Archaeological and Anthropological Sciences (2024) 16:185
https://doi.org/10.1007/s12520-024-02090-6

RESEARCH

Human-bird interactions in the Levant during the Late Pleistocene to Early Holocene: Multi-scalar analysis of avifaunal remains

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Received: 13 October 2023 / Accepted: 7 October 2024 / Published online: 22 October 2024

Abstract

This paper describes analyses of avifauna from Levantine Late Pleistocene and Early Holocene sites at contrasting scales. We present avian osteological data at Shubayqa, in northeast Jordan, illustrating human-bird-environment interactions over 4000 years offering interpretation of environmental change on avifaunal communities and reorientation in the nature of multi-species relationships at a wetland environment. Comparisons to published avifaunal assemblages investigates bird-human relationships across a broader temporal and geographical span. During the Late Pleistocene and Early Holocene, some of our species gradually transitioned to agriculture. People hunted birds for subsistence but extensive evidence for the symbolic importance of birds suggests complex relationships between species. Avifaunal evidence, therefore, presents insights into two commonly suggested primary causes for the shift from hunter-foragers to agriculturalists – resource pressure and symbolic expression. In this paper, we investigate and try to clarify the relationship between humans and birds at this transitional period in human history, furthering discussions of the shift towards agriculture. We argue humans gradually modified the landscape but this was not a reactionary response to resource stress. Nevertheless, this resulted in the productivity of the landscape increasing and allowed further intensification. Feathers and talons of birds were used for millennia preceding the shift to agriculture and the increase in bird hunting towards the end of the Pleistocene cannot be explained by the increased role of birds in the symbolic realm. The evidence from the avifauna adds weight to the idea of ecological niche construction activities, as people invested in specific locations, increasing productivity of habitats, thus encouraging further investment within some environments.

Keywords Avifauna · Symbolism · Subsistence · Quantification · Late Pleistocene · Early Holocene · Niche construction

Introduction

The relationship between humans and birds

Today, even with our understanding of the physics enabling bird flight and knowledge of avian migrations, birds fascinate us. To hunter-gatherers, well attuned to nature, the spectacle of these species was surely awe-inspiring. Migratory species appearing, seemingly out of nowhere, must have had an impact on people in the distant past. Ethnographic and historical case studies document how birds infiltrate belief systems (Balzer 1996; Clarke 2016; Parmalee 1977) and archaeologically, numerous examples of bird remains at many sites across Southwest Asia from the Upper Palaeolithic to Early Neolithic reflect symbolic or ritual behaviour. For example beads made from chukar partridge (*Alectoris chukar*) tibiotarsus bones in Natufian assemblages form part of headdresses incorporated in human interments (Pichon 1983). Mithen (2022) interpreted the large number of diurnal raptors within the avifaunal assemblage from Wadi Faynan 16 as linked to Shamanistic practices. To human groups that interacted with these birds, the symbolism represented by materials derived from these animals must have been influenced by a combination of behaviour, visual and audible characteristics of different species.

Aside from remains of birds themselves, iconographic evidence provides another insight into past human-bird relationships. Garfinkel and Krulwich (2023) recently published a synthesis of avian depictions across the Pleistocene/

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Holocene boundary arguing that birds, generally a marginal motif, became relatively common in the Pre-Pottery Neolithic A (PPNA). They suggested that this reflected the momentous transition towards settled life in agricultural communities with birds reminding people of seasonal cycles of activities. They went on to argue that assemblages of bird bones at many of the PPNA sites largely reflected the ritual importance of birds and "birds were of greater symbolic than economic value" (Garfinkel and Krulwich 2023:10) indicating that evidence of feather removal, high frequencies of raptors as well as over-representation of talons offered support for this interpretation.

Although not necessarily juxtaposed to symbolic or ritual association of birds and people, hunting birds primarily for subsistence needs was also common. Analysis of subsistence strategies is central to hunter-gatherer archaeology and zooarchaeologists have often focused on the role of animals, including birds, in past diets. The presence of avifaunal remains at some PPNA sites, such as Shubayqa 6, primarily relate to subsistence activities with large accumulations of bones in middens associated with food preparation (Yeomans and Richter 2020). It is impossible to divorce hunting for subsistence from the symbolic role of animals targeted and multi-species theoretical approaches have furthered discussion of the multitude of ways that humans and other species had entangled lifeways. This approach stresses the dynamic, multidirectional and mutual constitutive relationship between humans and other animals. Non-human animals act as agentive beings actively co-producing the world. This process of "world-making" is the result of historically situated, entangled inter-species relationships (Brittain and Overton 2013; Pilaar-Birch 2018; Hussain et al. 2022, 2023).

As Bishop (2022) notes, use of archaeological evidence to reveal human-bird intersections should move beyond subjective associations towards quantitative analysis. The problem of disentangling the interactions has been mentioned by researchers working in diverse locations. For example Sloan (2014:35) notes that "[a]lthough circumpolar bird subsistence encompasses intertwining economic, sociocultural, spiritual, and symbolic components, the dynamism and multidimensionality of these practices have been under recognized in academic discourse on subsistence." Bishop et al. (2018:314) highlight how human-bird interactions in Mesoamerica consist of "subsistence, social use and ritual engagement" with individual birds often hunted to fulfill more than one of these roles. Their paper (Bishop et al. 2018) provides a useful summary of archaeological evidence that helps identify motivations for bird hunting. When researchers have access to primary data this is a useful model but intricacies of assemblages are summarised in publications and often lack the detail necessary to investigate patterns across wider temporal and spatial boundaries. In an elegant study, designed to incorporate the agency of birds, Bishop (2022) developed a quantitative approach assigning procurement scores based on behaviour and physical characteristics of different species. This provided an assessment of difficulty in obtaining each bird species and, when combined with a standardised quantification of species in the archaeological record, showed that people inhabiting Chaco Canyon in New Mexico (850–1150 AD) were hunting birds, with the exception of turkeys, mainly for symbolic purposes. However, as Bishop (2022) notes, this method requires identification of avifaunal remains to species level so the unique characteristics can be modelled. Behavioural characteristics of different sexes of birds would also have been important, but this is an even more challenging level of detail to obtain. We have not applied the approach of Bishop (2022) in this paper because the geographical area covered by this review is varied and encounter rates for different species would have been dramatically different across the diverse environments. Furthermore, we have difficulties in species level identifications that currently limit the utility of the approach to our study region. In future, attempts to model expected frequencies of taxonomic groups in different locations incorporating these additional factors into the analysis would be a fruitful line of enquiry.

Previous synthesis of Levantine evidence

More than thirty years ago, Tchernov (1993) provided a synthesis of avifauna from Levantine sites noting how the diversity of birds increased from the Early Epipalaeolithic to Late Epipalaeolithic and into the Early Neolithic. The accompanying discussion focused on how this reflected human responses to decreasing abundance of larger bodied mammals with people resorting to hunting smaller prey with a lower return. The long-term trend in mammal body size in hunted prey is frequently interpreted as over-exploitation of larger mammals (e.g. Stiner et al. 2009; Stutz et al. 2009; Dembitzer et al. 2022). The symbolic role of birds is not in the foreground in many discussions grounded in optimal foraging theory (although see Meier et al. 2016 and Reshef et al. 2019 for regional examples incorporating the symbolic value of prey into human behaviour ecological models). This contrasts with interpretations for individual sites that frequently cite the role of symbolism as a driving factor in hunting species such as diurnal raptors (e.g. Martin et al. 2013; Mithen 2022). An alternative interpretation for the frequency of raptors during the Late Pleistocene and Early Holocene is the possible use of raptors in falconry (Dobney 2002). Dobney (2002:82) raises the idea of falconry as an intriguing theory but notes that we are unlikely to determine if such activities took place.

Scales of analysis

Differing views on informative analytical scales have led researchers to tackle archaeological questions using different methodological approaches. Some, such as Nims and Butler (2019:582) argue that "[m]any key questions that archaeologists seek to answer about past socio-ecological systems are best approached through comparative study, meta-analysis, and regional synthesis." A contrasting statement by Birks et al. (2015:4) emphasises how "[h]umans depend almost exclusively on their local environment, so the impacts of climate changes on both terrestrial and wetland habitats need to be reconstructed at local ecosystem scales in relation to habitation sites." Both approaches have merits and, in this paper, we have combined analysis of human-bird interactions across the Levant, at local and regional scales. These different scales provide alternative insights into the past. The current focus on big data does not sufficiently acknowledge how individual events are amalgamated during the formation of the archaeological record and intricacies of assemblages are often condensed. At the other end of the analytic spectrum individual events, when identified in the archaeological record, inform us about past human-bird interactions in detail. When preserved, a contextual analysis of discrete events and resultant avifaunal remains provides informative evidence. The numerous carpometacarpus bones of Eurasian jays (*Garrulus glandarius*) interred with human burials of Middle Neolithic date from Zvejnieki, northern Latvia, is an eloquent example of birds interpreted as representing totemism and shamanism (Mannermaa 2013). Within the Levant, the presence of a golden eagle (*Aquila chrysaetos*) wing in the burial of a possible shaman at Hilazon Tachtit dated to 12,400–12,000 cal BP illustrates the symbolic role of birds in the Early Natufian (Grosman et al. 2008). At the MPPNB (Middle Pre-Pottery Neolithic B) site of Nahal Efe, remains of nine raptors were recovered from the base of a storage pit (Alcàntara et al. 2023). Interpretation of the find awaits more detailed analysis although Alcàntara et al. (2023) suggest a mix of symbolic and dietary uses of the birds. Level of preservation in all these cases was exceptional but often we conduct analysis on time-averaged accumulations of material evidence, affected by a range of taphonomic processes as opposed to individual events. Deliberate burial or placement of remains associated with symbolic behaviour is also likely to result in these actions being well preserved in the archaeological record and care is needed not to overemphasise the symbolic and ritual associations between people and birds because impressive finds overshadow material accumulated from daily activities.

The aim of this paper is, therefore, to contrast two scales of analysis of avifaunal remains in an attempt to revisit the question of why humans hunted birds at the transitional period of the Late Pleistocene and Early Holocene. How important was symbolic behaviour, were some species more typically associated with these activities and was there any temporal and geographical variation in these associations? By beginning to address these questions, we hope the relationship between humans and birds will enable additional insight into the relative importance of symbolism and subsistence in this key period. To investigate these hypotheses, characteristics of faunal assemblages resulting from subsistence, utilitarian and symbolic association between birds and people are summarised in Table 1. In this paper we aim to test if the relationship between humans and birds can be clarified and contrast how meta-analysis and local diachronic analysis maybe informative.

Background: The four thousand year sequence of avifauna at Shubayqa

Two sites, Shubayqa 1 and 6, are situated at the edge of a Late Pleistocene and Early Holocene wetland in the basalt strewn desert of Eastern Jordan. Detailed description of the qa', a seasonally flooded silt pan that the sites border and the local geomorphology is discussed elsewhere (Yeomans et al. 2024 and references within). The stratigraphic sequence for both sites is currently divided into five broad phases. Early Natufian (14.4–14.1 cal BP), Late Natufian (13.1–13.3 cal BP) and Final Natufian (12.2–11.6 cal BP) at Shubayqa 1. At Shubayqa 6 there are two architectural phases from the Final Natufian to PPNA (12.0–11.2 cal BP) and Late PPNA (11.0–10.6 cal BP). These five stratigraphic groups correspond to four architectural phases (Fig. 1) with further subdivision of the assemblage of Shubayqa 1 (Yeomans et al. 2021, 2019, 2017; Yeomans and Richter 2020, 2018) illustrating minimal change in avifaunal composition within phases. Delays in obtaining radiocarbon dates have limited similar detailed phase analysis of the assemblage from Shubayqa 6. Further discussion of the sites, methodology of the faunal analysis and radiocarbon dates are published elsewhere (Richter et al. 2016, 2017; Yeomans et al. 2017, 2018, 2021; Yeomans and Richter 2018, 2020).

Yeomans et al. (2024) provide the number of identified specimens (NISP) for the avifaunal assemblage from the archaeological sequence from Shubayqa. Table 2 provides summarised data according to different structures for Shubayqa 6 allowing data to be further subdivided once dating of individual structures is refined.

Methods

Species abundance and skeletal element representation at Shubayqa

The faunal assemblage from Shubayqa is very fragmentary which has made identification very challenging. Previously

Table 1 Zooarchaeological evidence for bird hunting motives based on Table 1 in Bishop et al. (2018) but expanded to include other signatures investigated in this study and expanded from the details in Bishop (2022)

	Subsistence	Utilitarian	Symbolism
Species representation	Birds with significant meat available from carcasses or species common in the environment Birds seasonally abundant or present when other sources of food are limited Small species might be targeted by mass hunting methods Birds that can be easily caught	Birds with suitable feathers arrow fledges or skins can be turned into clothing (Oakes 1991)	Birds with large and colourful feathers Birds with impressive talons. Species that might be associated with oral traditions. Birds with behaviours that humans can relate to or inspire people Birds that are difficult to hunt and their capture illustrates the skill of hunters
Recovery context	Bones found with other subsistence waste in middens or hearths	Bones found with other waste including subsistence waste but maybe discarded in an activity area associated with production activities	Bones of birds found in burials and other caches If wings were displayed on walls, the wing elements might be found in building infill deposits
Skeletal element representation	Bias towards the meat bearing bones if preparation and consumption did not take place in the same location	Wing elements especially those attached to the primary flight feathers found together. Absence of these elements might suggest they were used elsewhere and did not end up in middens	Completely articulated birds or portions of birds (wing or foot) Ungual phalanges of raptors well represented High frequency of tibiotarsus bones representing waste from bead manufacture
Modification	Cutmarks associated with meat removal Gnaw marks especially on the ends of the long bones Bones might be burnt either from roasting with ends of bones exposed to heat Completely burnt bones might occur if consumption waste was discarded into a hearth	Cutmarks or peeling marks associated with feather removal or skinning for bird skin garments	Less likely to have evidence for butchery except those relating to feather or talon removal Holes drilled into talons for suspension or use wear indicating attachment to clothing Bones unlikely to be burnt unless a deliberate attempt to change their colour was made Polished bones or deep transverse cuts are evidence of bead manufacture

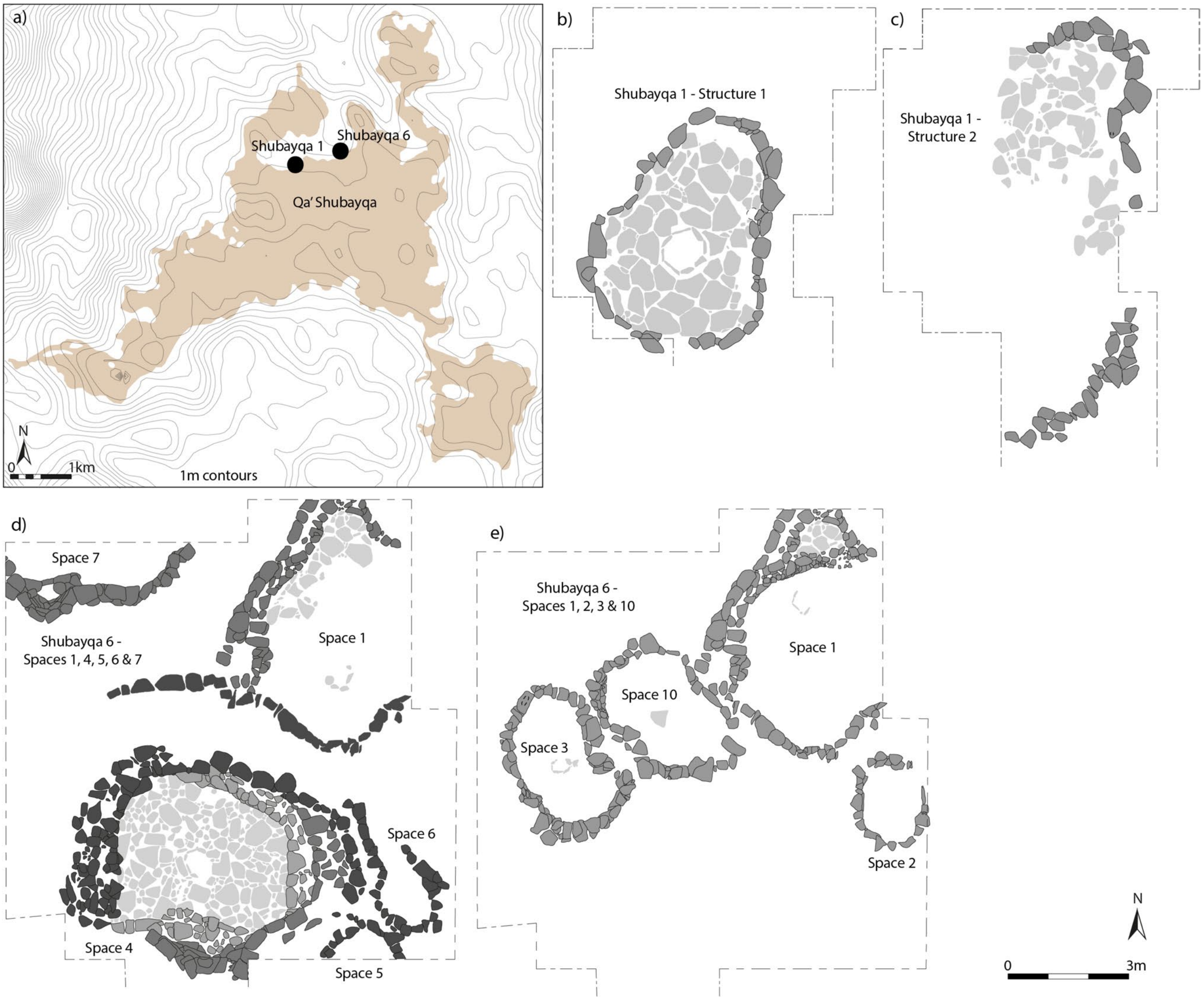


Fig. 1 **a**) Location of Shubayqa 1 and 6 on the edge of Qa' Shubayqa. **b**) Early Natufian structure at Shubayqa 1. **c**) Late Natufian structure at Shubayqa 1. **d**) Final Natufian to PPNA Phase of architecture at Shubaqya 6. **e**) LPPNA phase of architecture at Shubayqa 6

published NISP counts (Yeomans et al. 2024) are used to compare frequency of different taxonomic groups. Although there are multiple measurements of taxonomic evenness zooarchaeologists can use (Faith and Du 2018), a single statistic to measure diversity within an assemblage obscures detail in composition and we have the calculated Shannon's, Simpson's and Simpson's Evenness of taxonomic diversity for the four main phases of occupation at Shubayqa.

Skeletal element representation as a means to understand the primary reason for bird procurement has been frequently applied to zooarchaeological assemblages. This analysis is an effective way to argue for rationale during hunting (Bishop et al. 2018; Bovy 2012a; Finlayson et al. 2012; Lefèvre and Laroulandie 2014). Analysis has already been published for the Late Natufian period covering Anatidae, coot (*Fulica atra*) and Charadriiformes noting how the scapula, sternum and coracoid, together forming the triosseum complex, were significantly better represented. This suggests that birds were hunted in large numbers for subsistence—a pattern noted at other Natufian and PPNA sites (Tchernov 1993). In this paper, we present the data for Anatidae, except Anserinae for the four main phases of occupation and is based on the relative representation of the proximal and distal ends of the paired long bones as well as the axial elements of the furcula and sternum compared. Calculation is based on the minimum number of elements (MNE) as a proportion of expected representation given the minimum number of individual (MNI) calculations.

Table 2 Broad taxonomic groupings of avifauna by Phase and Space for Shubayqa 6. The Final Natufian to PPNA Phase at Shubayqa 6 needing additional dates for further subdivision

	Shubayqa 1 Early Natufian	Shubayqa 1 Late Natufian	Shubayqa 1 Final Natufian	Shubayqa 6 Test trench	Midden	Space 1	Space 4	Space 5	Space 6	Midden (LPPNA)	Space 1 (LPPNA)	Space 10 (LPPNA)	Space 2 (LPPNA)	Space 3 (LPPNA)
	14.4–14.1 ka cal BP	13.1–13.3 ka cal BP	12.2–11.6 ka cal BP	12.4-12 ka cal BP	12.0–11.7 ka cal BP		11.7–11.2 ka cal BP infilling					10.7–10.6 ka cal BP		11.0–10.6 ka cal BP
Cygnus spp.	2	5		1	90	1	17		1	23	1	6	2	7
Anser spp.	2	11			4		1		4	1				1
Other Anseriformes	630	2073	23	49	414	15	720	4	11	104	74	22	28	103
Phasianidae	30	20		4	4		24			8	14	5	1	28
Podicipedidae	57	89					5				1			4
Columbidae	2													
Pteroclididae	11	5			3		6							5
Gruidae	8	7			8		1							3
Rallidae	116	420		10	23	2	43			10	12		1	11
Charadriiformes	2000	738	5	5	11		93		1	11	16	1		14
Ardeidae	4	29			1						1			
Accipitridae	83	41		3	19		38			3	10	3	1	7
Strigidae	2			1	1		2							
Falconidae	2	1					1							
Corvidae	1	4			1		0					1		1
Other Passeriformes	37	20		1	1	1	39			7	7	2	4	16
Total	**2987**	**3463**	**28**	**74**	**580**	**19**	**990**	**4**	**17**	**167**	**136**	**40**	**37**	**200**

Network science methods for visualisation and analysis

Network analysis has been extensively applied to archaeological research and the entire toolbox of network methods has been efficiently used for visualisation and analysis of archaeological materials (Brughmans and Peeples 2023). Indeed, network science provides archaeological research with a variety of concepts and flexible analytical tools that proved to be useful for disentangling complex phenomena and for visualising relationships between multiple entities within complex systems of interactions (e.g. Giomi and Peeples 2019; Jayyab and Gibbon 2022; Mazzucato 2019; Mills et al. 2013; Pereira et al. 2023). Nevertheless, with few exceptions, network methods have been rarely applied to zooarchaeological assemblages (Crabtree et al. 2017; Holland-Lulewicz and Holland-Lulewicz 2023; Verhagen et al. 2021); in this context, network science methods are used to visualise and investigate long-term patterns of socio-ecological relations between humans and birds at an intra-site scale. Human-bird-centred socioecological networks are constructed to display changes through time within the Shubayqa 1 and 6 assemblages. We use network methods to visualise patterns of bird families co-occurrence through time and, from an analytical point of view, we use simple degree centrality to assess the role of specific families within the human-bird-centred system at Shubayqa 1 and 6. At a regional scale we construct similarity networks of sites based on the Morisita-Horn similarity index of zooarchaeological assemblages and we use the Louvain community detection algorithm to define community partitions based on similarities between sites (Fig. 11b). Methods of modularity maximization are able to define partitions in networks according to the density and strength of edges (Brughmans and Peeples 2023; Fortunato 2010). The Louvain algorithm, like other community detection methods, returns a community partition element that assigns each node to a module/community (Blondel et al. 2008). All our analyses are conducted in UCINET and VISONE (Borgatti et al. 2002; Brandes and Wagner 2004).

Regional analysis

To set the sequence from Shubayqa in context, meta-analysis of published avifauna assemblages across the Levant dating from Late Pleistocene and Early Holocene was conducted. Explorations beyond individual sites are relatively few with most avifaunal reports present data from a single site. Exceptions illustrate potential of regional analyses and for example, Finlayson et al. (2012) summarised data on presence of corvids and raptors over a wide geographical area demonstrating that Neanderthals specifically sought feathers of these species.

The regional analysis presented here utilises published data from avifaunal assemblages across the Levant dating from the Upper Palaeolithic, Early, Middle and Late Epipalaeolithic and PPNA (Table 3). This encompasses a large proportion of published data including the timeframe when human societal groups shifted from hunting towards agriculture. Important PPNB assemblages have not yet been fully published so inclusion of this period awaits reports on sites such Nahal Roded (Birkenfeld et al. 2019, 2020). Figure 2 shows location of sites included in the analysis as well as secondary sites mentioned but not included in the statistical analysis as they are outside the geographical focus of this analysis or only a small number of bird bones were identified (< 20). Assemblages dating to one of the chronological subdivisions were included in the analysis and temporally insecure data were excluded.

Meta-analysis requires data from different sites to be comparable and consequently reduces subtleties of each site. Identifications were grouped by family because of difficulty in identification and also it was necessary to limit subdivision of the data. Passeriformes were split into Corvidae and other Passeriformes since most reports do not attempt identification beyond this level. All Charadriiformes were grouped together because of difficulty in identification of fragmentary remains. Diurnal raptors (Accipitridae and Pandionidae) included falcons (Falconidae). Although it is now known that the Falconidae are closer to Psittaciformes than Accipitriformes, many early analyses included Falconidae with Accipitriformes and it is not possible to separate this data from published sources. Owls (Strigidae and Tytonidae) were also grouped because of infrequency and subdivision of data reduces statistical potential. The appropriateness of taxonomic categories could be debated but the aim here is a preliminary investigation to understand how and why humans interacted with birds. Although behaviour, colour and physical characteristics probably had more importance than their evolutionary relationship, it is impossible to group data into categories that reflect these characteristics because of the difficulty in identification. The data used in the analysis is given in Table S1.

Several analytical methods provide us with a better understanding of variation in human-bird associations across the Levant. Rarefaction is heavily dependent on sample size so ubiquity analysis of presence is limited to the 16 assemblages with over 100 identified bones. To investigate the relative proportions of the different taxonomic groups, correspondence analysis on the assemblages with more than 20 bones identified was undertaken. This exploratory technique allows investigation of associations between different sites and species. We also show a similarity index for the different assemblages highlighting those that have a comparable species represented. Many potential similarity indices can describe the degree that taxonomic groups occur at

Table 3 Chronological periods with approximate dates and summary of climatic and archaeological evidence. The sites and NISP used in this analysis (samples of more than 20 NISP only included) are indicated. *Only Minimum Number of Elements (MNE) was given in the Ohalo II publication (Data from Baadsgaard et al. 2010; Clark et al. 2024; Edwards n.d.; Gourichon 2002; 2004; Grosman and Munro 2007; Grosman et al. 2016; Horwitz et al. 2010; Janetski and Baadsgaard 2005; Kersten 1991; Kinzelman 2003; Kuhn et al. 2004; Martin et al. 2013; Munro 2012; Pichon 1987; 1994; Recchi and Gopher 2002; Simmons 2013; Simmons and Nadel 1998; Tchernov 1994; White et al. 2021a). Shubayqa 6 excludes the Test Trench

Date range (kyr cal BP)	45–25	25–19.0	19.0–14.6		14.6–11.7			11.7–10.9
Climatic period	Last Glacial Maximum		Post-glacial warming	Pre-Bølling warming	Bølling	Allerød	Younger Dryas	Early Holocene
Regional environmental data	Cold and lower evaporation		Slightly warming and dry	Warming and increased moisture	Warm and moist		Cool and dry but local data suggest less seasonal rain with lower evaporation	Warmer with increased rainfall
Period	Upper Palaeolithic (UP)	Early Epipalaeolithic (EEP)	Middle Epipalaeolithic (MEP)		Late Epipalaeolithic (LEP)			PPNA
Sites with avifaunal (NISP assigned to period), only phases where NISP > 20	Ksar'Akil (69) Mughr el-Hamamah (62)	Ayn Qassiya (126), Meged (71), Ohalo II* (467)	Wadi Jilat 22 (79), Wadi Mataha 2(32)		Ain Mallaha (1325), Bawwab al-Ghazal (94), El-Wad Terrance (77), Hatoula (161), Hayonim Terrace (168), Hilazon Tachtit (130), Mureybet (917), Nahal Ein Gev II (103), Qumran Cave 24 (38), Shubayqa 1 (6478), Wadi Hammeh 27 (23), Wadi Mataha 2 (89)			Gilgal (737), Jerf el Ahmar (1553), Mureybet (2745), Netiv Hagdud (1138), Hatoula (780), Shubayqa 6 (2257), Wadi Faynan 16 (7798)
Sites	2	3	2		12			7
Total NISP	131	644	111		9603			17008

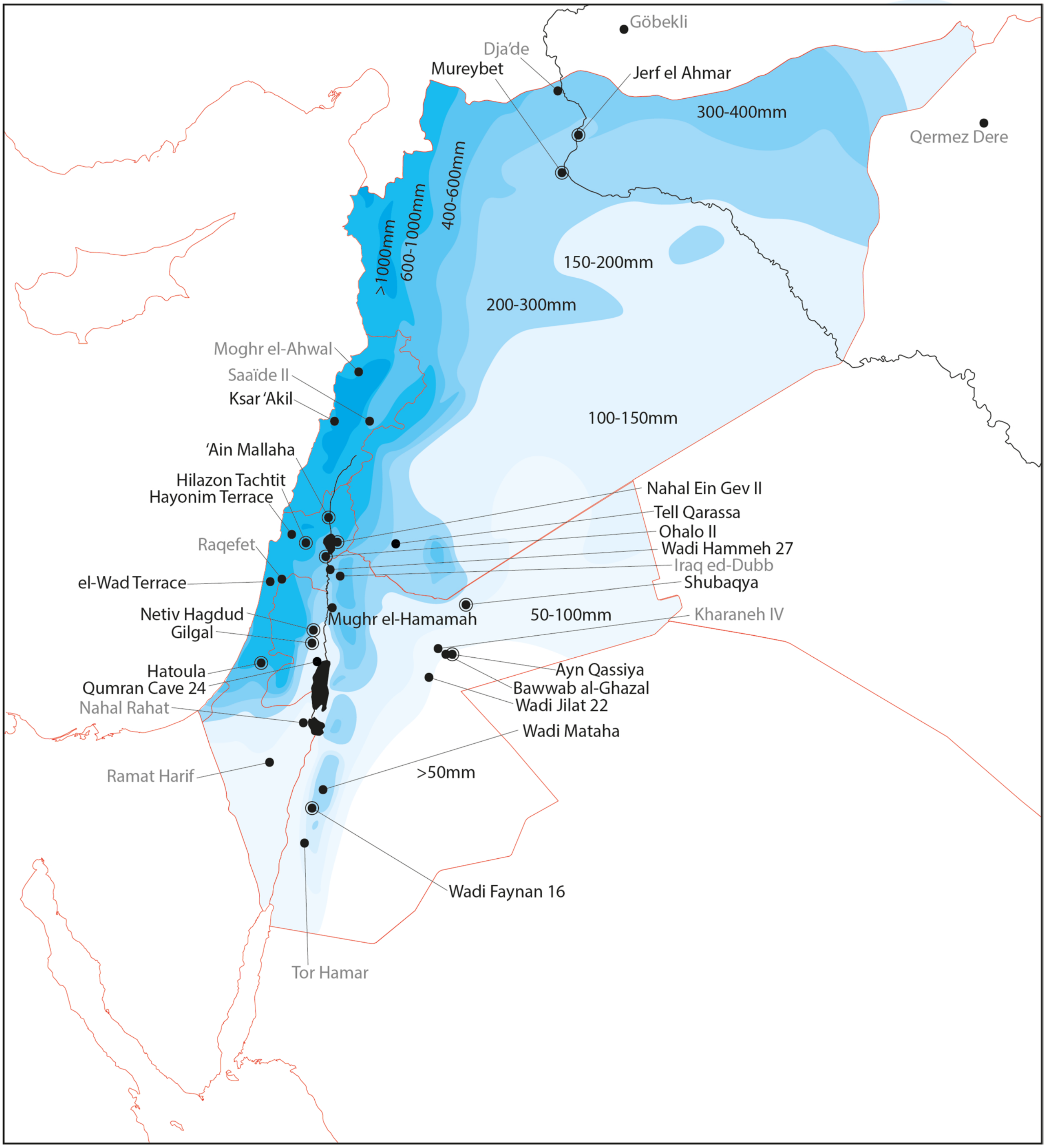


Fig. 2 Location of sites used in the correspondence and similarity index analysis shown in black text, others sites with small assemblages shown in grey. Assemblages with more than 100 NISP, included in the ubiquity analysis, shown by enclosed circles. Base colours reflect the current yearly rainfall

similar frequencies (Giovas 2021). For example, Sørensen index compares the similarity of two samples (Sørsensen 1948) but is vulnerable to sample size differences. Giovas (2021), in a review of the different techniques, advocates use of the Morisita-Horn index which emphases abundance of prevalent taxa and is less sensitive to the presence of rare taxa. Pairwise comparison of the taxonomic groups using the Morisita-Horn index compares different assemblages.

Correspondence analysis was performed in R version 4.3.1 using package *Factoextra* (Kassambra and Mundt 2020) and the Morisita-Horn used package *divo* (Sadee et al. 2019).

Several published avifaunal assemblages provide details of skeletal element representation and, to investigate the role of raptors in past human-bird associations, the number of ungual phalanges compared to other elements for sites was conducted where information was available.

Table 4 Taxonomic diversity in the bird assemblage for four main phases of occupation at Shubayqa. To avoid problems of identification level, species were grouped into the following: Accipitridae, Anatidae (Anserinae), Anatidae (non-Anserinae), Ardeidae, Charadriiformes, Ciconiidae, Columbidae, Corvidae, Falconidae, Gruidae, Passeriformes (non-Corvidae), Phasianidae, Podicipedidae, Pterociidae, Rallidae, Tytonidae and Strigidae

Period	Shannon's (J)	Simpson's (1-D)	Simpson's Evenness ($E_{1/D}$)
Early Natufian	0.535	0.504	0.135
Late Natufuan	0.598	0.581	0.183
FN-PPNA	0.401	0.312	0.112
LPPNA	0.67	0.572	0.195

Results

Analysis of the Shubayqa assemblage

Figure 3 shows relative change in different taxonomic groups of avifauna across phases of Shubayqa. This graph excludes the Final Natufian from Shubayqa 1, due to limited sample size, but allows visualisation of shifts in the representation of different bird groups. Table 4 provides statistical calculations of evenness using the groupings of taxa. A graphical representation of taxonomic diversity at Shubayqa (Fig. 4) illustrates there is change in the diversity within the avifaunal assemblage at Shubayqa but that the shift is not marked. The most common taxonomic group form more of the assemblage at the start of the occupation of Shubayqa 6 but there is also an increase in the total number of taxonomic groups represented and many of the lower ranked groups increase.

Figure 5 a) depicts a two-mode network with two entities, the chronological phases at Shubayqa 1 and 6 and the number of different bird families. Degree centrality performed on the network highlights the role played by specific families of birds throughout the entire sequence; the Anatidae both Anatinae and non-Anserinae which are present in all the five time-periods at the site and the Scolopacidae that are

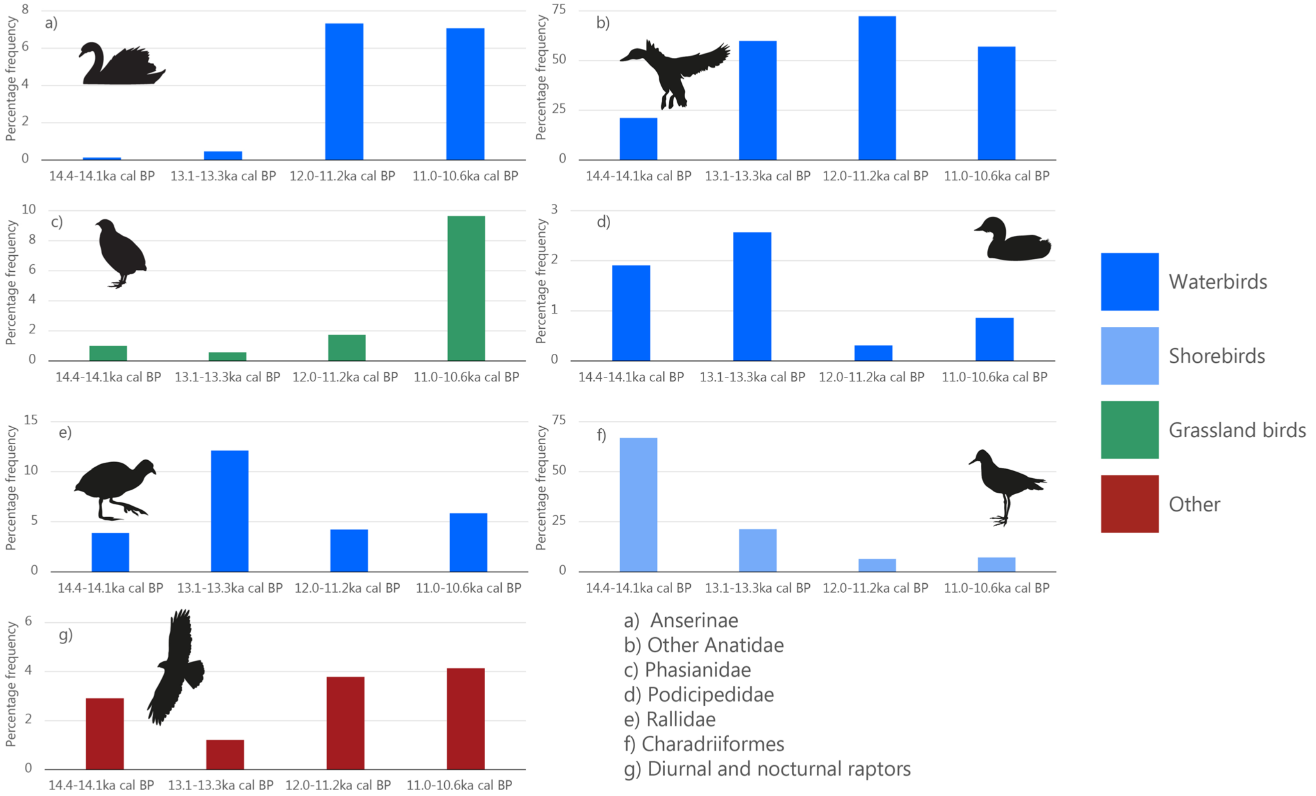


Fig. 3 Proportions of main taxonomic groups (and general habitat preferences) from Shubayqa in different phases, excluding Final Natufian at Shubayqa 1 when minimal avifauna was present

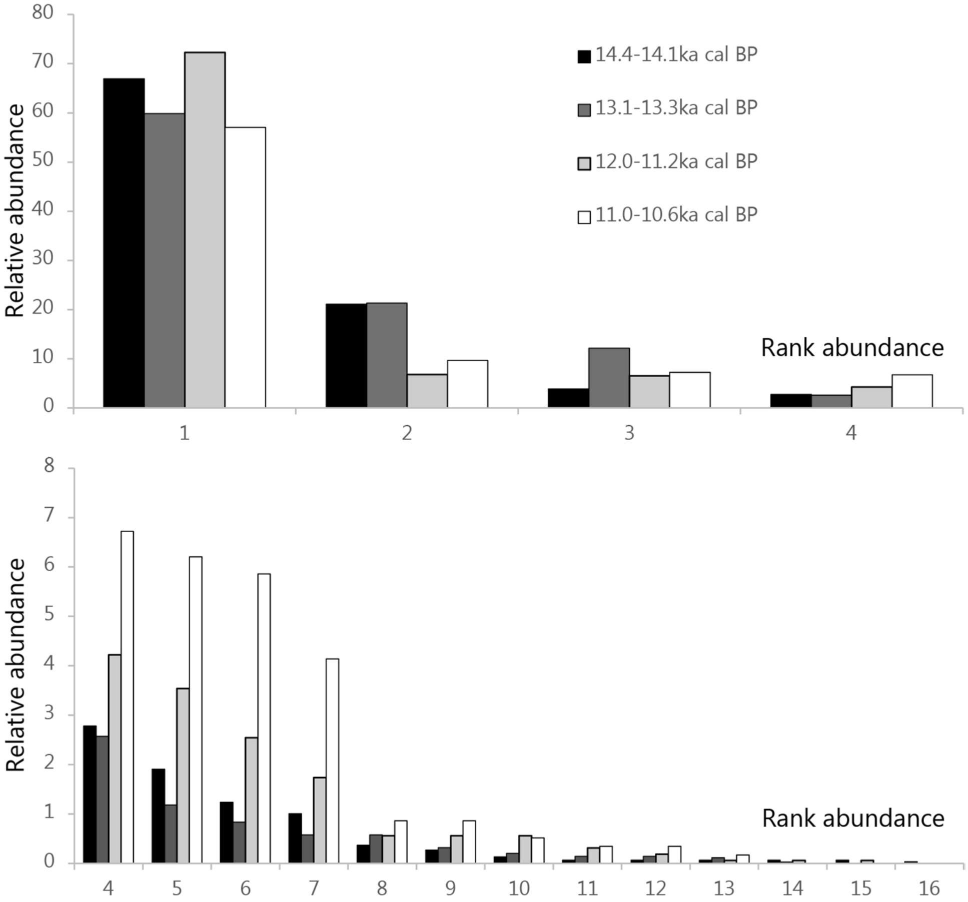


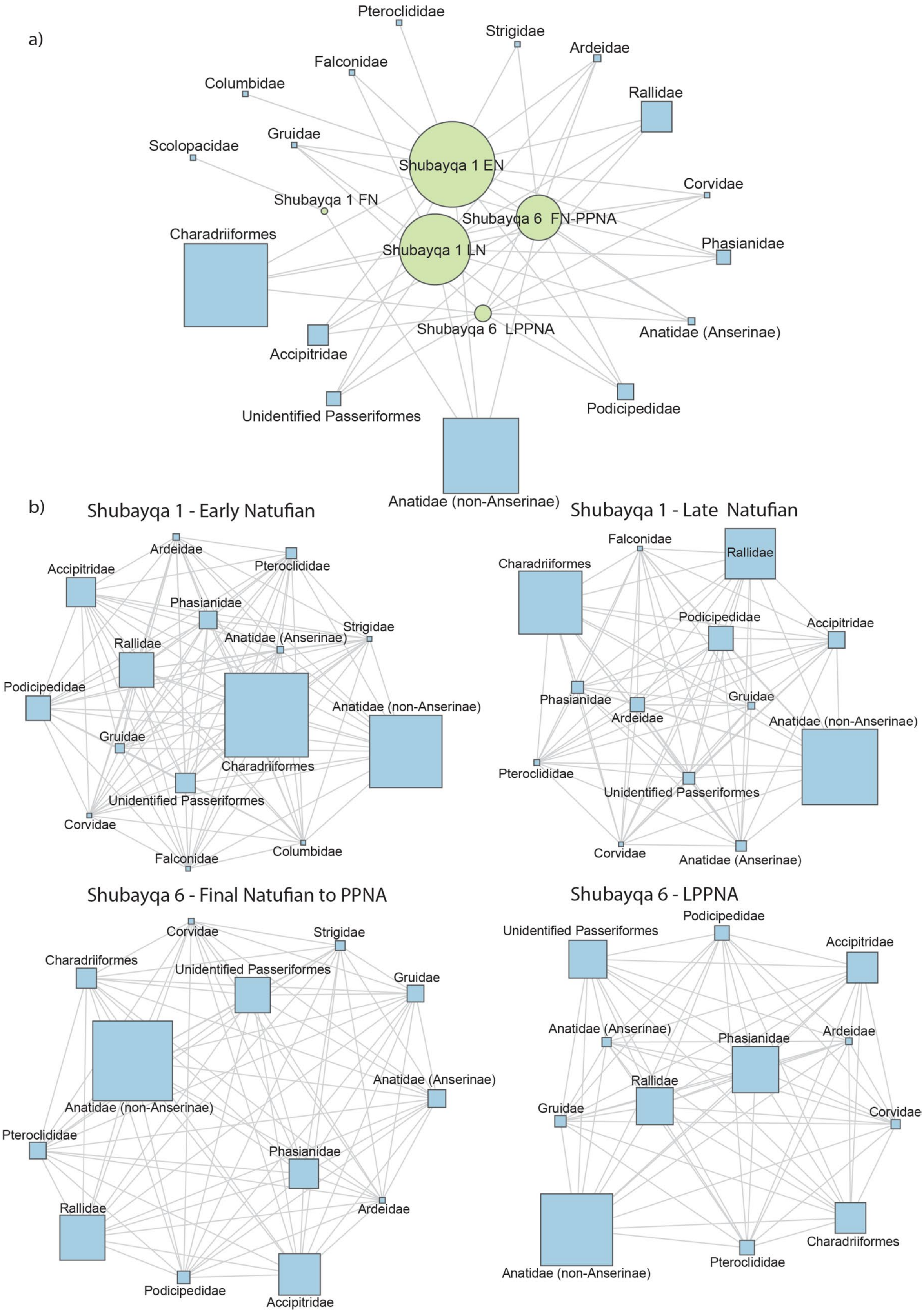
Fig. 4 Change in rank occurrence of the dominant taxa in the assemblage from time in the four main phases of occupation illustrates an overall shift towards reduced taxonomic variety in the frequent taxonomic groups but an increase in the overall range of taxa. Upper graph shows the four top ranked taxonomic groups and the lower shows the remaining taxonomic groups

predominant at Shubayqa 1. Figure 5 b) shows one-mode networks, where nodes represent numbers of bird bones recovered for each time-period, grouped by family. These networks depict human-bird-centred communities through time; similarly to the previous networks, a simple exploratory degree centrality analysis gives the opportunity to easily visualise the shifting importance of specific birds through time. Very clear in numbers, is the increase of Anserinae at Shubayqa 6 and the decrease of Charadriiformes after the Early Natufian (see discussion).

Figure 6 provides results of the body part analysis and shows that bones of the triosseum of Anatidae are well represented in all phases of the occupation sequence. By the later part of the sequence, represented by the material from Shubayqa 6, there is an increase in the proportion of other bones including the carpometacarpus and, to a lesser extent, the tibiotarsus and tarsometatarsus that were less well represented in earlier phases.

Regional analysis

Ubiquity analysis (Fig. 7a) provides several insights into the association between people and birds. It is notable that diurnal raptors and Phasianidae are universally present at sites with more than 100 identified bones. Anatidae are present at the majority of sites and even at Hilazon Tachtit, a Late Natufian burial ground (Grossman et al. 2008), this group is present but represented by a single bone. Pairwise Morisita-Horn similarity is shown in Fig. 7b. Correspondence analysis (Fig. 8) shows that several taxonomic groups, positioned further from the graph origin, are probably discriminating between assemblages. Some of these, Charadriiformes, Gruidae and Threskiornithidae are only present in significant numbers in one assemblage, Shubayqa 1, Jerf al-Ahmar and Wadi Faynan 16 respectively reflecting local environments of these sites. Several assemblages are dominated by diurnal raptors, Wadi Jilat 22 (both Middle and Late Epipalaeolithic phases), Wadi Faynan 16 (PPNA) and Meged Rockshelter (Early Epipalaeolithic). Both correspondence and similarity analyses suggest that the assemblages from Wadi Mataha (Middle and Late Epipalaeolithic), Hatoula (Late Epipalaeolithic and PPNA), Hilazon Tachtit (Late Epipalaeolithic), el-Wad Terrace (Late Epipalaeolithic) and, to a lesser extent, Nahal Ein Gev II (Late Epipalaeolithic) yielded assemblages with similar taxonomic characteristics. Phasianidae form the major component of all these assemblages and, when examining the original data, it is clear these are mainly chukar. Figure 8 provides a visual representation of the similarity


a)
Pteroclididae
Strigidae
Ardeidae
Falconidae
Columbidae
Rallidae
Gruidae
Scolopacidae
Shubayqa 1 EN
Shubayqa 1 FN
Corvidae
Shubayqa 6 FN-PPNA
Charadriiformes
Shubayqa 1 LN
Phasianidae
Shubayqa 6 LPPNA
Anatidae (Anserinae)
Accipitridae
Podicipedidae
Unidentified Passeriformes
Anatidae (non-Anserinae)
b)
Shubayqa 1 - Early Natufian
Ardeidae
Accipitridae
Pteroclididae
Phasianidae
Strigidae
Anatidae (Anserinae)
Rallidae
Podicipedidae
Anatidae (non-Anserinae)
Gruidae
Charadriiformes
Unidentified Passeriformes
Corvidae
Falconidae
Columbidae
Shubayqa 1 - Late Natufian
Falconidae
Charadriiformes
Rallidae
Podicipedidae
Accipitridae
Phasianidae
Gruidae
Ardeidae
Anatidae (non-Anserinae)
Pteroclididae
Unidentified Passeriformes
Corvidae
Anatidae (Anserinae)
Shubayqa 6 - Final Natufian to PPNA
Corvidae
Strigidae
Charadriiformes
Unidentified Passeriformes
Gruidae
Anatidae (Anserinae)
Anatidae (non-Anserinae)
Pteroclididae
Phasianidae
Rallidae
Ardeidae
Podicipedidae
Accipitridae
Shubayqa 6 - LPPNA
Podicipedidae
Unidentified Passeriformes
Accipitridae
Anatidae (Anserinae)
Ardeidae
Phasianidae
Rallidae
Gruidae
Corvidae
Anatidae (non-Anserinae)
Pteroclididae
Charadriiformes

◂**Fig. 5** **a**) Two-mode network depicting chronological periods at Shubayqa 1 and Shubayqa 6 (green dots) and the avifauna recovered within each period grouped by family (blue squares). The size of nodes is proportional to their degree centrality scores. Degree centrality refers to the number of edges each node has. The bigger the time-period nodes (green dots), the higher the amount of bird families recovered within the specific chronological assemblage. Differently, the size of the blue squares refer both to the ubiquity of bird families within each period at Shubayqa 1 and 6 and to the number of individuals recovered. Anatidae (non-anserinae) appears to be the bird family present in all the time-periods and with the largest number of individuals. **b**) one-mode co-occurrence networks of bird families by time-period at Shubayqa 1 and 6. The size of nodes corresponds to the centrality degree score for each node. The larger the size of nodes, the higher the number of specimens recovered for each time-period assemblage

between assemblages based on the Morisita-Horn pairwise comparison with the values also provided in Table S2.

Body-part representation of raptors

Figure 9 provides the body part representation of the Accipitridae and Falconidae combined or for individual species when published data focused on specific species. The red shows the ungual phalanges with light red filled colour showing the other posterior phalanges and white outlined with red those where differentiation was not made in publication. The two sites in the northern Levant have the highest frequency of phalanges.

Discussion

Previous work on the avifaunal sequence at Shubayqa suggested that the flooded habitat around the wetland diminished following the Early Natufian. This resulted in a lower frequency of waders that forage in shallow pools (Yeomans 2018). The lower frequency of Charadriiformes continued into the PPNA suggesting that, following the Younger Dryas, seasonal flooding of the qa' providing habitats for waders was further reduced. A modern correlate for this change in habitat availability is Lake Agmon where absence of mudflats and seasonally flooded areas clear of vegetation resulted in a decline of nesting and feeding Charadriiformes (Shy et al. 1998). An almost complete absence of avifauna remains, compared to frequent mammalian bones, from the period of occupation coinciding with the Younger Dryas at Shubayqa 1 were initially suggested to reflect drying of the wetland with migratory birds rarely visiting. Additional data, discussed in detail below, may now offer a different interpretation. There is growing evidence to suggest that effects of the Younger Dryas in the Levant was characterised by reduced seasonality of rainfall and a lower evaporation rate could have resulted in wetlands being better watered (Orland et al. 2012; Lui et al. 2013; Hartman et al. 2016; Langgut et al. 2021).

The larger sample of bones recorded and published recently (Yeomans et al. 2024) and the species representation at Shubayqa (Figs. 3-5), Table 4) could have a range of underlying causes; changing subsistence patterns, variation in hunting technology, reflect changing symbolic role of birds or correlate to alteration in the ecological community because of habitat alteration. There is also the question of how other species in the wetland affected the avifauna. Most likely, a combination of many factors were responsible and it is extremely difficult to tease apart causes. Examining shifts between the Late Natufian at Shubaqya 1 and the two successive phases of occupation at Shubayqa 6 provides some insights. The decrease in Charadriiformes after the Early Natufian is replaced by an increase in the non-Anserinae Anatidae and Rallidae (primarily *Fulica atra*). Compared to the Late Natufian, the avifaunal assemblage from Shubayqa 6 (Final Natufian to PPNA phase) is characterised by a further increase in Anatidae and Anserinae together with a further decrease in Charadriiformes and Rallidae and fewer Podicipedidae. A slight increase in the frequency of raptors is documented in the bone assemblage. Representation of Anserinae (swans and geese) increased from 0.46% to 7.39% between the Late Natufian and the first phase of Shubayqa 6 with the majority of the increase represented by swans. Today, mute swans (*Cygnus olor*) are rare winter visitors to the Levant but can occur in large flocks (Shirihai 1996). Remains of swan identified at other sites include Bewick's swan (*Cygnus columbianus bewickii*) at Gilgal I (Horwitz et al. 2010) and Ohalo II, and whooper swan (*Cygnus cygnus*) at Ohalo II (Simmons and Nadel 1998) and Ayn Qassiya (Edwards n.d.) although the method for species level determinations are not clear. Today, these two species only occur as very rare vagrants (Shirihai 1996). 'Ain Mallaha (Simmons 2013) and Ksar 'Akil (Kersten 1991) also yielded unspecified swan remains. Bacher (1967) provides measurements for the three species of swans and the limited preserved measurements from Shubayqa allows us to discount the smaller Bewick's swan but, given the fragmentary nature of the faunal remains, species level identifications are problematic.

In seeking an ecological explanation for the increase in swan remains, it is notable that the mute swan has sometimes been considered a pest species damaging aquatic vegetation beds and driving away other waterfowl. In Europe, the protected status of mute swans, warmer winters and autumn sown cereals led to an increase in their population (Guillaume et al 2014). Numerous research papers focusing on the effects of mute swans on wetlands and waterbird communities were summarised by (Guillaume et al. 2014). They note how mute swans can be territorial towards other waterfowl especially in the breeding season but also outside the

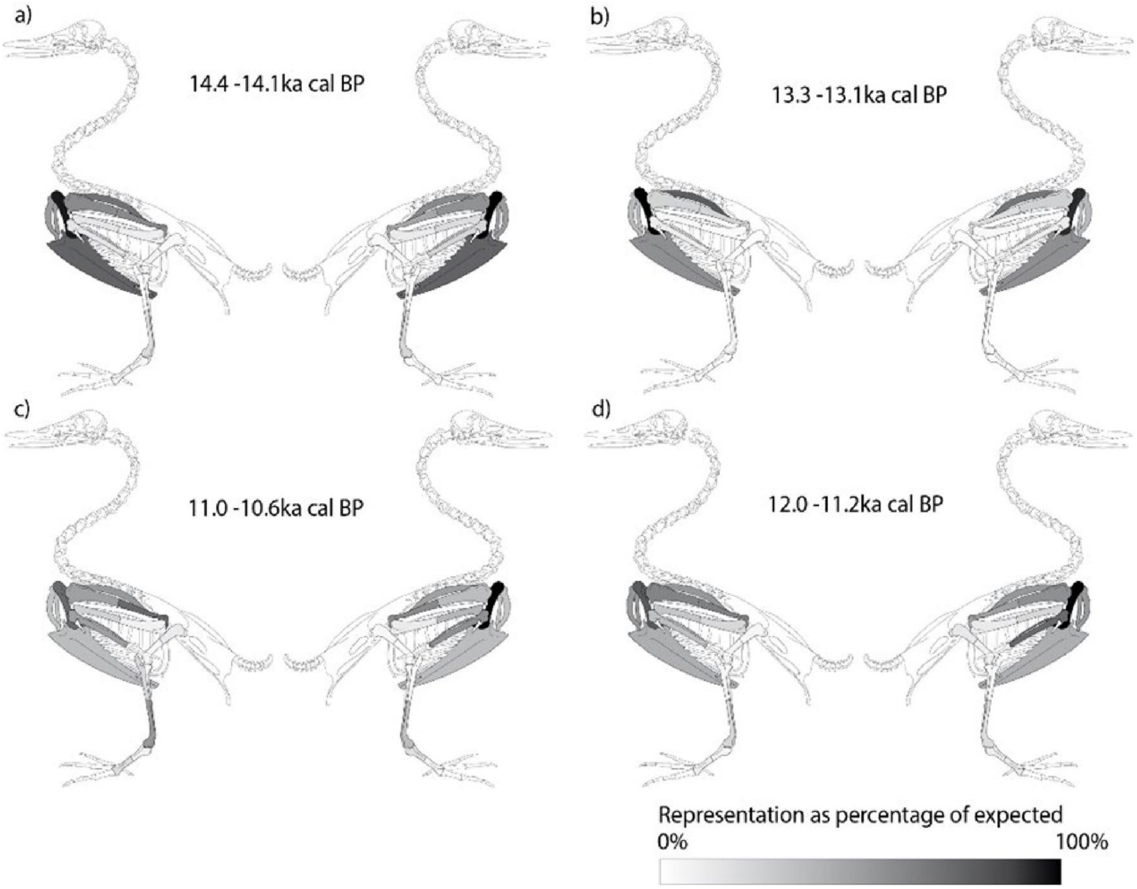


Fig. 6 Body-part representation of Anatidae, except Anserinae, from the four main phases at Shubayqa. a) Early Natufian, b) Late Natufian, c) Final Natufian to EPPNA and d) LPPNA. Illustrations modified from vector graphics (ArcheoZoo.org/Michel Coutureau http://dx.doi.org/https://doi.org/10.5962/bhl.title.61021). Axial bones are shown in both left and right views

breeding season in order to ensure food supply. Compared to whooper and Bewick's swans, mute swans do not trample substrate to gain access to roots and tubers, but feed on stems and leaves, resulting in greater competition to other waterbirds. Guillaume et al. (2014) found that mute swans are more likely to behave territorially towards similar sized species such as greylag geese, but they may have an indirect effect on other waterbirds by depleting food supply. As Guillaume et al. (2014:199) state, "By grazing aquatic plants, the swans can indirectly alter the biotic properties of aquatic ecosystems, and thus be considered ecosystem engineers", but note that the effect depends on the individual ecological context. In the Final Natufian to PPNA phase at Shubaqya, decline in other species of Anatidae, grebes, geese and coots might be explained by competition for resources with an increased number of swans. It is also worth noting that, following decline in swans in the LPPNA phase, other species of Anatidae, coots and grebes increase in frequency. These interpretations have to be taken with caution as we are dealing with archaeological evidence based on frequencies of identified bones in an assemblage rather than counts of different species of birds from an ecological survey of a wetland. Nevertheless, the waterbird community structure seems to have been influenced by mutual ecologies of different species and their behaviour characteristics. Furthermore, we have evidence that swans were breeding at Shubayqa (Yeomans et al. 2024), hence at their most territorial.

Taphonomic evidence, as exemplified by a recent study of avifaunal remains from Shuidonggou Locality 12 in China (Zhang et al. 2022), provides further details of human-bird relationships. There is evidence (Fig. 10a) in the form of peeling marks (Pedergnana and Blasco 2016; Blasco et al. 2019) resulting from feather removal on a swan carpometacarpus from Shubayqa. The body part representation for swans does not suggest that the birds were only hunted for feathers, but this taphonomic evidence shows that the feathers were also utilised. This find speaks to the complex entangled relations that linked humans and waterfowl at Shubayqa. Being alive at Shubayqa in the Final Natufian/PPNA would have entailed the frequent encounter and active engagement with mute swans which contributed to the shaping of the environment around the site. The inhabitants of

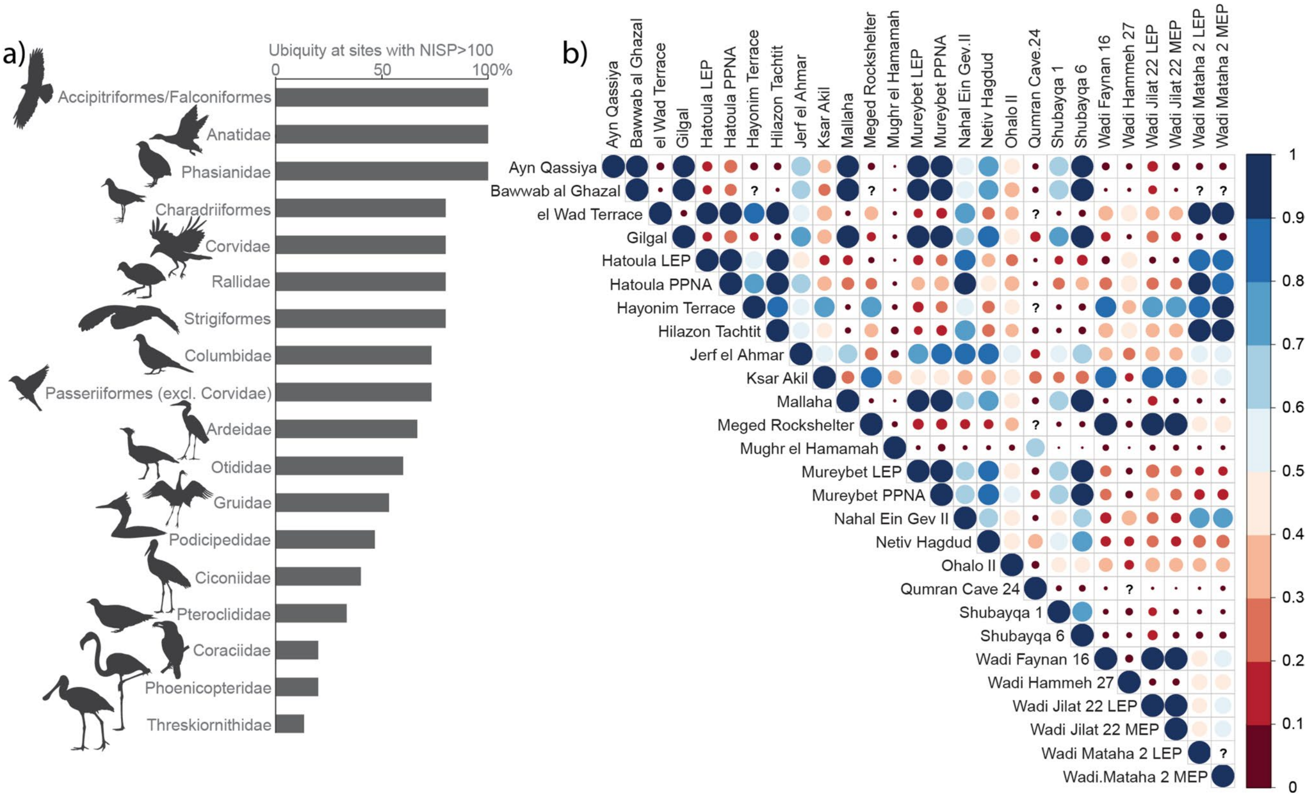


Fig. 7 **a**) Ubiquity of taxonomic groups within assemblages with more than 100 bones identified. **b**) Morisita-Horn similarity indices of Levantine avifauna assemblages from the Upper Palaeolithic to PPNA with darker and larger dots indicating greater similarity

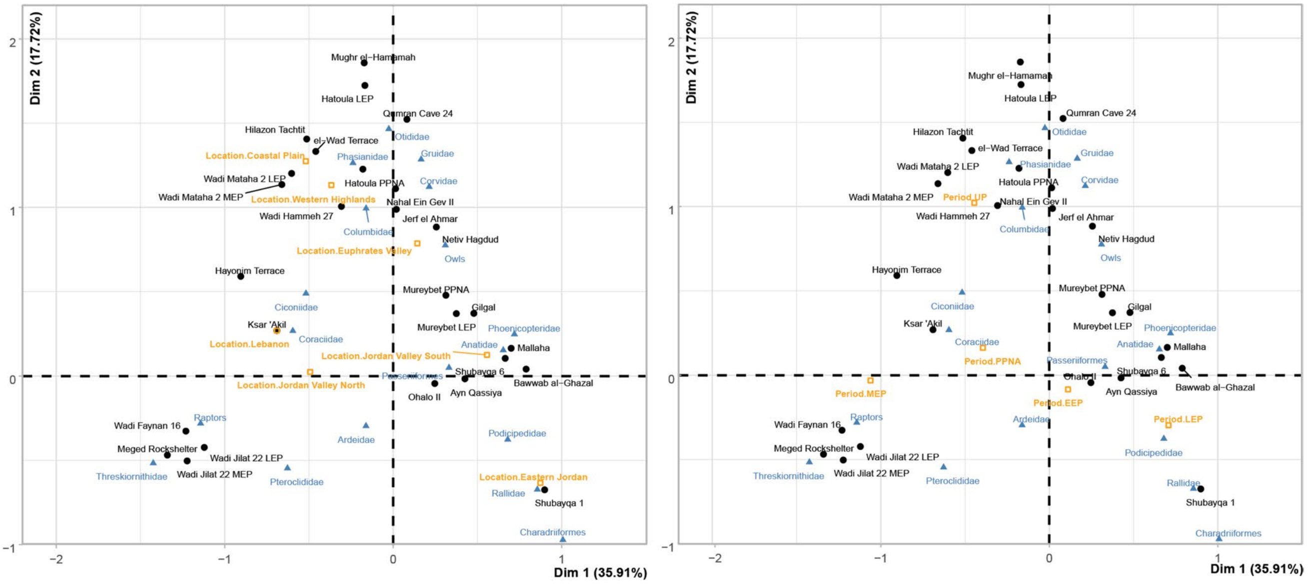
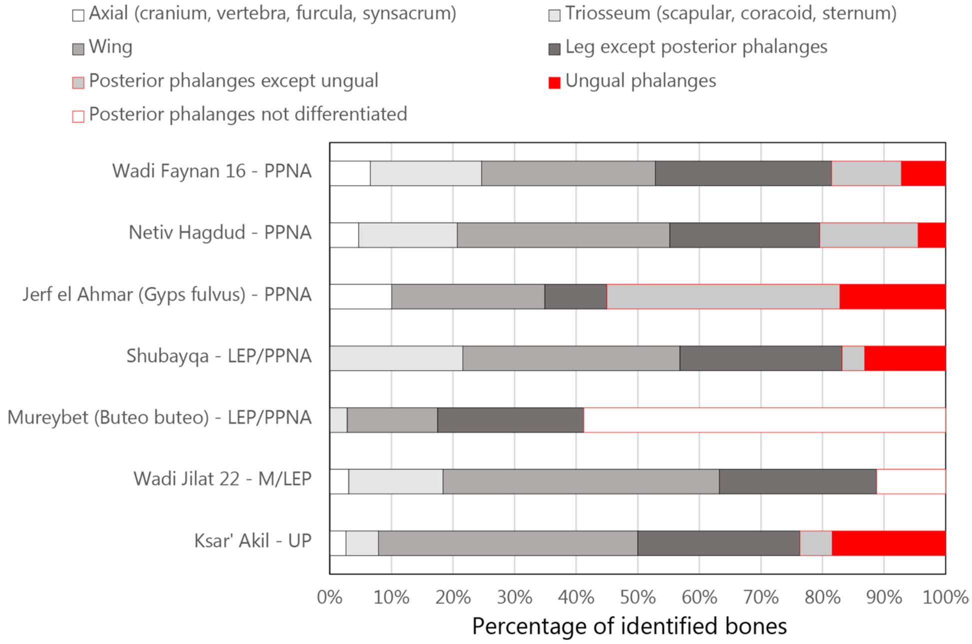


Fig. 8 Correspondence analysis of the identified number of bones in taxonomic groups shown against average for taxonomic groups (left) and period (right)

Fig. 9 Comparison of frequency of raptor ungual phalanx frequency in assemblage across the southern Levant (data fromGourichon 2002, 2004; Kersten 1991; Martin et al. 2010; Tchernov 1994; White et al 2021b), grouped by period



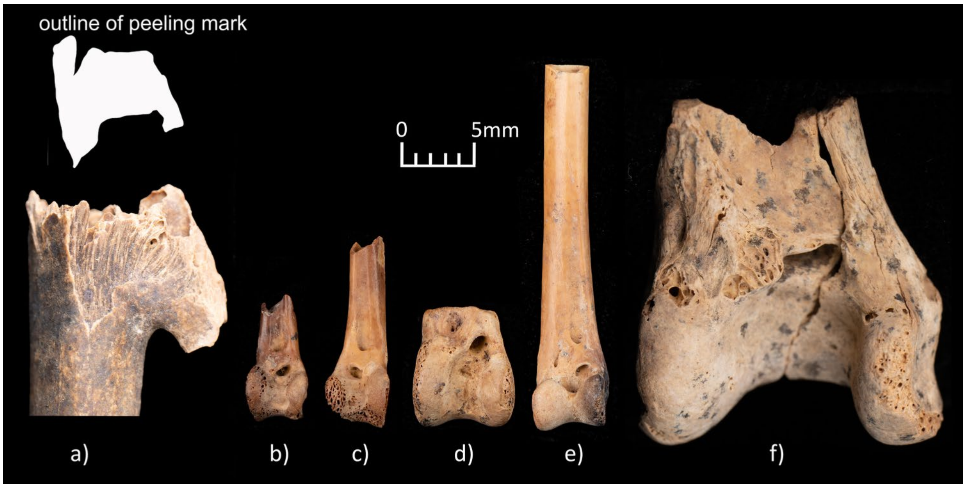


Fig. 10 **a**) Swan (*Cygnus* sp.) carpometacarpus from the Final Natufian/Early PPNA phase with evidence of peeling marks resulting from feather removal. b-c) two polished quail tibiotarsus bones from the LPPNA floor (153) in Space 3 found with beads manufactured from bones of small animals, mostly mammals where identifiable, but some could be birds bone (see Yeomans et al. 2019, Fig. 11). d) bead made from the distal end of a chukar partridge tibiotarsus from the Early Natufian hearth fill (43) in Structure 1. e) polished sandgrouse tibiotarsus, possibly a preform for bead manufacture from backfill in the construction cut the Late Natufian wall of Structure 2. f) Crane, Gruidae, tibiotarsus from Shubayqa 6, Space 4 (309)

the small Shubayqa community dwelt in a landscape where mute swans were an integral part at least for some of the year (Ingold 1996, 2000). These large birds which dominated the wetland in this period, very likely, contributed to define the identity of the community. The incorporation of swan feathers in the Shubayqa material culture may reflect the importance of these birds as human companions (Haraway 2008) during the Younger Dryas. The later (LPPNA) use of quail bones to produce beads (Fig. 10b and 10c) speaks to a different encounter and to different materialities that emerge from it. These materialities reveal the intimate engagement and the preoccupation with a type of bird usually attracted by cereal crop habitats. This shift may reflect changing activities and webs of interspecies participation at Shubayqa alongside the first experiments in the cultivation of cereals (see below).

The skeletal element representation changes slightly for the Anatidae over the sequence at Shubayqa. An explanation could be that the overall numbers of waterfowl hunted were fewer and therefore entire carcasses were transported to occupation locations for processing rather than initial butchery taking place at the capture site (Fig. 6). Few Anatidae tibiotarsus bones found at Shubayqa 6 displayed the distinctive cuts marks associated with bead manufacture that had been found at Shubayqa 1 in the Late Natufian (Yeomans and Richter 2018). The polished tibiotarsus bones of quail from the LPPNA phase at Shubayqa 6 were found in a floor with numerous bone beads from small mammals, mainly hares (Yeomans et al. 2019). There seems to be a shift in the habitats represented by the bone beads at the two sites – bones from animals generally inhabiting the wetland to animals that inhabit the grasslands. Was there a symbolic connection to this change? Perhaps it reflected the increased importance of the zone around the wetland as people started cultivation. In the LPPNA people were hunting numerous wetland birds, but for some reason, their bones were less likely to be turned into items of personal adornment even though the whole carcasses were brought back to the settlement.

The proportion of Phasianidae in the Shubayqa assemblage increased significantly in the LPPNA phase where they formed nearly 9.7% of identified remains. Where identifiable these were common quail (*Coturnix coturnix*). Quail is considerably smaller than sand partridge (*Ammoperdix heyi*) although the latter is more frequent in Jordan's eastern desert today. Quail is a migratory species present in the spring and autumn (Rabou 2021). The numbers of quail recorded in recent history has been impacted by their extensive hunting during migration especially along the north coast of the Sinai where, at least since the early twentieth century, tens of kilometres of bird nets targeted the migration route (Shirihai 1996). Eason et al. (2016) estimate that, between 2008 and 2012, 2.0 million quail were killed annually in this area during autumn migration. In 2012, with widespread use of MP3 players to attract the birds, the estimate was 3.3 million birds. The relative proportion of quail in the assemblage compared to other Phasianidae could therefore illustrate how this species has been targeted in recent history.

Green and Thomas (2008) surveyed the Jordanian Badia region in 1997 noting that quail were commonly flushed from patches of crops. Quails prefer cereal crop habitats (usually wheat and barley) and, during breeding seasons, remain hidden within dense vegetation (Sardà-Palomera et al. 2012). There is clear evidence for pre-domestication cultivation in the PPNA in other areas of the Southern Levant (Asouti and Fuller 2013) and, although the Shubayqa botanical assemblage has not been published, significant increase in frequency of quail must have corresponded to change in the availability of different habitats within the vicinity of the qa' Shubayqa. A synanthropic relationship, with quail benefiting from new niches offered by crop cultivation is an obvious explanation. Similar niche construction behaviour associated with the development of rice paddies resulting in an increase in frequency and year-round presence of geese is interpreted as early evidence for goose domestication in China (Eda et al. 2022). This illustrates how we need to consider the impact of changing habitats resulting from human activity on the long-term evolution of the relationship between humans and birds. We have also argued elsewhere (Yeomans et al. 2019) that dogs later in the sequence might have allowed quail to be flushed from the undergrowth increasing the encounter rate between humans and quails. If change in hunting method or habitat alteration is ultimately responsible will need reconsideration when botanical evidence is available. Two polished tibiotarsus bones from occupation deposits in Space 3 dating to the LPPNA were probably bead preforms (Fig. 10b and 10c) may have been a purely incidental use of suitable materials but choice may also reflect behavioural characteristics of these birds.

An example of a bead made from a chukar tibiotarsus (Fig. 10d) is the only bone from this species of Phasianidae in the assemblage from Shubayqa and dates from the Late Natufian. Chukar are more common in the Mediterranean zone of the Southern Levant. The bead made from a chukar tibiotarsus from Shubayqa is most probably evidence of contact with Natufian groups further west as it is stylistically very similar to those found at el-Wad and Hayonim Cave which were part of headdresses (Davin 2019). Given the absence of any other remains of chukar at Shubaqya, Natufian groups to the west probably traded this item with people living around the wetland at Shubayqa or the population brought important items with them as they moved in the landscape. There is other evidence, in the form of dentalium beads and Cervidae remains for an extensive trade network in the Natufian (Yeomans et al 2017).

Sandgrouse are uncommon throughout the entire Shubayqa sequence. The presence of a polished tibiotarsus of a sandgrouse from the Late Natufian phase at Shubayqa 1 may be an indication of a symbolic link to the hunting of these species (Fig. 10e). The low frequency of sandgrouse is in contrast to Qermez Dere where they form 77% of the assemblage and apparently hunted primarily for subsistence (Dobney et al. 1999). Sandgrouse are adaptable to a range of temperatures feeding on dry seeds, which like the quail, may have benefited from early cultivation. Sandgrouse also have the ability to store water in their belly feathers so the young can be provided with water without the requirement of being adjacent to a source (Maclean 1983). Explanation for the slight increase in the frequency at Shubayqa might relate to changing habitats or potentially the use of dogs to facilitate the tracking and capture of these birds (Yeomans et al. 2019).

Rallidae represented at Shubayqa are dominated by coots (*Fulica atra*) and they are especially well represented during the Late Natufian. Due to the effort expended in diving for food, coots prefer shallower waters with larger areas of reed beds (Talbi et al. 2020) and these specific habitats were therefore probably well represented in the later part of the Bølling-Allerød in Shubayqa. There is a gap in the occupation sequence between the Early Natufian and Late Natufian phases so an absence of human presence and harvesting of emergent vegetation, together with a reduction in water levels of wetland, might have encouraged coots to winter at Shubayqa. We do not know if the human residents completely left the area between the two phases but the increase in the frequency of coots tentatively suggests a period of lower anthropogenic impact on the wetland.

Cranes are often argued to have a symbolic importance to Early Neolithic communities across southwest Asia. At Çatalhöyük, two common crane tarsometatarsus bones were worked into bone points and a wing, placed on top of cattle horncores, is interpreted as part of a costume that may have been used by humans as they recreated mating dance of cranes (Russell and McGowan 2003). At Hallan Çemi (11,700–11,400 cal BP), crane is represented by a higher proportion of bones in a large communal structure (Zeder and Spitzer 2016). Cranes are also depicted on pillars at Göbekli Tepe (Garfinkel and Krulwich 2023). Currently, common cranes are passage migrants in the Southern Levant (Shirihai 1996) but have not been documented breeding and therefore dancing. However, we do have evidence that cranes bred at Shubayqa at least in the LPPNA (Yeomans et al. 2024). The limited knowledge we have of breeding ranges of past distributions of cranes is highlighted by Bovy's analysis of juvenile sandhill crane (*Grus canadensis*) in Washington, demonstrating a wider distribution 1500 years ago when a shell midden on Lopez Island formed (Bovy 2012b). Although most of the material is fragmentary, there is no evidence for a symbolic association of cranes to humans at Shubayqa (Fig. 3f) and therefore the symbolic relationship might be localised.

There is a slight increase in the proportion of raptors at Shubayqa 6 compared to Shubayqa 1. Compared to other sites in the Southern Levant, people were not targeting these species extensively. The frequency of Accipitridae varies throughout the entire sequence at Shubayqa but they are never common. The body part frequency is skewed towards terminal phalanges (Fig. 8) and, given the weight of a common buzzard (only 0.55–0.9 kg for captive birds and possibly less for wild birds (Okoli & Aiyedun 2014), the amount of meat obtained by hunting this species is low. The difficulty in obtaining these birds means it is unlikely that these birds were extensively hunted for food. There is also the possibility that claws and feathers were collected from birds that died from natural causes. The main migration route for raptors in the Levant follows highlands where soaring birds benefit from updraft. The encounter rate between humans and raptors is lower in the Badia region of Jordan but, when feathers and talons of these impressive birds could be obtained, people seem to have gathered these items. Based on the body-part representation, these birds were also consumed when hunted despite the relatively limited meat the carcasses provided. Furthermore, none of the ungual phalanges were found in contexts that were not general refuse locations and some bones were burnt (Fig. 11) as is typical for bones where food preparation was taking place. The best evidence for symbolic use of bird remains at Shubayqa derives from a cluster of material, probably placed inside a bag of perishable material that was placed against the wall of Space 1 during the PPNA. This find has been discussed in detail elsewhere (Yeomans et al. 2021) but contained possible figurines made from the worked foot bones of gazelle and sheep, worked bone items and at least one ostrich eggshell. These items were deliberately broken and seem to represent a closure event associated with the abandonment of the site.

In the taxonomic diversity at Shubaqya (Table 4 and Fig. 3), there is a change with an increase in the proportion of the assemblage that one family comprises, especially in the Late Natufian to PPNA phase at Shubayqa 6. This is possibly reflecting how some species adapt to the long-term presence of humans. By the LPPNA phase, cultivation created new habitats suited to species with different ecological niches and there is an increase in other taxonomic groups. The taxa present seem to be an interplay of reductive homogenisation whereby human activity reduces the richness, abundance and evenness of ecological communities either intentionally or accidentally (Crabtree et al. 2023) together with an increase in foraging opportunities for some of the less common species.

The younger dryas: Preliminary observations based on the shubayqa sequence

Unfortunately the stratigraphic sequence from the Final Natufian to PPNA phase at Shubayqa 6 cannot yet be subdivided. In 2020, a paper (Yeomans and Richter 2020) investigated the difference between a large midden (context 220) that has now been dated to the Final Natufian phase (12,000–11,700 cal BP) within the Younger Dryas (Yeomans et al. 2024) and midden deposits infilling Space 4 suggested different use of two areas within the settlement. The Space 4 midden resulted from extensive processing of carcasses, perhaps to store meat and fat for the lean season, whereas in the midden (220) there were less frequent avifaunal remains and the bones of mammals were not intensively processed (Yeomans and Richter 2020). We now suspect a temporal difference between the two middens with the wall of Space 4 cut into the (220) midden. As the wall of Space 4 was not excavated, it was impossible to stratigraphically demonstrate the relationship between the two (no construction

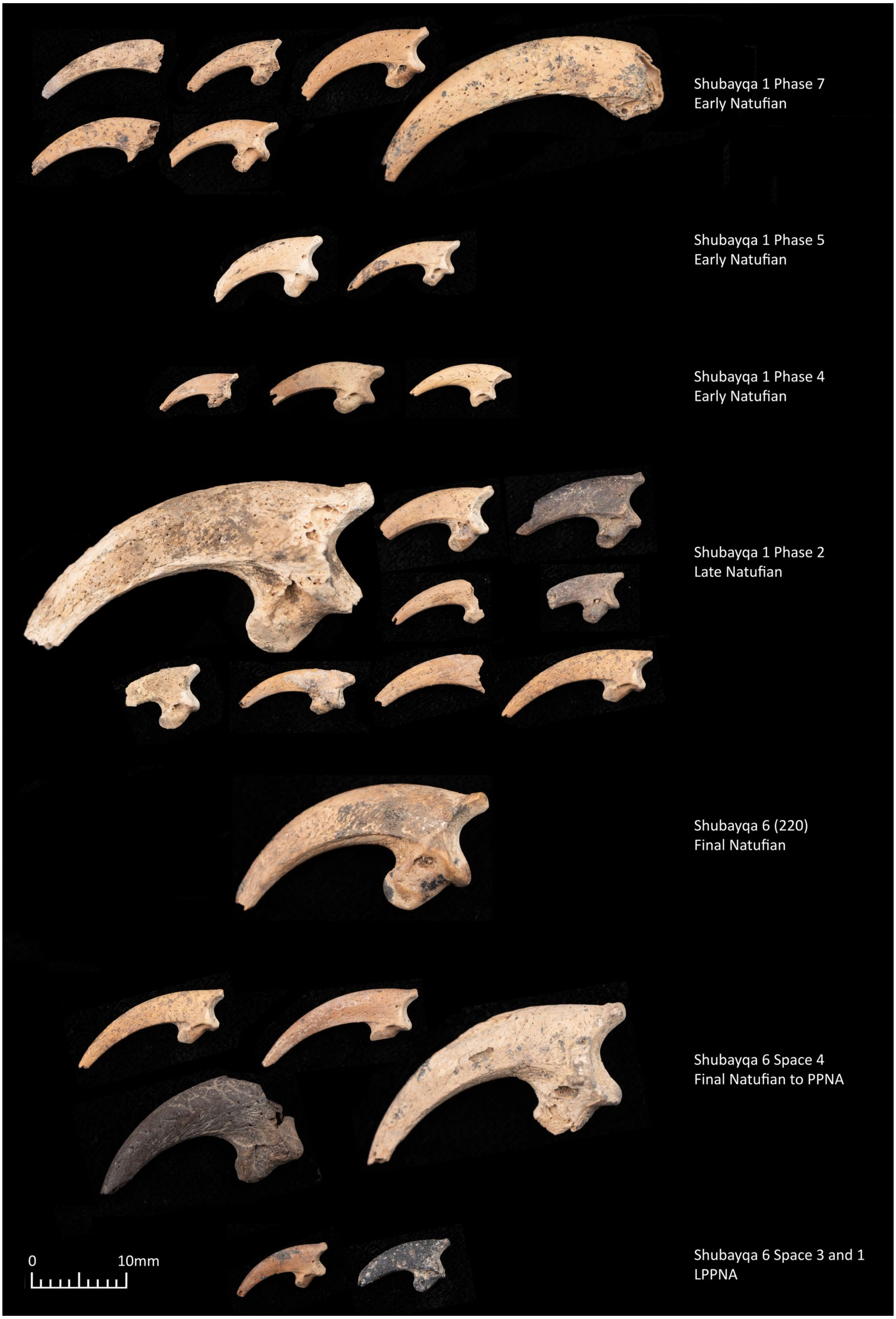


Fig. 11 Best preserved ungual phalanges from Shubayqa, for subphases at Shubayqa 1 see Richter et al (2017)

cut was evident). Dates from the Space 4 midden seem to spread from the very end of the Natufian to the mid PPNA but the earliest midden layers, as well as the hearth from initial use of Space 4 as an occupation structure, have not been dated. Avifauna was less frequent in the (220) midden and, similar to the Final Natufian midden at Shubayqa 1—this was initially interpreted as evidence of the environment becoming drier. However, this contrasts with evidence for more frequent wild cattle, a water dependent species, during the Younger Dryas phase at Shubayqa 1 and in the (220) midden. Struggling to explain this increase led to the idea that wild cattle were concentrating around wetland areas less prone to drying out during the period often considered as colder and drier. However, identification of fragments of eggshells from a breeding waterfowl in the Shubayqa 1 Final Natufian midden disputes this reconstruction (Yeomans et al. 2024). What is exceptional about the Final Natufian material from Shubayqa 1 and the Younger Dryas (220) midden at Shubayqa 6, is the clear difference in the processing of mammalian carcasses (Yeomans and Richter 2020). The faunal material from both were not extensively processed for the extraction of grease as they were in the earlier and subsequent phases. There is also no evidence for architecture in these phases so there is tentatively also a shift in the nature of occupation and this is another possible explanation.

Whilst there are relatively few avifaunal remains in the (220) midden (Fig. 12), there is an increase in the frequency of swan bones as well as bones of juvenile waterfowl (Yeomans et al. 2024) indicating the presence of conditions suitable for breeding—i.e. water availability. Several other papers (Orland et al. 2012; Hartman et al. 2016; Langgut et al. 2021) focusing on localised sequences of occupation suggest that the impact of the Younger Dryas in the southern Levant created wetter conditions with less seasonal rainfall. Did the effects of the Younger Dryas further north push the range of swans further south? We know that there must have been good conditions for ducks during the Younger-Dryas at Shubayqa, but these were not hunted as extensively as in the Bølling-Allerød or Early Holocene. As discussed above, changes to the waterfowl community structure may have come into play with influx of swans influencing the occupation of the wetland by other birds. Many questions remain as to effects of the Younger Dryas on the range of ecosystems of the Southern Levant that require consideration of multiple lines of evidence. Based on the data presented here, the Qa' Shubayqa during the Younger Dryas was still a viable wetland encouraging significant biodiversity and was a productive location for humans to hunt prey. The current faunal and architectural evidence suggested that the Younger Dryas occupation was seasonal in the dry season which would explain the absence of wintering birds but people were gathering the eggs and hunting the birds that remained through the summer months to breed. This model needs testing with archaeobotanical and other data in the future.

Regional analysis

The results of the regional analysis suggests that there was an important association between diurnal raptors and humans throughout the Late Pleistocene and Early Holocene on the basis of the ubiquity analysis. At some sites, there was evidently a very strong association between these humans and raptors. Wadi Jilat 22 has been interpreted as a hunting camp where procurement of feathers was paramount. Martin et al. (2013) speculated that distinctive and unique Jilat knives (Garrard and Byrd 1992) found at the site could resemble flight feathers of eagles. In this context, the possible flint figurines from Early Neolithic site of Kharaysin (Ibáñez et al. 2020) should also be mentioned and representation of bird elements in cultural material is highlighted by Beothuk pendants representing bird feathers, feet, and tails (Kristensen and Holly 2013). Representation of feathers in

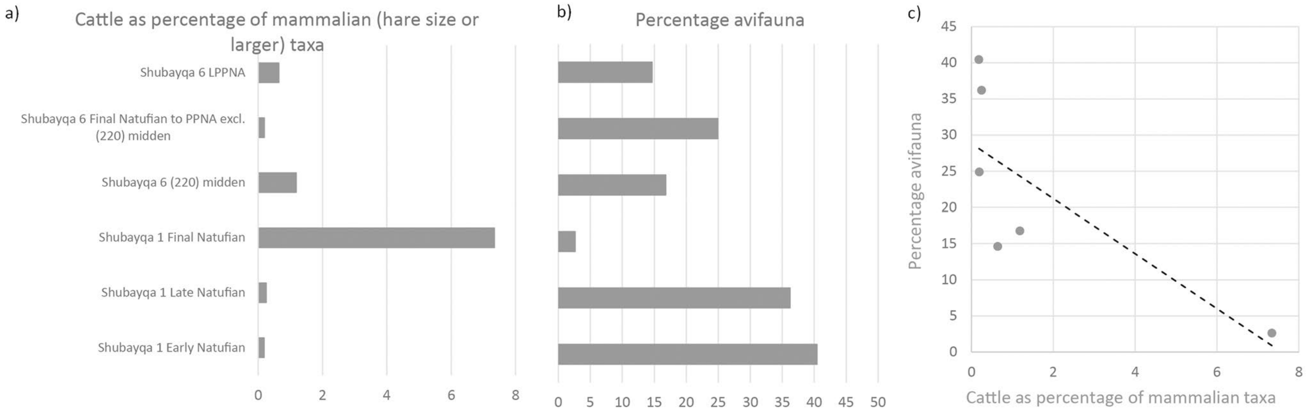


Fig. 12 Comparison of the frequency of a) cattle within the mammalian assemblage by phase, b) frequency of avifauna by phase and c) relationship between the two frequencies with trend line

tools is therefore possible and it would not be surprising that birds infiltrated the symbolic ideology of cultural artefacts manufactured from non-osseous materials as well as osseous materials.

Another Levantine site dominated by diurnal raptors is Meged Rockshelter with "identifiable avian body parts … strongly biased in favor of foot bones, in particular terminal phalanges" (Kuhn et al. 2004:35). These included one notched specimen but, as Kuhn et al. (2004) mention, the bulbous articulation at the proximal end of the terminal phalanx forms an ideal natural anchor point. The dominance of diurnal raptors at Wadi Faynan 16 has also been noted and the body-part analysis suggests that whole carcasses were often brought to the site allowing use of feathers and talons, although there is some evidence that these birds were occasionally consumed (White et al. 2021b). Mithen (2022) developed an idea that feathers and talons were important in shamanistic rituals at the site promoting symbolism as the focus of human-bird interactions. Results of Morisita-Horn analysis shows overall similarity of the Wadi Jilat 22, Wadi Fayan 16 and Meged Rockshelter assemblages but Ksar 'Akil is also highlighted as having an assemblage with taxonomic groups represented in similar proportions. Kersten (1991) notes that more material, not analysed, consists chiefly of phalanges of large birds of prey from the Upper Palaeolithic phase which, if included, would probably have resulted in a greater similarity between this site and others dominated by diurnal raptors. The body part analysis shows that at Jerf el Ahmar and Mureybet (Gourichon 2002, 2004), phalanges were more common than at other sites (Fig. 9). However, these sites clustered with sites such as Shubayqa in the Morisita Horn hierarchical clustering (see below) with avifauna dominated by wetland birds which may relate more to the local environment.

The presence of beads made from the tibiotarsus bones of chukar expresses a symbolic association of these species to humans and they have been found with burials at Hayonim Cave, 'Ain Mallaha and el-Wad, with a few additional beads manufactured from raptor tibiotarsus bones (Pichon 1983; Davin 2019). The taste of chukar meat and difficulty in hunting these birds is also notable (Eid and Handal 2018). Arguably, the symbolic importance of chukar seems widespread across southwest Asia in the Late Pleistocene and Early Holocene, perhaps relating to the behaviour and/or physical characteristics of the birds. Reconstruction of human-bird interactions can be developed with knowledge of bird life histories, physical traits and behaviour (Overton and Hamilakis 2013). Chukar are striking birds with bold, black bars on their sides, a dark band runs across the eye encircling the white cheek and connecting under the throat. The red bill and borders of eyes provide conspicuous markings. Males are territorial and vocal when alerting others to the presence of predators. At the PPNA site of Wadi Faynan 16, chukar would be expected given the local environment and they were present in the assemblage but White et al. (2021b) analysed the body-part and butchery evidence to conclude the species was hunted for consumption. The association between humans and chukar was not limited to the symbolism but subsistence rationale for humans hunted this species may not have been as important as interpreted by proponents of the Broad Spectrum Revolution (Flannery 1969). There seems to have been a dual purpose; humans to hunted chukar as they provide tasty meat but the difficulty in hunting them and perhaps their physical and behavioural characteristics resulted in a symbolic association reflected by the use of body-parts from this species.

The assemblages dated to the Late Epipalaeolithic at Qumran Cave 24 and Mughr el-Hamamah stand out as different from others within our study area with a domination of Columbidae and, at Qumran Cave 24, Corvidae. This has similarities to the assemblage at Göbekli Tepe located further to the north, spanning the Late PPNA to Middle PPNB with an avifaunal assemblage dominated by Corvids (Peters and Schmidt 2004). The much larger PPNB assemblage from Qumran Cave 24 was also dominated by Columbidae and Corvidae (Recchi and Gopher 2002) suggesting that the composition of the earlier assemblage was related to the taxa found in the immediate environment. Evidence of a symbolic relationship is provided by a polished Corvidae bone from Qumran Cave 24 in the PPNB phase. Overall, Corvidae increase as percentage in assemblages dating to the PPNA and might be related to the fact that these birds thrived in new anthropogenic niches created by agricultural activity. However, the symbolic importance of the taxa is noted in other prehistoric settings (Finlayson et al. 2012; Serjeantson and Morris 2011).

Several assemblages have similar species compositions indicated by a dendrogram showing Morisita-Horn similarity between assemblages (Fig. 13a). Figure 13b shows a similarity network of sites (nodes) based on the Morisita-Horn similarity scores (links) colour coded according to the community partitions detected by the Louvain algorithm. Sites that are part of the same community are strongly associated according to their similarity scores. These communities of sites mirror the clusters highlighted in the dendrogram in Fig. 13a. Some aspects of these assemblages, such as the chukar tibiotarsus beads at 'Ain Mallaha and the use of bird bones to manufacture beads at Shubayqa 1 and 6, illustrate the symbolic associations between humans and birds but generally, the avifaunal assemblages seem to mainly relate to subsistence activities and reflect the broad environment of site location (Fig. 14). At Shubayqa 6, for example, many of the remains of the birds were found in middens that accumulated because of intensive carcass processing (Yeomans and Richter 2020). Horwitz et al. (2010:269) note that it is "most likely that the majority of

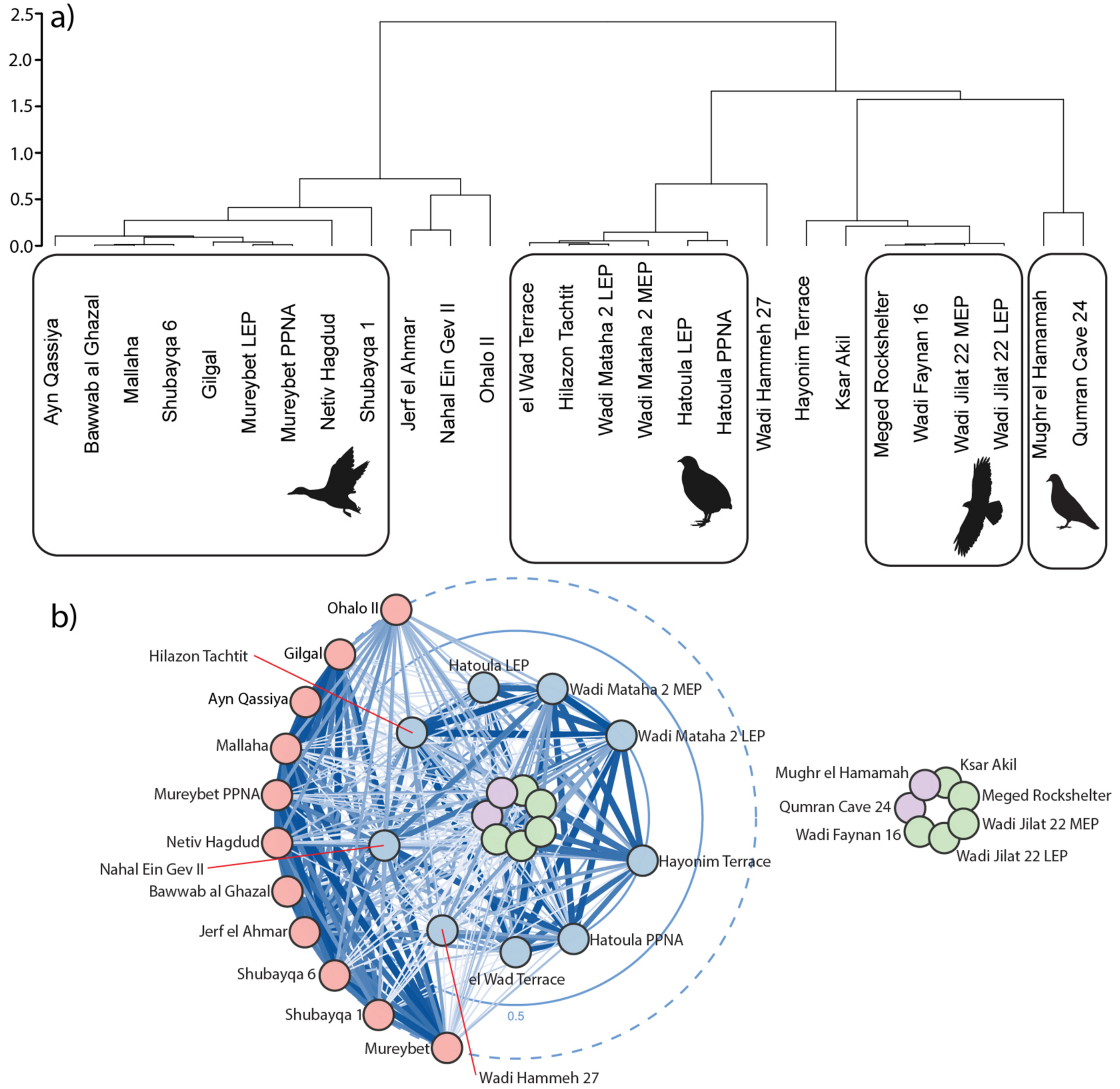


Fig. 13 Dendrogram showing the hierarchical clustering of assemblages based on the Morisita-Horn similarity index with silhouettes to indicate dominant taxonomic groups. b) Similarity network of sites (nodes) based on the Morisita-Horn similarity index (links). The colour of links is proportional to the degree of similarity between pairs of sites and the colour of nodes corresponds to the community partitions each site has been assigned by the Louvain algorithm. Nodes with the same colour define groups of sites that strongly correlate because of their Morisita-Horn similarity scores.These partitions mirror the clusters highlighted by the hierarchical clustering in 11a

the bird remains served as dietary items and were intentionally trapped or hunted by the inhabitants of Gilgal." Although there is range of human-bird interactions, the results seem to suggest sites fall at one end of the spectrum; those where symbolic association of birds and humans was stronger and those where subsistence utilisation of birds was more important perhaps reflecting a division in the how different people viewed avian inhabitants of the world. Perhaps this is evidence that when birds were consumed more regularly, strength of symbolic connections to birds was weaker. The routes of migration are also likely to be important with certain species following constrained routes leading to different geographical and seasonal variation. It is notable that some sites are relatively close to other sites where there is a stronger subsistence association between humans and birds. A recent summary of the evidence of

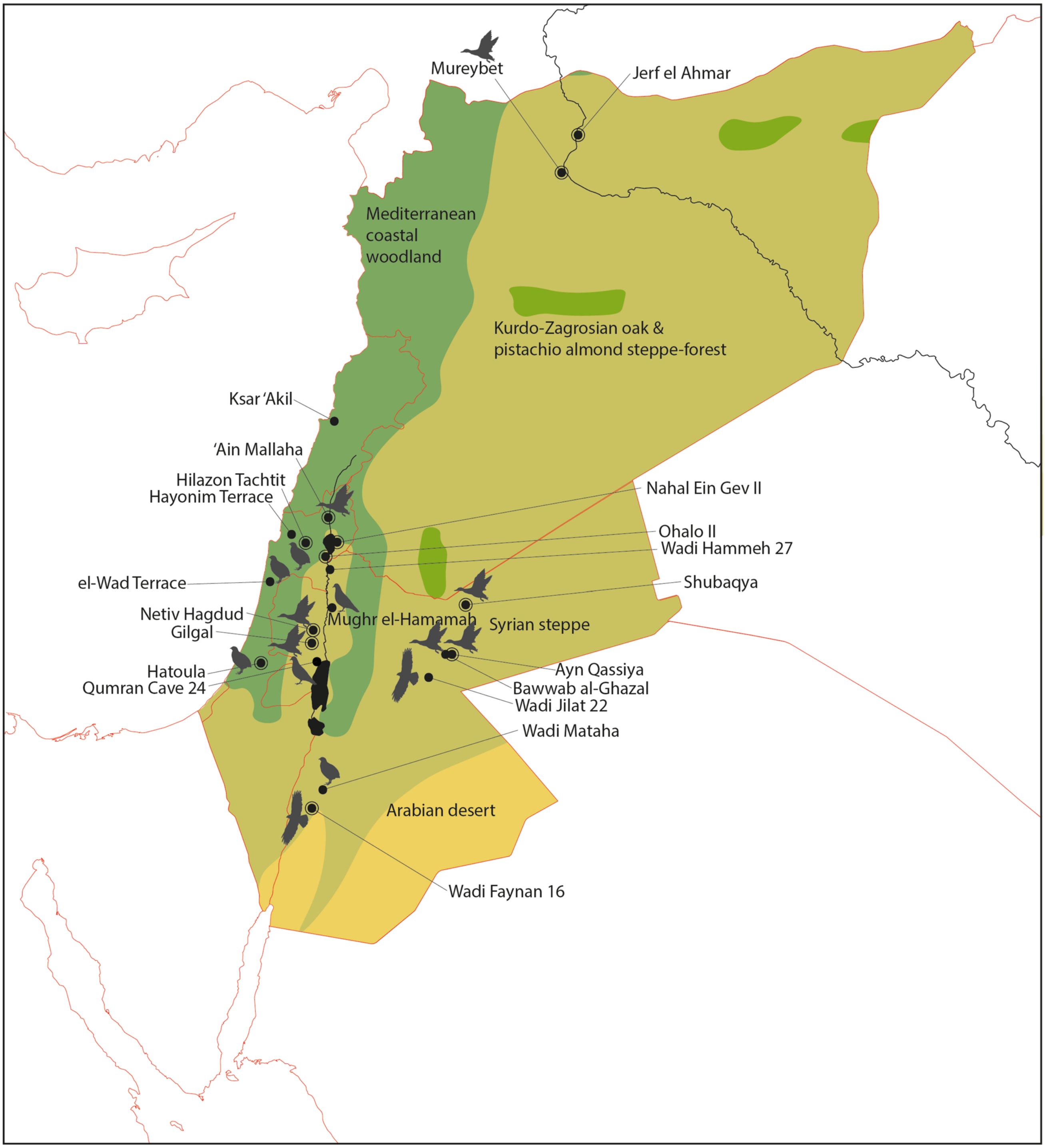


Fig. 14 Vegetation zones and location of sites with a similar dominant taxonomic group within assemblage shown in the Fig. 13 dendrogram allowing visualisation of the effects of environment on the species representation

human-avian interaction in the upper Euphrates and Tigris river basins argued that distinct modes of bird exploitation occurred in the two areas. This was unrelated to the ecological characteristics of the two environments and "bird hunting does not seem to have been conducted to fill major gaps in the supply of animal proteins" (Pöllath and Peters 2023: 154). Although this study primarily assumed a subsistence basis for the human-avian interactions, the analysis demonstrated that intensity of bird hunting was linked to cultural traditions.

Sample size issues meant that several sites were not included in the statistical analysis. The few bones from Iraq ed-Dubb (Martin et al. 2013), Moghr el-Ahwal (Edwards et al. 2017), Ramat Harif (Munro et al. 2020) and Raqefet Cave (Yeshurun et al. 2013) are tentatively closer to sites with a stronger symbolic association between humans and birds. Nahal Rahaf 2 (Marom et al. 2022), Saaide II (Churcher 1994) and Wadi Jilat 6 (Martin et al. 2010) could arguably be more subsistence based association and the nature of associations other sites such as Kharaneh IV (Martin et al. 2010) and Tor Hamar (Hirose et al. 2022) remain obscure. Beyond the geographic boundary of sites included in the statistical analysis is the site of Dja'de (Gourichon 2004) dating to the Late PPNA and Early PPNB with a high representation of Great bustard (*Otis tarda*) and Qermez Dere, dated to the Early Neolithic, dominated by sandgrouse (Pteroclidae) (Dobney et al. 1999). The dominance of these species might reflect the effect of agricultural activity providing opportune foraging habitats for these species of birds with both groups of birds attracted to these niches. At Körtik Tepe, interpretation (Emra et al. 2022) discussed the avifauna in relation to subsistence economy of the settlement despite ritual activities being well attested (Clare et al. 2019). Interestingly, the assemblage dominated by Great Bustard (*Otis tarda*) during the Younger Dryas phase, has an increase in Greylag goose (*Anser anser*) in the Early Holocene. Attraction of the geese to agricultural activities could be considered as a potential factor.

Preconceptions of species identified as symbolically important

The symbolic role of raptors and corvids are often highlighted in literature as symbolically powerful or charged species (Mannermaa 2013) but other species may have filled a similar role. Waterfowl do not always come to the fore in such interpretations as these species are often linked to subsistence but several archaeological cases studies challenge this notion. The importance of Anatidae is highlighted by the Upper Palaeolithic site of Mal'ta, 160 km from Lake Baikal in Siberia and dated to 23,000 to 21,000 cal BP (Khenzykhenova et al. 2019). Sixteen carved avian figurines were recovered from the site and, of these, 13 pendants depicted waterfowl in flight with elongated necks suggestive of swan representations (Abramova et al. 1967). These items, carved from mammoth ivory, had a hole at the distal end and recovery of one from a grave placed on the chest of the interment, suggests how these items were worn (Abramova et al. 1967). In this example, the importance of waterfowl infiltrated into the symbolic realm and based on the three species identified in the faunal assemblage (*Anser anser*, *Larus argentatus* and *Corvus corax*) the swan pendants did not reflect the importance of the species to diet and must therefore have had a meaning beyond subsistence (Khenzykhenova et al. 2019). Preserved feathers allowed Urquiza and Echavarria (2018) to show how Anatidae as well as Phoenicopteridae and Rheidae feathers were used for paraphernalia and weapons in Argentina. An example of a loon skull with inlaid ivory eyes placed in a human burial at Ipiutak, Alaska provides an illustration of how behaviour of a species provided a foundation for their importance (Morrow and Volkman 1975). The loon is difficult to hunt and only occasionally represented in midden deposits but its hunting prowess may have led to its symbolic importance for humans. From these few case studies, it is clear that the range of species that embedded symbolic or ritual meaning to past human groups is diverse. The approach here was to attempt to analyse the data without preconceived ideas of the value (economic, symbolic or ritual) of different species and then, based on quantitative analysis, explore underlying characteristics to highlight potential significance. The results suggest that diurnal raptors did have a symbolic importance throughout the Late Pleistocene and Early Holocene with chukar also perceived as important especially in the Late Epipalaeolithic. There also seems to be a divergent pattern – sites where humans have a stronger symbolic association with birds do not appear to have relied on birds for subsistence to the same extent as sites without but this might relate to the local environmental conditions. Even at sites where birds were important as part of people's diet, birds still influenced other aspects of people's behaviour. This is unsurprising given what we know of the beneficial effects of birds on humans (Whelan et al. 2008) and the ecosystem services that avifauna provide would have been equally important in the past. Overall, we have tried to use Table 1 to test the hypothesis that certain bird species were hunted for symbolic reasons and others were hunted for subsistence reasons and the analysis has shown that it is very difficult to separate subsistence from symbolism.

Conclusion

The presence of wetland birds at Shubayqa in the Younger Dryas and evidence from carcass processing suggests that resource pressure was not significant and offers support to other criticisms focusing on the timing of the Younger Dryas as a factor in the shift to agriculture (Maher et al. 2011). Evidence for synanthropic adaptations of animals have been the focus of recent publications (summarised by Baumann 2023) highlighting the importance of understanding human ecological niche creation on carnivores and omnivores which benefited from scavenging opportunities and protection from predators. Anthropogenically altered environments benefited many species (e.g. Zeder & Lemoine 2022) not just those of higher trophic level as the summary by Baumann (2023) highlights. Niche construction activities by humans may have promoted certain natural-cultural contact zones to offer increasingly productive environments and hence encourage further investment. As Zeder (2017) suggests, the increase in symbolism as people invested more time into certain locations and modifying these habitats, could be explained as a means for traditional ecological knowledge to be passed down to the next generation. Whilst there is cultural evidence that bird symbolism increased during the shift to the transition to agriculture (Garfinkel & Krulwich 2023), comparison of avifaunal assemblages suggests that throughout the Late Pleistocene and Early Holocene birds had a symbolic role for humans. Even in locations where bird hunting was primarily for subsistence, birds still had a symbolic role for people.

This study has shown that the association between birds and humans over the course of the Late Pleistocene and Early Holocene is part of a complicated web of interactions. The people occupying the vicinity of a wetland at Shubayqa had a complex knowledge of subsistence strategies allowing them to mitigate short- and long-term climatic fluctuations (although local impact of these is open to debate). Many birds were drawn to this wetland and varied according to habitat availability as well as human presence and their ecosystem engineering activities. These birds were hunted for food but other roles of birds, as we see from ethnographic examples where people are better connected to the environment, would have been equally important. Crabtree et al. (2023) have suggested that the closer a society is to other species in their environment the more likely they are aware of the impact of their actions on other species. They argue that, because of the migratory nature of many birds, past populations will have less knowledge of the ecological impact of their multispecies interactions with these animals. This does not necessarily seem to be the case for the Late Pleistocene and Early Holocene of Shubayqa. Yet, the sequence at Shubayqa, with the increased representation of one taxonomic group through time and the overall decrease in birds through the sequence despite prevalence of suitable environments, might be evidence for human activity affecting the community of avifauna. The long-term sequence at Shubayqa shows the changing relationships between humans and birds through time and this may have been related to the influence that the humans had on the environment and habitat availability. At the same time, the shift in human activities may have changed their patterns of interspecies participation as the case for the large and small waterfowl demonstrates.

The entwined lives of humans and non-human animals as reflected in the archaeological record is difficult to interpret but there is now greater discussion of how the interwoven lives of different species was multifaceted (e.g. Pilaar-Birch 2018). It is impossible to separate symbolism and subsistence as the two are inextricably linked, but perhaps people in the Late Pleistocene and Early Holocene differentiated between species to a certain degree. We agree with the position of Bishop (2022) that the use of statistics is needed to avoid making assumptions on the relationship between humans and birds in the past and to move away from subjective associations. However, this currently is problematic as without species level identification, we cannot use the specific behaviour and physiological characteristics of birds to investigate how birds and humans interacted. Our current study suggests that, like much of the literature before, certain species such as raptors and chukar, may have held specific significance to people during the Late Pleistocene and Early Holocene. However, the results also underline that it is extremely difficult to separate symbolism and ritual from food and subsistence. Humans hunted birds for food but their importance as fellow inhabitants of various environments requires greater acknowledgment in archaeological discourse. From the archaeological evidence, relationships between the humans and non-human animals were intimate and this is best seen from the situated zooarchaeological evidence investigated at the microscale. Both regional and local approaches to the analysis of archaeological data have proved information to a certain extent, but our case study illustrates that the intra-site scale of analysis ultimately pushed our understanding of human-bird interactions further. This scale of analysis should not be undervalued as the level of information we can gain is high, even if we are restricted to a specific locality. All-encompassing narratives of transitions in human history are often reductionist and micro-analytic scales give us the opportunity to observe idiosyncratic variation of phenomena and the complexities of human behaviour trajectories. Environmental reconstruction at the broad scale may not take into consideration local variations that were more perceivable to individuals and had a larger impact on the life of individual communities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12520-024-02090-6.

Acknowledgements We are grateful to the Department of Antiquities of Jordan for granting permission to excavate at Shubayqa 1 and 6. We would also like to thank the local community in Safawi for their hospitality and Tobias Richter as well as all the archaeologists that have contributed to the project. This paper benefited from discussions with Beatrice Demarchi, Maria Codlin and Ashleigh Haruda as well as comments made by three anonymous reviewers improved the paper. Funding was provided by an Independent Research Fund Denmark grant (1024-00032B).

Author contribution LY—Conceptualization, Methodology, Investigation, Writing—Original Draft, Writing—Review & Editing, Visualisation, Project administration, Funding acquisition. CM—Formal analyses, Writing—Original Draft, Writing—Review & Editing, Visualisation.

Funding Open access funding provided by Copenhagen University. Funding was provided by an Independent Research Fund Denmark, Research Project 2 Grant (1024-00032B).

Data availability All data used in this paper is available from the Supplementary Information.

Declarations There are no financial or non-financial interests that are directly or indirectly related to this work submitted for publication.

Competing interest The authors declare no competing interests.

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