Waterfowl Eggshell Refines Palaeoenvironmental Reconstruction and Supports Multi-species Niche Construction at the Pleistocene-Holocene Transition in the Levant

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Abstract

Utilising multiple lines of evidence for palaeoenvironmental reconstruction improves our understanding of the past landscapes in which human populations interacted with other species. Illuminating such processes is key for a nuanced understanding of fundamental transitions in human history, such as the shift from hunting and gathering to farming, and allows us to move beyond simple deterministic interpretations of climate-driven innovation. Avifaunal remains provide detailed indications of complex multi-species interactions at the local scale. They allow us to infer relationships between human and non-human animals, but also to reconstruct their niche, because many bird species are sensitive to specific ecological conditions and will often relocate and change their breeding patterns. In this paper, we illustrate how novel evidence that waterfowl reproduced at Levantine wetlands, which we obtained through biomolecular archaeology, together with modern ornithological data reveals conditions of wetlands that are conducive for breeding waterfowl. By understanding the interplay between wetland productivity cycles and waterfowl ecology, we argue that human modifications to the environment could have promoted wetland productivity inviting waterfowl to remain year-round. Within this landscape of "mutual ecologies", the feedback resulting from the agency of all species is involved in the construction of the human niche.

Keywords Avifauna · Eggshell · Palaeoproteomics · Niche construction · Wetland management · Mutual ecologies

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Introduction

This paper considers human-waterbird interactions in the Levant at the transition between the Late Pleistocene and the Holocene. The main scope of the research is to begin building a more nuanced understanding of environmental and cultural change in this area, which was an important locus of social and economic change, particularly during the Bølling-Allerød, a warm and wet period dated to approximately 14,700 to 12,900 cal BP (Bar-Yosef, 1991; Maher et al., 2011). Shifts in human behaviour at the Pleistocene-Holocene transition—including reduced levels of seasonal mobility and shifts in subsistence activities—lay the foundations for the adoption of agriculture (Bar-Yosef, 1991; Belfer-Cohen, 1991; Belli et al., 2023; Yeshurun & Bar-Oz, 2018). These preemptive changes are linked to, although not necessarily caused by, an increase in resource abundance resulting from "favourable" environmental conditions of the Bølling-Allerød, which was followed by the "less favourable" Younger Dryas (Maher et al., 2011). But how did global climate change impact the local environments inhabited by human and non-human animals as well as a myriad of plant and microbial life forms? Avifaunal remains from archaeological sites are crucial but underutilised proxies which can provide precise supporting evidence for localised palaeoenvironmental reconstruction in the Levant. Furthermore, human-bird interactions can reveal complex human-animal-environment relationships that played an important role in affording these shifts, allowing us to move beyond deterministic interpretations of climate-driven societal change.

Avifauna is important in modern ecology as well as palaeoecology because birds are extremely sensitive to environmental change (Amat & Green, 2010), to which they respond through biological and behavioural adaptation (Guillemain et al., 2013). Body-size change is one example of the former, *e.g.* it has been argued that reduction in size of mute swan (*Cygnus olor*) documented since the Neolithic/Bronze Age in Cambridgeshire, UK, was probably the result of habitat impoverishment (Northcote, 1981). However, migration is the key strategy employed by many birds to adapt to environmental conditions (Newton, 2010). Migration requires enormous energy reserves but allows birds to take advantage of seasonal variation in different geographical regions. Birds can change patterns of migration at breeding, staging or wintering grounds (Alerstam, 1990), shifting the timing and distance of voyage (Coppack & Both, 2002). Migration is hazardous; hence, some birds opt for remaining at wintering or breeding grounds throughout the year, thus avoiding long distance movement but facing the uncertainty of finding resources locally. Here, we focus on migratory waterfowl (Anatidae) in the wetland environment of the Qa' Shubayqa (Eastern Jordan; Fig. 1) and on the potential relationships between climate, people, birds and wetland vegetation, which may have contributed to creating suitable conditions for birds to breed from the Bølling-Allerød to the Early Holocene and for people to construct and modify their cultural and ecological niche.

Today, as in the past, the Levant is a major corridor (flyway) of bird migration between Eurasia and Africa—despite the impact of anthropic activity, which
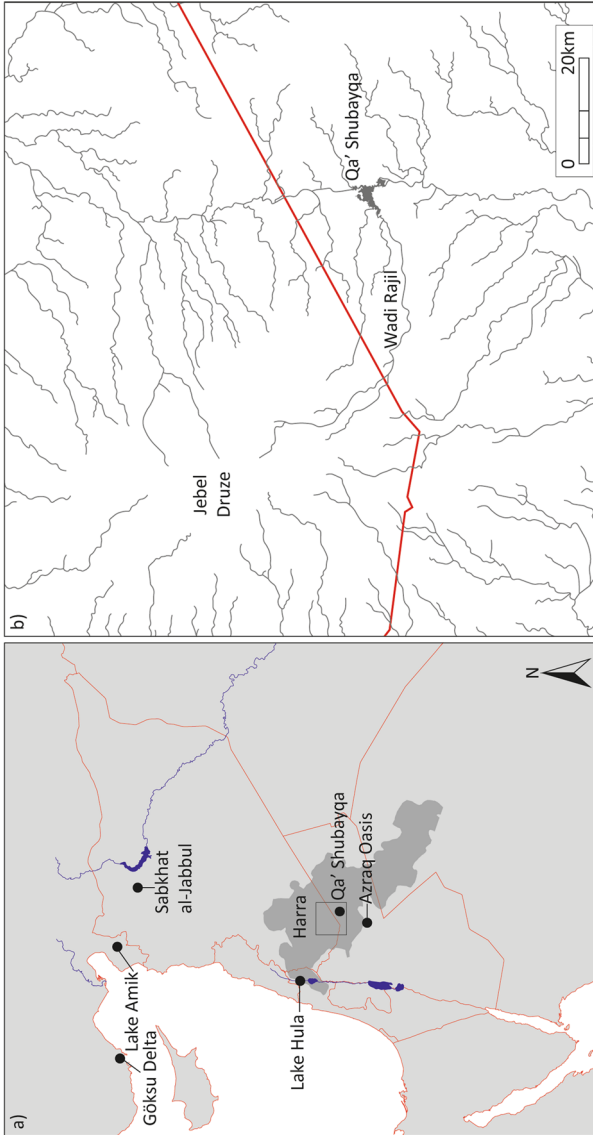
Fig. 1 Location maps. **a** Major wetlands in the Levant and southeast Anatolia that provide modern ecological data and their position in relation to the Qaʾ Shubayqa. **b** Wadi drainage system around the Qaʾ Shubayqa

has caused wetland loss in recent decades and centuries (Fleut-Chouinard et al., 2023; Lotze et al., 2006). Numerous avian species depend on the region's wetlands during their journey to wintering grounds in Africa. Others remain in the Levant for the coldest months, returning to breeding grounds in northern Europe. The abundance of avian remains in archaeological sites in the Levant (Gourichon 2004; Mithen, 2022; Pichon, 1987; Simmons & Nadal, 1998; Tchernov, 1993; White et al., 2021; Yeomans et al., 2017) clearly demonstrates that this area was also a fundamental flyway for birds in the past, although environmental conditions would have been significantly different from present-day ones. If we assume niche conservatism, *i.e.* that avian responses to environmental change do not vary over time, then, we can use bird remains as valuable proxies for tracking such changes diachronically. Importantly, this yields a high-resolution picture of environmental change in a localised setting as opposed to describing broad patterns occurring globally or regionally.

Rather than interpreting the data within a solely palaeoecological framework, we prefer to adopt the concept of "mutual ecologies" (Fuentes, 2010) to infer dynamic encounters between humans and waterbirds. Within this "multispecies" perspective, changes in human behaviour developed within dense webs of entangled relations with other species that equally acted as agents and participants in shaping environments and in the creation of cultures (see Fuentes, 2010; Fuentes & Baynes-Rock, 2017; Haraway, 2008; Taylor & Signal, 2011; Tsing, 2015). This redirects attention to the knotted relations between humans and non-human animals and challenges human exceptionalism and the anthropocentric discourse that dominated Western culture in the modernist period (Coole & Frost, 2010; Descola, 2013; Kohn, 2013; Taylor & Signal, 2011). Mutual ecologies are the inextricable and contingent entanglement of different organisms' world-creating processes (Fuentes, 2010; Hussain et al., 2022). The intertwined relations between humans and non-human animals and other living-beings produce mutual ecologies (Fuentes, 2010: 600) within which the integrated organisms co-determine and co-make each other's niches (Fuentes, 2010; Fuentes & Baynes-Rock, 2017; Odling-Smee et al., 2003). Mutual ecologies encompass both the ecological niches and the socio-material entanglement between humans and non-human animals and as, Fuentes (2010) states, the idea of "mutual ecologies … keeps the forces of history, political economy, interindividual relationships, and culture clearly in view" (Fuentes, 2010: 600).

A key element of mutual ecologies is therefore the process of niche construction. Niche Construction Theory developed as scholars began to conceptualise the environment as a relational entity in constant dialectical relationship with other organisms. Niche construction is the process through which organisms, intervening in the environment and participating in the construction/destruction of their niches, alter the selection pressure for themselves and other organisms (Laland & O'Brien, 2010; Laland et al., 2016; Odling-Smee et al., 1996). Through constant interaction with their environment and the intense work of engineering on their niches, organisms are able to co-determine or co-direct their own and other organisms' evolution (Rendell et al., 2011). This co-direction is achieved by changing the way selective pressure operates, both on the organisms that construct the niche, on other organisms that share the same niche

and on their offspring who inherit the modified selective environment. The niche construction process includes an array of behaviours from "animal manufacturing nests, burrows and webs" or "plants modifying nutrient cycles" to "migrations, dispersal and habitat selection" (Rendell et al., 2011:823). As such, organisms do not simply adapt to an environment by responding to external stimuli but actively operate *to modify their habitat*, which could then be passed down to their offspring, producing, in this case, a sort of "extragenic inheritance" (Odling-Smee et al., 1996: 642).

In this paper, we examine new scientific evidence for waterfowl breeding in the Levant in the context of mutual ecologies. Firstly, we present preliminary analysis of avian bone and eggshells from the Late Pleistocene and Early Holocene sites of Shubayqa 1 and 6, which demonstrate breeding populations of waterfowl in Eastern Jordan, thus indicating that the environment had been suitable for sustaining avian life, from egg laying through to development of the young. Secondly, we review present day and historical ecological data for breeding waterfowl in the Levant, which serve as modern analogues for the reconstruction of past habitats that supported breeding waterfowl populations. Finally, we interpret these novel data in the framework of mutual ecologies and niche construction theory, highlighting some potential interactions that may have contributed to the overall process of niche construction, and use examples from several areas of the world and historical periods to argue in favour of human management of the wetlands.

Background

Geographical and Ecological Setting of the Qa' Shubayqa

The landscape of the Harra, in eastern Jordan, is a basalt-strewn desert resulting from eruptions of long extinct volcanoes. Today, it is virtually impenetrable for humans—as attested by the local name, *Bilad esh-Shaytan*, meaning "Land of the Devil". Set in the middle of this basalt landscape is the Qa' Shubayqa, a clay pan measuring 12 km^2 (Jones et al., 2016). The Qa' Shubayqa is located in the north of the Azraq drainage basin with the Jebel Druze foothills to the north and northwest (Fig. 1). During the wet season (November to April), three wadis feed water into the qa'. The most significant is the Wadi Rajil draining from the Jebel Druze (Fig. 2a) where rainfall is considerably higher (500–600 mm annually). Upon reaching the qa', the waters spread into a broad alluvial fan forming multiple small channels. Localised flooding occurs after rains and pools of standing water can remain until late spring or early summer. Water exits the Qa' Shubayqa to the south (Fig. 2b), eventually reaching the Azraq Oasis. In the summer months, water is scarce with no precipitation and extensive evaporation. Vegetation supported by this hydric regime is typical of the Mesopotamian shrub desert zone and include tamarix bushes, tussock-grass, Chenopodiaceae, *Artemisia* sp. with reeds and rushes around wetland areas.

Fig. 2 The Wadi Rajil in full flow after a heavy spring rain at the start of March 2017. **a** Photograph taken upstream of where the wadi spreads out in the Qa' Shubayqa. **b** Photograph taken to the southeast of the Qa' Shubayqa after the rain runoff has forced through a gap in the basalt and continues towards the Azraq Oasis

Previous Archaeological Evidence for Wetlands at Qa' Shubayqa

Whilst water is scarce in the Harra today, there is evidence that the region was more hospitable in the past. Upstream of the Qa' Shubayqa, the Wadi Rajil once supplied water to the Bronze Age settlement of Jawa where the population constructed an extensive series of pools, dams and canals to capitalise on the floodwater (Meister et al., 2018). During the Early Bronze Age occupation, the system provided water to an estimated population of ~6000 and their livestock (Whitehead et al., 2008). The faunal assemblage from Jawa is dominated by caprines, but the significant number of cattle would have required a consistent water supply (Köher, 1981). If the water resources at Jawa did attract waterfowl, the absence of their bones from the excavations suggests that they were not hunted or the excavation methodology was not fine-grained enough to ensure recovery. This region also supported other settlements, including a Middle Bronze Age walled site a few kilometres upstream of Jawa (Braemer, 1988) and a hillfort, Khirbet al-Ja'bariya, close to the Wadi Rajil (Müller-Neuhof & Abu-Azizeh, 2016). The hillfort is argued to have been occupied throughout the year by a portion of the population indicating that settlement of the Harra was not entirely abandoned in the dry season. The extensive landscape of Bronze Age occupation, supported by the Wadi Rajil, indicates that this landscape was more suitable for human habitation in the past.

Upon visiting the semi-arid landscape today, it is difficult to picture an environment that attracted stable human occupation. Models have attempted to hindcast past rainfall in this area based on speleothem data, but these do not stretch as far back as the Bølling-Allerød (Hewett et al., 2022) and the local environment of the Harra is clearly very complex. Reconstructions of vegetation based on precipitation and temperature on a regional scale do not take into account local geomorphology. Moreover, the hydrology of the Harra region has been altered many times. Most recently, in the middle of the twentieth century, construction of large reservoirs in Syria modified the runoff characteristics of the Wadi Rajil, resulting in reduced seasonal flooding in the Qa' Shubayqa. Furthermore, the silts infilling the qa' date to the Holocene, suggesting that its water capacity has reduced over time, and in the early Holocene, the basin could have held at least double the amount of water as possible today (Jones et al., 2022). Climatic changes affecting rainfall and vegetation cover at the end of the Pleistocene would have had an impact on the hydrology, influencing runoff and absorption of water into the sediments, as would have intensive grazing on the landscape by herds of sheep and goat since the Late Neolithic. Given these factors, it is extremely probable that the Qa' Shubayqa stored considerably more water in the Late Pleistocene and Early Holocene, but the morphology of the ancient basin remains unknown.

Two sites on the edge of the Qa' Shubayqa, Shubayqa 1 and 6 (Fig. 3) (Richter et al., 2012, 2014, 2016a, 2016b, 2017) have yielded abundant evidence of waterfowl remains (Yeomans, 2018; Yeomans & Richter, 2018, 2020), demonstrating the long-term presence of a wetland. At Shubayqa 1, the Early and Late Natufian occupation (14,400–14,100 cal BP and 13,300–13,100 cal BP) mainly occurs within the relatively wet and warm Bølling-Allerød interstadial (14,700–12,900 cal BP). The Older Dryas, a brief colder and dryer spell that lasted ca. 200 years separates the
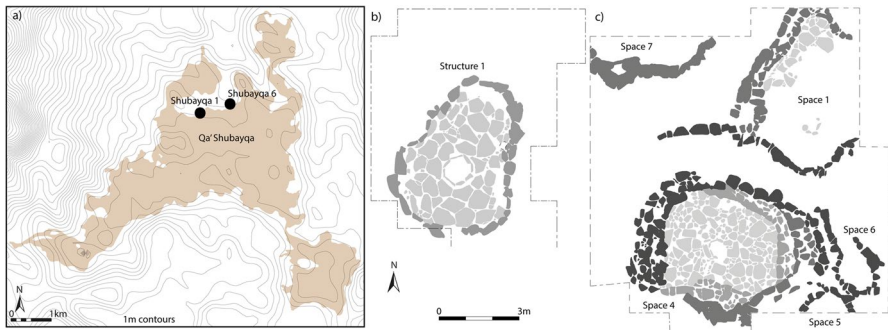
Fig. 3 a Location of Shubayqa 1 and Shubayqa 6 on the northern side of the Qa' Shubayqa. **b** Structure 1, dated to the Early Natufian at Shubayqa 1. **c** Earliest architectural phase at exposed at Shubayqa 6 with benches and walls shown in darker colours to paved floors

Bølling and the Allerød, but this short interlude is insecurely dated and its effects in the Levant poorly understood; hence, the Bølling-Allerød is usually seen as one climatic phase (Maher et al., 2011). A large pit at Shubayqa 1, dated to the Final Natufian (12.2–11.6 kya cal BP), pertains to the Younger Dryas (12,900–11,700 cal. BP)—generally understood to be colder and dryer on the basis of global and regional records, including Soreq Cave (Fig. 4).

Two architectural phases are represented at Shubayqa 6; the Final Natufian to Pre-Pottery Neolithic A (ca. 12,000–11,200 cal BP), thus falling within the cool and dry Younger Dryas and the start of the Holocene, and the Late Pre-Pottery Neolithic A (LPPNA) (11,000 to 10,600 cal BP).

The frequency of wetland birds in the archaeological bone assemblage (Table 1), particularly the abundance of Charadriiformes, which are autumn and spring visitors and Anatidae, suggests that both shallow water or mudflats as well as deeper water was available in the Qa' Shubayqa during the Early Natufian (González & Green, 2014). The presence of wetland features is also supported by the finding of large numbers of tubers from bulrush (*Bolboschoenus glaucus*) (Arranz-Otaegui et al., 2018a, 2018b, 2023a, 2023b), a wetland species commonly found at Epipalaeolithic sites in the Southern Levant (Wollstonecroft et al., 2011). Conversely, the lack of avifaunal remains from contexts dating to the Younger Dryas occupation at Shubayqa 1 might suggest a dryer environment at this time. At Shubayqa 6, the increased presence of wetland birds in the Early Holocene implies a return to wetter conditions. Figure 4 illustrates the changing proportions of Anatidae, Rallidae, and Charadriiformes compared to other birds and mammals in the faunal assemblage in relation to regional climatic sequence provided by the Soreq Cave (Bar-Mathews & Ayalon, 2011) and Lake Lisan (Neugebauer et al., 2014). Figure 5 provides a summary of the main mammalian taxa through the sequence as well as the proportion of avifauna according to the preferred habitat type as a summary of the previously published work on the faunal assemblage.
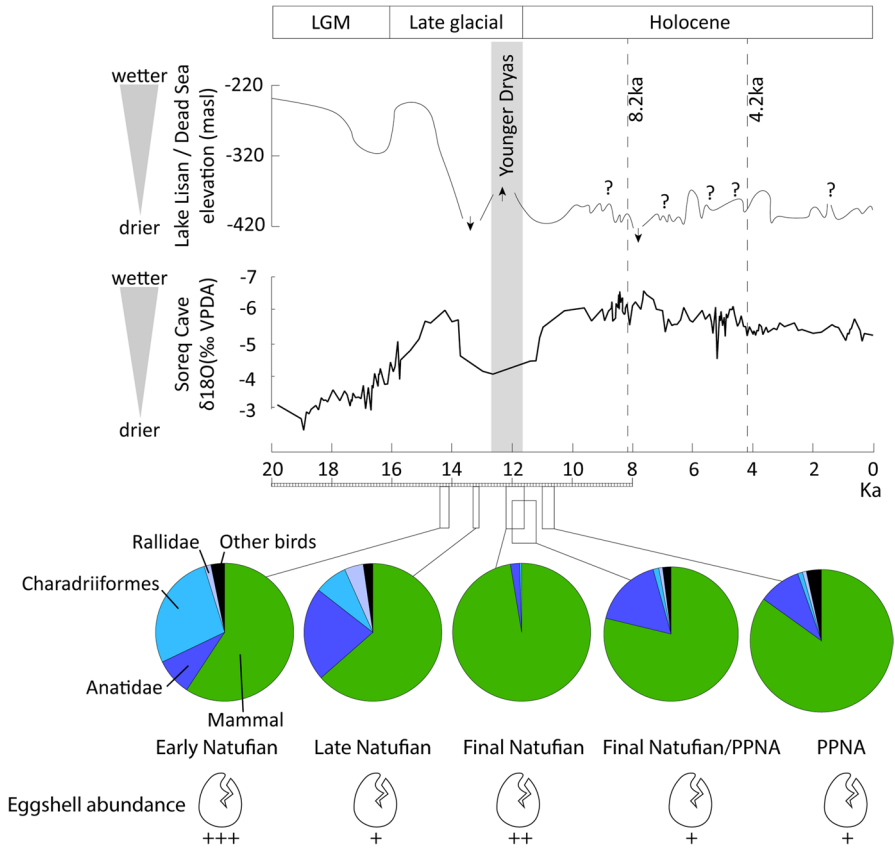
Fig. 4 Frequency of Anatidae, Rallidae, and Charadriiformes vs other birds and mammals in the Shubayqa assemblage compared to the regional palaeoenvironmental sequence. Excludes cluster of worked bone from Shubayqa 6 (Yeomans et al., 2021). Climatic proxy data from Bar-Matthews and Ayalon (2011), Jones et al. (2019), Neugebauer et al. (2014) and references within. Eggshell relative abundance: + + + indicates very frequent, + + indicates present and + indicates occasional

Identification of Eggshell

To maximise the palaeoenvironmental information that can be retrieved from avian eggshell, taxonomic identifications of the fragments is paramount. Here, we present evidence obtained using proteomics-based methods for the determination of a subsample of the abundant avian eggshell assemblage from the excavations at Shubayqa 1 and 6. An important caveat is that whilst both fine-screening (4 mm mesh), and flotation sampling was employed on site, thin eggshell fragments of small birds are unlikely to be recovered. The majority of eggshell fragments recovered date to the Early Natufian period (Fig. 4), and work is ongoing to determine whether excavation context, recovery methods or social and environmental changes are responsible for the decrease in eggshells recovered in later time periods. A sample of 35 eggshell fragments were selected for biomolecular analysis pertaining to seven excavation

Table 1 Number of identified specimens (NISP) of bird bone

			Shubayqa 1			Shubayqa 6		
Order	Family	Species	Early Natufian	Late Natufian	Final Natufian	Test trench Final Natufian	Final Natufian to PPNA	LPPNA
Anseriformes	Anatidae (Anserinae)	Cygnus spp.	2	5		1	109	39
		Anser spp.	2	11			9	2
		Unidentified					1	
		Large (cf. Anas platyrhynchos)	22	14		2	107	42
		Medium (cf. A. acuta, Mareca penelope/strepera, Spatula clypeata)	139	73		20	299	70
		Small (Anas crecca/Spatula querquedula)	64	59		5	243	55
		Unidentified	154	906	12	4	260	65
	Anatidae (Aythyinae)	Aythya spp.	7	46		1	23	3
		cf. Netta rufina		3			1	
	Anatidae (Mergini)	cf. Bucephala clangula	3	7			3	
	Anatidae (Tadorninae)	Tadorna spp.		9				1
	Anatidae (Oxyurini)	cf. Oxyura leucocephala						1
	Anatidae (not Anserinae)	Unidentified	241	956	11	17	227	94
			21.2%	60.3%	82.1%	67.6%	79.6%	64.1%
Galliformes	Phasianidae	cf. Alectoris chuckar	1					
		Ammoperdix heyi	3					
		Coturnix coturnix	26	13		4	28	53
		Unidentified		7				3
			1.0%	0.6%		5.4%	1.7%	9.7%
Podicipediformes	Podicipedidae	Tachybaptus ruficollis	10	34				
		Podiceps nigricollis	39	50			3	4
		Unidentified	8	5			2	1

Table 1 (continued)

Order	Family	Species	Shubayqa 1			Shubayqa 6		
			Early Natufian	Late Natufian	Final Natufian	Test trench Final Natufian	Final Natufian to PPNA	LPPNA
Columbiformes	Columbidae		1.9%	2.6%			0.3%	0.9%
		Columba sp.	1					
		Streptopelia sp.	1					
Pteroclidiformes	Pteroclididae		0.1%					
		Unidentified	11	5			9	5
			0.4%	0.1%			0.6%	0.9%
Gruiformes	Gruidae	Unidentified	8	7			9	3
			0.3%	0.2%			0.6%	0.5%
	Rallidae	Fulica atra	83	404		7	65	24
		Gallinula chloropus	3	2				1
		Crex crex	7	5		3	3	1
		Rallus aquaticus	1	3				1
		Porzana spp.	11	2				3
		Unidentified	11	4				4
			3.9%	12.1%		13.5%	4.2%	5.9%
Charadriiformes	Recurvirostridae	Himantopus himantopus	4	2				
	Charadriidae	Charadrius spp.	11	3			1	2
		Pluvialis spp.	3					
		Vanellus spp.	8					
		Unidentified	15			1	3	11
	Scolopacidae	Calidris spp.	115	15			8	5
		Limosa spp.	3				2	

Table 1 (continued)

Order	Family	Species	Shubayqa 1 Early Natufian	Late Natufian	Final Natufian	Shubayqa 6 Test trench Final Natufian	Final Natufian to PPNA	LPPNA
		Philomachus pugnax	1318	266	1	2	65	10
		cf. *Tringa* spp.	15	76				1
		Numenius spp.	10	21				
		Unidentified	349	325	4	1	17	3
	Glareolidae	Unidentified	43	4			2	3
	Sternidae	Unidentified						
		Unidentified	106	26		1	7	7
			67.0%	21.3%	17.9%	6.8%	6.5%	7.2%
Pelecaniformes	Ardeidae	*Ixobrychus minutus*	1					
		Ardeola spp.	2	3				
		Ardea spp.		8				
		Unidentified Ardeidae	1	18			1	1
			0.1%	0.8%	0.0%		0.1%	0.2%
Accipitriformes	Accipitridae	*Aquila chrysaetos/nipalensis*		2		2	3	1
		Aquila spp.	3	2			6	1
		Circus sp.	4					
		Accipiter nisus/brevipes	1	2		1	1	1
		Buteo spp.	3	6			11	8
		Unidentified Accipitridae	72	29			36	12
			2.8%	1.2%		4.1%	3.5%	4.1%
Strigiformes	Strigidae	cf. *Asio flammeus*	2			1	3	
			0.1%			1.4%	0.2	

Table 1 (continued)

Order	Family	Species	Shubayqa 1			Shubayqa 6		
			Early Natufian	Late Natufian	Final Natufian	Test trench Final Natufian	Final Natufian to PPNA	LPPNA
Falconiformes	Falconidae	cf. *Falco tinnunculus*					1	
		Falco spp.	2	1				
			0.1%				0.1%	
Passeriformes	Corvidae	*Garrulus glandarin*						1
		Unidentified	1	4			1	1
				0.1%			0.1%	0.3%
	Unidentified	Unidentified small Passeriformes	37	20		1	41	36
			1.2%	0.6%		1.4%	2.5%	6.2%
		Total avifauna	2987	3463	28	74	1610	580
		Total mammal excluding microfauna	4346	6035	1035	487	5976	3276
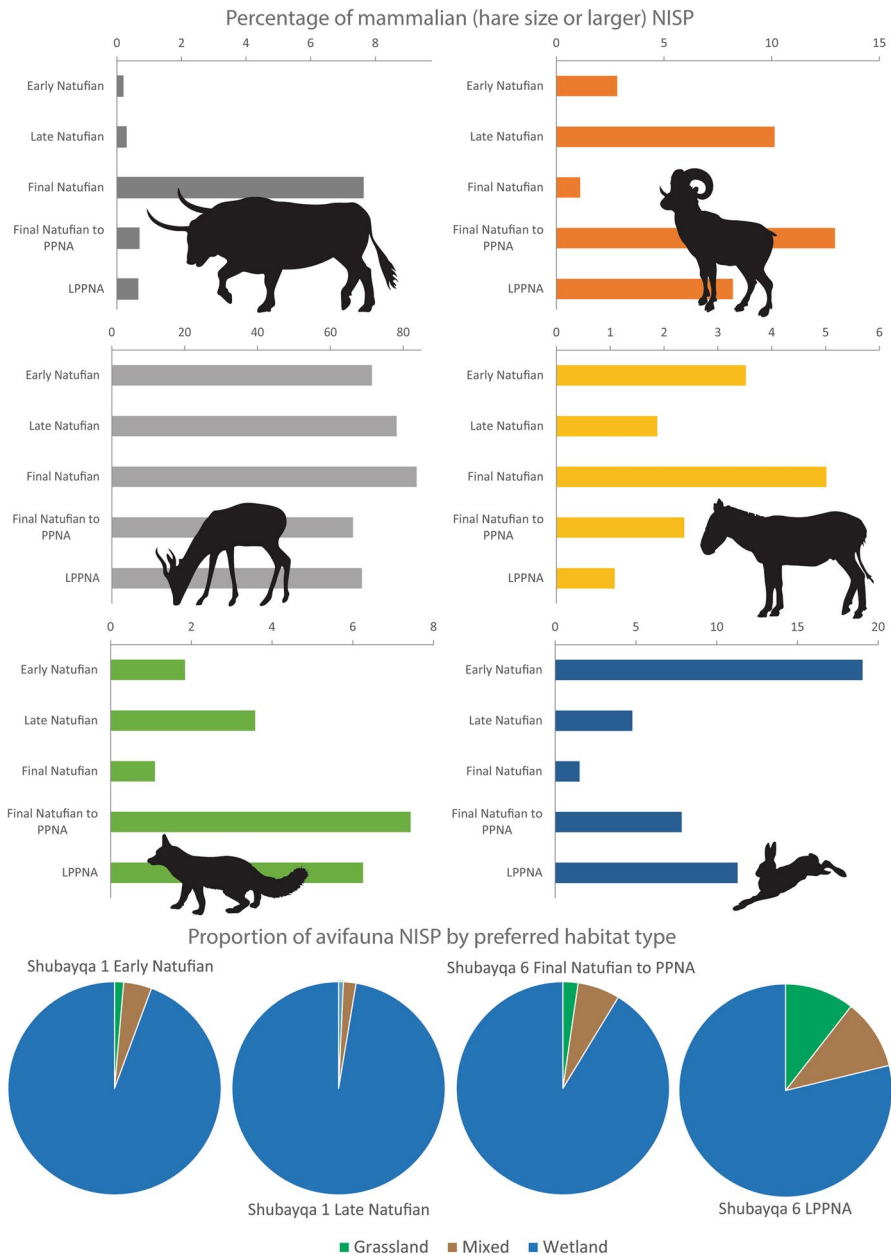
Fig. 5 Frequency of the main mammalian taxa through the sequence at Shubayqa and frequency of preferred habitats of avifauna (excluding the Final Natufian Phase of Shubayqa 1 due to small sample size)

contexts (Table 2) and processed according to the protocol described in Demarchi et al., (2022; see SI for complete methodology) for palaeoproteomics-based identification by MALDI-TOF mass spectrometry.

Table 2 Summary of Anatidae and Grus peaks identified in Shubayqa eggshell fragments and taxonomic assessment. Peaks unique to identified taxa are indicated with [Ans.] for *Anser*, [Cyg.] for *Cygnus* and [Gru.] for *Grus*. Notes: "Thin" refers to eggshell thickness assessed visually

Sample ID PALTO#	Time period	Site context	Thickness (mm)	Identification	892.4 [a]	960.6 [Gru.]	1255.6 [Ans.] [a]	1256.6 [a]	1400.6 [Cyg.]	1564.7 [+0.98] [ab]	1709.8 [Gru.]	1722.8 [Ans.]	1723.8	1845.8 [Gru.]	2050.9	2220.0 [+0.98]	2392.2	2461.2	2489.0 [+0.98]	2551.2 [Cyg.]	2567.2/3 [Ans.] [b]	2915.4 [Cyg.]
112A	Early Natufian	SHUB1 (128)		Poor spectra																		
112B	Early Natufian	SHUB1 (128)		Poor spectra																		
112C	Early Natufian	SHUB1 (128)		Poor spectra																		
112D	Early Natufian	SHUB1 (128)	0.35	Not identified																		
114A	Early Natufian	SHUB1 (157)	0.32	Anatidae						x			x					x				
114B	Early Natufian	SHUB1 (157)	0.33	Anatidae						[x]			x					x				
114C	Early Natufian	SHUB1 (157)	0.35	Cf. Anatidae									x									
114D	Early Natufian	SHUB1 (157)	Thin	Anatidae	x			x		x			x			[x]	x	x	[x]			
115A	Final Natufian	SHUB1 (174)	0.37	Anatidae				x		[x]			x				x	x	[x]			
115B	Final Natufian	SHUB1 (174)	Thin	Poor spectra																		
115C	Final Natufian	SHUB1 (174)	0.36	Poor spectra																		
116A	Early Natufian	SHUB1 (132)	0.44	Poor spectra																		
116B	Early Natufian	SHUB1 (132)	0.38	Poor spectra																		
116C	Early Natufian	SHUB1 (132)	Thin	Poor spectra																		
116D	Early Natufian	SHUB1 (132)	0.44	Anatidae	x			x		[x]			x					x				
116E	Early Natufian	SHUB1 (132)		Poor spectra																		
117A	Early Natufian	SHUB1 (132)		Cf. Anatidae	x					[x]			x				x					
118A	Early Natufian	SHUB1 (157)	0.31	Anatidae	x			x		[x]			x			[x]		x				
118B	Early Natufian	SHUB1 (157)	0.36	Anatidae	x			x		[x]			x			[x]	x	x				
118C	Early Natufian	SHUB1 (157)	0.33	Anatidae	x			x		x			x		x	[x]		x	x			

Identified peak *m/z*, x=present, [x] =deamidated peak present

Table 2 (continued)

Sample ID PALTO#	Time period	Site context	Thickness (mm)	Identification	892.4[a]	960.6 [Gru.]	1255.6 [Ans.][a]	1256.6[a]	1400.6 [Cyg.]	1564.7 [+0.98][ab]	1709.8 [Gru.]	1722.8 [Ans.]	1723.8	1845.8 [Gru.]	2050.9	2220.0 [+0.98]	2392.2	2461.2	2489.0 [+0.98]	2551.2 [Cyg.]	2567.2/3 [Ans.][b]	2915.4 [Cyg.]
119A	Early Natufian	SHUB1 (157)		Poor spectra																		
119B	Early Natufian	SHUB1 (157)		Poor spectra																		
119C	Early Natufian	SHUB1 (157)	0.32	Anatidae						[x]			x					x				
119D	Early Natufian	SHUB1 (157)	0.34	Anatidae						[x]			x			x		x	x			
119E	Early Natufian	SHUB1 (157)	0.35	Anatidae	x			x		[x]			x			[x]		x	x			
119F	Early Natufian	SHUB1 (157)	0.32	Anatidae	x			x		x			x		x	[x]	x	x	x			
119G	Early Natufian	SHUB1 (157)	0.41	Anatidae	x			x		x					x	[x]	x	x	x			
119H	Early Natufian	SHUB1 (157)	0.55	Not identified												x						
121A	Early Natufian	SHUB1 (195)	Thin	Poor spectra																		
121B	Early Natufian	SHUB1 (195)	Thin	Poor spectra																		
121C	Early Natufian	SHUB1 (195)		Poor spectra																		
121D	Early Natufian	SHUB1 (195)		Poor spectra																		
680A	LPPNA	SHUB6 (205)	0.56	Cf. *Grus*.		x					x			x								
689	Early Natufian	SHUB1 (132)	0.69	*Cygnus* sp.					x			x								x		x
693	Early Natufian	SHUB1 (26)	0.55	*Anser/Branta*			x					x	x		x		x		x		x	

[a] peptide derived from diagenesis-induced hydrolysis of peptide bond

[b] two peptides with unresolvable m/z values in MALDI-MS data

This approach, known as peptide mass fingerprinting (PMF), exploits the taxon-specific variation in the amino acid sequences of the proteins embedded within the calcite crystals. These proteins are extracted and processed in the laboratory, in order to obtain shorter fragments, *i.e.* peptides, which are analysed by MALDI-TOF–MS to produce a spectrum where peaks correspond to the mass of individual (charged) peptides in the sample (*m/z*). These peaks can then be matched to characteristic *m/z* values from reference taxa, for identification purposes (Demarchi et al., 2020; Presslee et al., 2017). Amongst the protein sequences that can be used for this scope, C-type lectins (XCA1 and XCA2, Le Roy et al., 2021) are usually preferred, because they are ubiquitous, abundant and typically well preserved (Demarchi et al., 2016).

Fifteen eggshell specimens produced low quality MALDI-TOF spectra and were excluded from further analysis. Many of these samples were found in the same contexts of eggshells that produced identifiable spectra. One hypothesis for the differential molecular degradation is that some of these fragments had been exposed to high temperatures, *e.g.* due to cooking. The remaining samples yielded good-quality spectra, with distinct peptide mass fingerprints. Four representative specimens were analysed by high-resolution LC–MS/MS (liquid chromatography coupled to tandem mass spectrometry), and the raw data were searched against a database including all avian proteins available on NCBI as well as previously published C-type lectin sequences (Demarchi et al., 2022; Grealy et al., 2023). This allowed us to identify and confirm potential taxon-specific (*i.e.* "marker") peptides (Table 2, see also, S.I.) from XCA1 and XCA2 protein sequences for *Grus americana*, *Anser cygnoides*, *Anas platyrhynchos*, *Aythya fuligula* and *Cairina moschata*, as well *Cygnus* spp. (*Cygnus olor*, XCA1 and *Cygnus atratus* XCA2). The peaks observed in MALDI-TOF mass spectra of archaeological samples were then compared to these marker peaks in order to determine the avian taxa (Fig. 6).

Thirteen eggshell pieces were identified as Anatidae based on the presence of the marker at *m/z* 1723.7 (Demarchi et al., 2020; Presslee et al., 2017) and several additional Anatidae peaks (Table 2). Two samples were identified as "possible Anatidae" due to the presence of the marker peak at *m/z* 1723.7, but the relatively
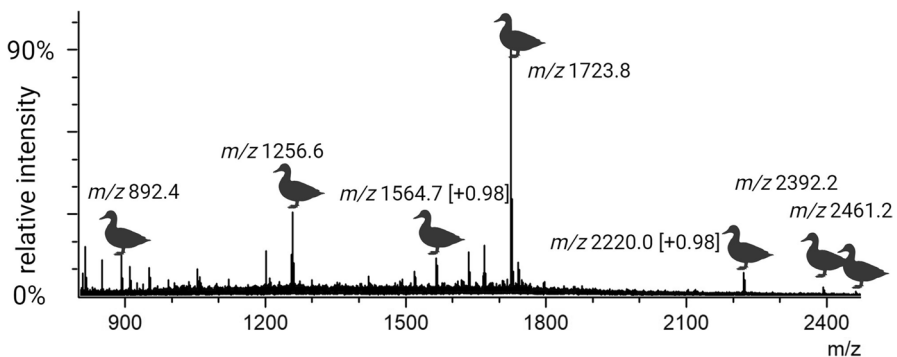

Fig. 6 MALDI-TOF mass spectrum of sample PALTO 114D illustrating some of the peaks typically found in Anatidae eggshell (created with Biorender.com)

low quality of their spectra hampered more precise identification. Furthermore, the tandem mass spectrometry data obtained on two of these putative Anatidae samples (PALTO 114D and 119D; see SI) confirmed that all observed peaks except that at *m/z* 2461.2 derived from known Anatidae eggshell peptides. Peak *m/z* 2461.2 was present in all spectra of the archaeological samples identified as Anatidae. Assisted *de novo* sequencing indicates that this peak likely derives from a peptide sequence that is homologous to that found in several Anatidae species (which implies that the reference sequence for this species is not yet publicly available; see S.I.). All thirteen of the eggshell samples identified as Anatidae had thin eggshells—generally between 0.3–0.4 mm in thickness, which is within the range of multiple duck species that could have bred at Shubayqa in the past (Fig. 7).

Two specimens could be determined more precisely (see details in S.I.). PALTO 693 was identified as a goose belonging to genera *Anser* or *Branta*, on the basis of PMF data matching that of reference *Anser* sp. This identification was confirmed with tandem MS analysis and is consistent with the measured eggshell thickness of 0.55 mm. PALTO 689 was assigned to genus *Cygnus* based on both PMF and tandem MS data matching the reference proteins for swan (*Cygnus* spp.) and an eggshell thickness of 0.69 mm (Fig. 7). One final specimen was identified as a possible *Grus* (crane), due to the presence of peaks at *m/z* 960.6, 1709.8 and 1845.8 which match theoretical peptide masses for *Grus* protein sequences. This
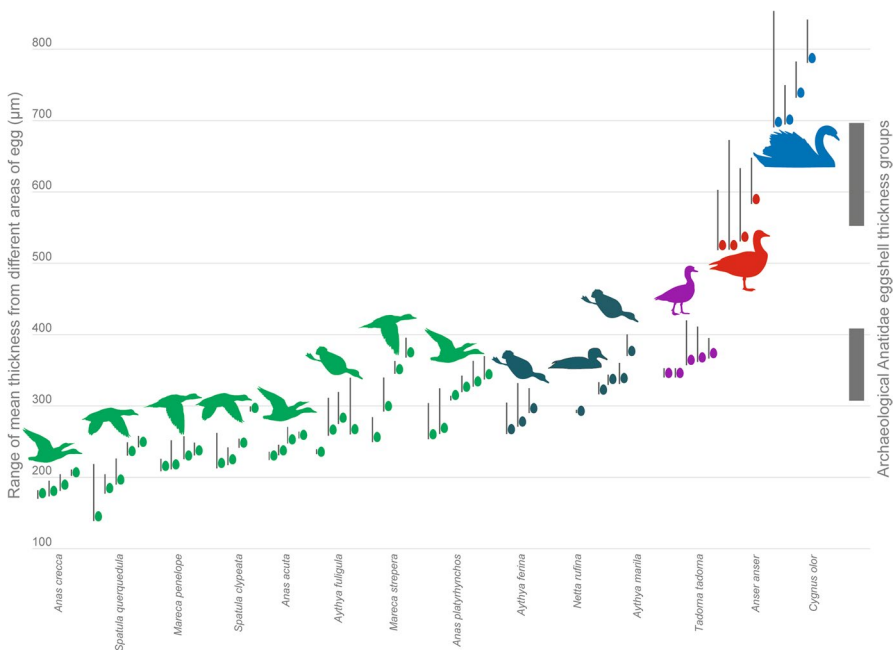
Fig. 7 Thickness of eggs from Levantine species of Anatidae (Maurer et al., 2012) compared to the thickness groups of the archaeological eggshell fragments

sample had a shell thickness of 0.56 mm, which is consistent with that of eggshell of *Grus* genus (Maurer et al., 2012). An additional two samples could not be assigned to any of the taxonomic groups for which we have reference sequences.

Modern Ecological Data

Four major wetlands in the Levant, as well as the Göksu Delta in Anatolia, provide data on the ecological conditions necessary for different species of Anatidae (Fig. 8) to reproduce in the area today (or in recent history)—Azraq Oasis, Lake Amik, Lake Hula and Sabkhat al-Jabbul. Modern ecological data show the presence of four groups of taxa (Table 3) breeding nowadays, thus providing analogues for the

Fig. 8 Photographs of species mentioned in the text. **a** Mute swan (*Cygnus olor*) with cygnets photographed on 23 May 2022 in Denmark. **b** Juvenile mute swan (*Cygnus olor*) photographed on 25 September 2022 in Denmark. **c** Mallard (*Anas platyrhynchos*) with duckling photographed on 6 August 2022 in Denmark. **d** Female tufted duck (*Aythya fuligula*) wintering in Denmark and photographed on the 5 March 2023. © Lisa Yeomans

Table 3 Summary of ecological requirements of Anatidae documented breeding in the Levant, data from Bowler (2005), Cramp and Simmons (1977) and Hughes and Green (2005) unless specified

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Anatini (*Anas crecca*)	Teal	Azraq?, Lake Amik	8–11	Prefers diminutive water bodies that might be part of a larger wetland	Up to 50 m from standing water (Fox, 1986), on ground in thick cover	Omnivore	In semi-desert areas is often outnumbered by garganey. Adverse to frequent or intense human presence
Anatini (*Anas acuta*)	Northern pintail	Azraq?	7–9	Prefers open shallow waters that are at least moderately biologically productive; 10–31 cm with most food obtained from mud bottom and long neck may provide advantage over other species	Nests in dense but not tall vegetation, not near trees and on ground as close as 2–3 m from water	Omnivore. Also can feed on land for grain and by digging up rhizomes/tubers	Droughts create northward shifts in breeding range (Smith, 1970). Preferred habitats are susceptible to drought so species is mobile and will move to equivalent conditions
Anatini (*Anas platyrhynchos*)	Mallard	Azraq, Lake Hula, Lake Amik	5–13	Open water bodies with emergent vegetation preferably of multiple species (Pöysä et al., 2001); Shallow (30–40 cm), with emergent vegetation (Pöysä et al., 2001)	Hidden nests in vegetation, up to 100 m away from the water	Insects (brood) and vegetation(adults)	Preference for small patches of wetlands scattered through the landscape or when there is a high edge-to-area ratio provided by larger wetlands with complex shapes (Newbold & Eadie, 2004)

Table 3 (continued)

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Anatini (*Mareca penelope*)	Eurasian widgeon	Lake Hula?	8–9	Breeding habitat quite near shallow waters of medium quality with ample submerged and floating vegetation but without dense emergent strand	Nests on ground in thick cover, nest up to 250 m from water	Almost entirely vegetarian; grazes whilst walking or feeds from water surface, often associates with coots and swans that bring food to surface	Does not habitually upend so water depth a controlling factor; individuals infrequently summer in winter areas
Anatini (*Mareca strepera*)	Gadwall	Lake Amik?	8–12	Strong preference for shallow standing or slow-moving water with ample cover provided by patches of emergent vegetation	On ground usually less than 20 m to water in dense vegetation	Mostly feeds on plant parts obtained whilst swimming with head under water	Conservative and reluctant to shift from regular haunts; less tolerant of bad weather than other species of Anatini
Anatini (*Spatula clypeata*)	Northern Shoveler	Sabkhat al-Jabbul	9–11	Prefers permanent but very shallow waters fringed by dense reed strands; tolerates floating vegetation if enough open water available	Nests on ground in grass or rushes as close as 5 m to water	Omnivorous feeding mainly on surface plankton	Readily moves between sites

Table 3 (continued)

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Anatini (*Spatula querquedula*)	Garganey	Azraq?	8–9	Shallow fresh water with low extensive cover; avoids deep water without aquatic vegetation; high productivity wetlands preferred	On ground usually within 20 m of water in thick vegetation, grass or rush tussocks	Omnivorous with food collected whilst swimming with head below water; upending not common	Spends minimal time on land
Aythyini (*Aythya fuligula*)	Tufted duck	Lake Amik	8–11	Can dive 3–14 m; fresh water free of floating vegetation without emergent vegetation encroaching; in nesting season usually in waters 3–5 m in depth	Prefers islets for breeding; on ground or in water in reeds or grass tussocks; less than 20 m from water	Omnivorous taking slow moving items from bottom; ducklings take more food from surface	Avoids extremes of heat and cold; tolerant of human presence
Aythyini (*Aythya nyroca*)	Ferruginous duck	Lake Hula, Lake Amik	8–10	Shallow expanses of water rich in submerged and floating vegetation and fringed by dense strands of emergent vegetation	Nests on anchored floating vegetation; floating islands of waterlily with depth below nest commonly 1.3–1.6 m (Loucif et al., 2021); also nests on islets	Omnivorous but heavily plant based taking food from surface, by upending and diving	Only needs small patches of open water

Table 3 (continued)

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Aythyini (*Netta rufina*)	Red-crested pochard	Sabkhat al-Jabbul, Lake Amik	8–10	Freshwater with extensive reed cover; moderately deep water and not adverse to slow moving waters; for breeding prefers small pools with ample submerged vegetation and open areas surrounded by dense emergent vegetation; dives 2–4 m	On ground in dense vegetation close to water	Mainly vegetarian obtaining food by both dabbling and diving	Walks more easily than other Aythyini
Aythyini (*Marmaronetta angustirostris*)	Marbled duck	Azraq, Lake Hula, Lake Amik	7–14	Prefers small to medium shallow freshwater with frequent submerged and fringing vegetation; likes to have instant access to shade; often associated with *Scirpus* (Green, 1998a)	Nests on ground under low bushes in thick vegetation; broods select water of about 35–45 cm (Sebastián-González et al., 2012)	Feeds amongst vegetation but not much known about diet; feeds by upending and diving and grubbing in the shore muds; feed in different parts of the water column (Green, 1998a)	Populations move to suitable breeding grounds taking advantage of ephemeral wetlands after rainfall

Table 3 (continued)

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Tadorninae (*Tadorna tadorna*)	Shelduck	Azraq, Sabkhat al-Jabbul?	5–11	Outside of Asia only uses freshwater sparingly; forage in areas with high biological productivity	Nests in the old burrows of other animals (Nouidjem & Mimeche, 2021) usually nests close to water by up to 1 km away	Mainly vertebrates obtained by digging in mud	
Oxyurini (*Oxyura leucocephala*)	White-headed duck	Lake Hula, Sabkhat al.Jabbul, Lake Amik?	5–10	Freshwater lakes fringed with reeds and ample pond weeds; needs tracts of open water; despite its diving abilities it prefers water less than 1 m in depth as it surface dives	Nests over water on platform made of dead reeds or in old nests from other species; bends vegetation to form roof	Omnivore but lacking data; surface diving over long tracts rather than diving deep; Broods often associated with water depth of 50–65 cm (Sebastián-González et al., 2012)	The species is not suited to walking and prefer to swim to cover than take flight
Anserinae (*Cygnus olor*)	Mute swan	-	4–8	Prefers regulated rivers and streams or ponds created by subsidence	Nests within 100 m and generally closer to water in a mound constructed from rushes, reeds and other vegetation	Mainly aquatic food and emergent vegetation at the water's edge. Cygnets feed of aquatic vegetation torn off by adults but probably insects as well; feeds at depths up to 1 m	Adapts well to presence of humans

Table 3 (continued)

Tribe and species	Common name	Breeding grounds in Levant	Clutch size	Preferred habitat and foraging	Nesting environment	Feeding	Other
Anserinae (*Anser anser*)	Greylag goose	Sabkhat al-Jabbul	4–6	Dependence on aquatic location and grassland results in patchy distribution	On ground in sheltered hollow, under brush or in reeds	Soft vegetation clipped with side of bill and roots scraped with terminal nail on upper mandible	Adapts well to presence of humans

archaeological record. At the same time, such data also highlight that a major influence on the presence of breeding waterfowl is human activity, and especially those activities that create open water environments. Currently Anatidae typically migrate north to reproduce, but ornithological data illustrates that, when certain water availability and vegetation requirements are met, then some waterfowl are encouraged to remain through the breeding season and stay in the Levant year round. In general, wetlands in areas with greater rainfall, such as Lake Amik and Lake Hula, have a higher variety of species that are securely documented to breed locally, but human activity is also important in encouraging waterfowl to breed. Vegetation management had a significant impact in changing the breeding patterns of the waterfowl (Ashkenazi, 2004).

Azraq Oasis, located in the limestone plateau (Hammada) southwest of the Qa' Shubayqa, was once a "glimpse of heaven" (Mountford, 1965: 51). The oasis, fed by springs and seasonal rains, included "marshes that beckoned millions of migrating birds to its shimmering ponds" (Janssens & Thill, 2013: 322). More recently, the Azraq Oasis and the bird population has been heavily reduced by agricultural activities and water usage (Janssens & Thill, 2013; Payne, 2011). Regardless, winter duck hunting was very popular prior to its ban in 1985 (Disi et al., 2004), and a few instances of waterfowl breeding have been recorded in the twentieth century. For example, Wallace (1983) documented breeding birds of Azraq over three spring seasons after a "normal" winter in 1962/3, a "wet" winter in 1964/5 and a "dry" winter in 1965/6. Resident mallards (for Latin names see Table 3) bred in all 3 years in the oasis and freshwater marshes. Some garganey were documented in courtship flight but breeding was not confirmed (Andrews, 1995; Wallace, 1983). Shelduck were seen courting in the "normal" and "wet" years, but again, it remained uncertain if this resulted in a nest. However, 15 shelduck chicks were seen on the flooded qa' in 1990, as well as several marbled duck chicks sighted in mid-summer (Andrews, 1995). After the complete drying up of the aquifer in 1993, a small area of the original oasis was re-flooded in 1994. A later study of the breeding birds in Azraq between 1999 and 2011 did not record any breeding waterfowl (Ellis, 2014) suggesting that the reduction in the water levels had an impact on the breeding ecology of the waterfowl. Others have suggested that teal (Clarke, 1980) and pintail might breed in the region (Ashkenazi, 2004), but the current evidence suggests that mallard and shelduck are the most likely to breed particularly in years of elevated rainfall. Since species recorded breeding include mallard, marbled duck, shelduck and potentially garganey, teal and pintail, the wetland needs to provide water of at least 30–40 cm in depth with areas of emergent vegetation around the edges as part of a biological productive wetland (Green, 1998b).

A description (Yom-Tov et al., 2012) of breeding avifauna across Palestine/Israel between the 1930s and 2010s found that, despite many natural water bodies—such as a Hula Lake and adjacent swamps—drying up, breeding of many aquatic birds increased because of the creation of artificial fish ponds and reservoirs. Weed beds dominated the older, dryer water bodies whereas the newly created water-bodies provide large expanses of open water that encourage breeding. Hatzode and Yom-Tov (2002) note that mallard readily adapted their breeding range within the country as a response to these changes. Other ducks that

bred in Lake Hula include the ferruginous duck (Ashkenazi, 2004), and as well as marbled ducks within the region's papyrus swamps (Tristam, 1884). Birds also flocked to Lake Hula as a wintering and breeding ground following the drainage of Lake Amik in Southern Turkey (Ashkenazi, 2004; Çalışkan, 2008). Prior to the drainage of Lake Amik, the wetland was an integral part of the wetland network of the region, supporting breeding populations of red-crested pochard, ferruginous duck and perhaps also gadwall (Ashkenazi, 2004; Meinertzhagen, 1935). Chicks from one pair of breeding marbled ducks were also seen in the Agmon wetland in 1994 (Shy et al., 1998). These species require shallow expanses rich in submerged vegetation, areas of water with a depth of 2 to 4 m and areas of dense surrounding emergent vegetation. Study of the feeding ecology of post-breeding marbled duck, mallard, garganey and ferruginous duck in the Göksu Delta illustrated the resource partitioning between species (Green, 1998b).

At Sabkhat al-Jabbul, just southeast of Aleppo, irrigation activities since the mid-1980s have transformed the habitat from a seasonal saline lake to a complex wetland ecosystem (Serra et al., 2006). In 2005, 725 white-headed ducks were seen wintering on the lake supported by the development of reed beds. The species was very infrequent prior to influx of fresh water into the system, with only single birds reported in spring 1965 and summer 1994 (Serra et al., 2006). This change in migration pattern was also likely driven by the drainage of Lake Amik, encouraging white-headed ducks to winter at Sabkhat al-Jabbul instead. White-headed duck chicks were also spotted at Sabkhat al-Jabbul in 2005, together with a significant population of red-chested pochard breeding pairs (Serra et al., 2006). Serra et al. (2006) report that several other species of ducks could have bred at the wetlands in the mid-2000s, but inconsistent spring and summer observations make breeding difficult to prove. Other species that may breed here include grey-lag goose, shelduck and northern shoveler (Serra et al., 2006). The species that have been documented breeding require wide expanses of shallow open waters and some water of around 2 to 4 m in depth with submerged vegetation, emergent vegetation and reeds to provide nesting materials.

Overall, four subfamilies/tribes of Anatidae are known to have bred in the Levant in the recent past (Andrews, 1995; Shirihai, 1996) and are likely candidates for the taxonomic groups represented in the archaeological record. Members of each subfamily or tribe share some physical characteristics relating to feeding behaviours and habitat preferences (Green et al., 2001: Fig. 1). More detailed data on the general ecological preferences of the species documented breeding in the Levant in recent years is summarised in Table 3.

- The Anatini, dabbling ducks, feed in relatively shallow water by upending and dabbling at the surface. These species have powerful wings that facilitate taking off from water.
- The diving ducks, Aythyini, have smaller wings—to reduce drag when diving. This makes take-off more cumbersome, and diving ducks are more vulnerable to predators. Therefore, diving ducks prefer larger water bodies allowing them to stay away from predators that lurk at the edge and enabling them to gather the speed needed for take-off. Deeper water is also preferred as the species dive

for food. Two species within the Aythyini, the red-chested pochard and marbled duck, feed by diving and dabbling.

- Tadornini, shelducks, are grazers and dabblers and their morphology suits both walking on land and swimming on the surface.
- The white-headed duck is a member of the Oxyurini or stiff-tailed ducks and very well suited to diving with a low wing length and high tarsus length relative to body mass.

Discussion

The eggshell data clearly show that ducks, geese and swans all bred near the Qa' Shubayqa during the Early Natufian; therefore, the environmental requirements of these species must have been met. Samples analysed from the Final Natufian and LPPNA contexts were also identified as aquatic species (Anatidae/ crane). Although few eggshell samples were identified from these contexts, the evidence for breeding aquatic bird populations is strengthened by the presence of several bones of juvenile waterfowl in the assemblage from these later periods (Figs. 9 and 10). The eggs of *Fulica atra*, in particular, are less likely to be recovered archaeologically than many Anatidae species, due to their thin and

Fig. 9 Examples of juvenile waterbird tarsometatarsal bones. **a** Coot (*Fulica atra*) and **b** duck from Late Natufian phase at Shubayqa 1. **c**, **d** Juvenile tarsometatarsal and tibiotarsus of ducks from the earlier part (Younger Dryas) of the Final Natufian to PPNA phase at Shubayqa 6. **e** Juvenile tarsometatarsus of a duck from the Final Natufian to PPNA phase at Shubayqa 6

Fig. 10 Juvenile swan (*Cygnus* spp.) bones from an external midden deposit, dated to the Younger Dryas, in the Final Natufian to PPNA phase at Shubayqa 6. **a**, **b** Tarsometatarsus bones. **c** Tibiotarsus

fragile eggshells. No examples of medullary bone (Rick, 1975) in the waterfowl remains have been found but, as Serjeantson (2009) notes, it is uncommon to find medullary bone in faunal remains of wild birds, because medullary bone forms for a short period, perhaps only a matter of days, in the time before egg-laying. Furthermore, it is typically found in the femur and tibiotarsus (Canoville et al., 2019), elements that are poorly represented in the Shubayqa assemblage due to fragmentation and selective carcass processing and transport (Yeomans & Richter, 2018, 2020).

Humans inhabiting the edge of the Qa' Shubayqa were collecting eggs for food and discarded the shell fragments in middens. These remains provide important evidence that populations of waterfowl (Anatidae including swan and goose, *Fulica atra* and *Grus*) bred at a Late Pleistocene and Early Holocene wetland within the Qa' Shubayqa. This finding indicates that:

(i)   migration patterns for some species might have been different during this period compared to today. For example, the evidence of breeding swans in the Final Natufian at Shubayqa 6 might relate to the fact that colder conditions of the Younger Dryas pushed the breeding range of a species of swan (probably the mute swan) further south.

Today, mute swans (*Cygnus olor*) are rare visitors to the Levant in the winter months but they can occur in large flocks (Shirihai, 1996). Whilst there is no documented breeding of swans in Jordan in the ornithological literature, the mute swan breeds in Anatolia and is present there year-round (Arslan et al., 2022). This species has an irruptive nature and migration or movement of a large number of individuals south of their normal range is mainly due to a lack of availability of food in winter or unusual winter quarters (Blasco et al., 2019). Archaeologically, identification of swan remains at Qesem Cave, Ohalo II and Gilgal (Blasco et al., 2019; Horwitz et al., 2010; Simmons & Nadel, 1998) suggest that in the Pleistocene and Early Holocene swan was present at least occasionally. There is no methodology to determine the age of swan bones as juveniles, the only published study data is for geese. For this species, bones mature by 16 weeks of age, in order for the young birds to undertake their first autumn migration (Serjeantson, 2002). "Living (neornithine) birds grow up rapidly and without interruption, terminating their growth within one year and, with a few secondary exceptions, starting to fly only after or near the completion of growth" (Chinsamy & Elzanowski, 2001: 402). The swan bones shown in Fig. 8 are therefore birds that died before undertaking a long-distance migration. Two radiocarbon dates from the midden containing the remains (RTD-9656 10,126 $\pm$ 28 bp and RTD-9657 10,242 $\pm$ 29 bp) suggest that the deposit dates to the earlier part of Younger Dryas (12,000–11,700 cal BP).

(ii)   the wetland was able to sustain populations of waterfowl at least from egg laying in spring to chick development in late summer, which implies the presence of significant water in the Qa' Shubayqa through much of the breeding season, providing sufficient food sources and appropriate shelter for various waterfowl species. Despite the Final Natufian Phase at Shubayqa 1 indicating a decrease in the frequency of waterfowl, the presence of Anatidae eggshell in context with a date of 12,000–11,700 cal BP (RTD-8902 10,107 $\pm$ 53 bp, Richter et al., 2017) and additional data from Shubayqa 6, suggests that, even in the Younger Dryas, water was present for much of the seasonal cycle. This supports findings by Hartman et al., (2016) in a study of oxygen isotopes values from gazelle teeth from Hayonim and Hilazon Tachtit indicating that the Younger Dryas was cooler but not drier than previously suggested in western Galilee. It also highlights the value of techniques that can provide environmental reconstruction at the settlement level, to complement broader environmental proxies. Whilst precipitation may have reduced during the Younger Dryas, water levels within the hydrological system and present in larger wetlands may have not been immediately affected.

The timing of waterfowl mating, egg laying, incubation and development of juvenile ducklings/goslings/cygnets is important since these can infer conditions of the past wetland in different seasons. Based on the length of the incubation period and time needed for the juveniles to fledge in the potential species once breeding at the Qa' Shubayqa, a reasonable estimate is that the wetland would need to contain significant water through the height of summer and probably even longer. The mute swan requires water throughout the year to breed with substantial quantities of submerged and emergent vegetation to support feeding and nesting requirements (Bowler, 2005; Cramp & Simmons, 1977; Hughes & Green, 2005), and the confirmed presence of breeding swans illustrates the healthy state of the wetlands through the year with considerable vegetation available. Today, greylag goose (*Anser anser*) are reported as occasional winter visitors to the southern Levant with no documented evidence of breeding (Andrews, 1995; Shirihai, 1996).

The identification of eggshell and/or juvenile bones of species other than Anatidae is also important, and the ecology of these species provide insights into conditions of the Late Pleistocene and Early Holocene. In the spring of 1963 to 1966, a small number of coots were seen at Azraq with a few pairs suspected as breeding (Andrews, 1995). In Israel, a few pairs are occasionally documented breeding in the 1920s to 1950s. In the 1980s, there was a notable increase of summer visitors, mostly non-breeders, but a few pairs were recorded as breeding (Shirihai, 1996). A study of the breeding ecology of coots in Algeria found that they are often associated with *Phragmites* vegetation with egg laying between 8 March and 2 July in nests associated with low water depths making them easily predated (Samraoui & Samraoui, 2007). Common crane (*Grus grus*) is a very regular winter visitor to Eastern Jordan and found in the basalt desert as well as areas of flooded qa' (Andrews, 1995). The Demoiselle crane (*Grus virgo*) is a rare passage migrant on route through the region (Shirihai, 1996), and neither species have been documented breeding as far south as the Levant. The common crane breeds in eastern Turkey (Akarsu et al., 2013) but has not been documented breeding in the Southern Levant.

Overall, the presence of both avian eggs and juvenile bones in the archaeological site, together with other zooarchaeological evidence, such as the high frequency of gazelle under 7 months of age following a spring birth (Yeomans et al., 2017), implies that human occupation at Shubayqa was year-round. Any consideration on the role of wetlands in encouraging or sustaining waterfowl breeding needs to be founded on the understanding that wetland ecology is highly dynamic. Some wetlands undergo cycles of regeneration that can be related to episodes of drought and deluge, with fluctuations combining over many years to form a wetland cover cycle with temporary optimal conditions (Poiani & Johnson, 1993). Without fluctuations in water level and the resultant dynamic vegetation successions (Fig. 11), many wetlands degenerate (Werner et al., 2013). Eventually, standing water will cause a reduction in the amount of emergent vegetation, and dissolved oxygen in the water will decrease. This cycle has a strong impact on the distribution of waterfowl and other wetland birds, which will alter their distribution in response to changing habitat availability. Ideal locations for many of these birds are provided by hemi-marsh conditions, *i.e.* with a ratio of emergent vegetation to open-water approximately 1:1.
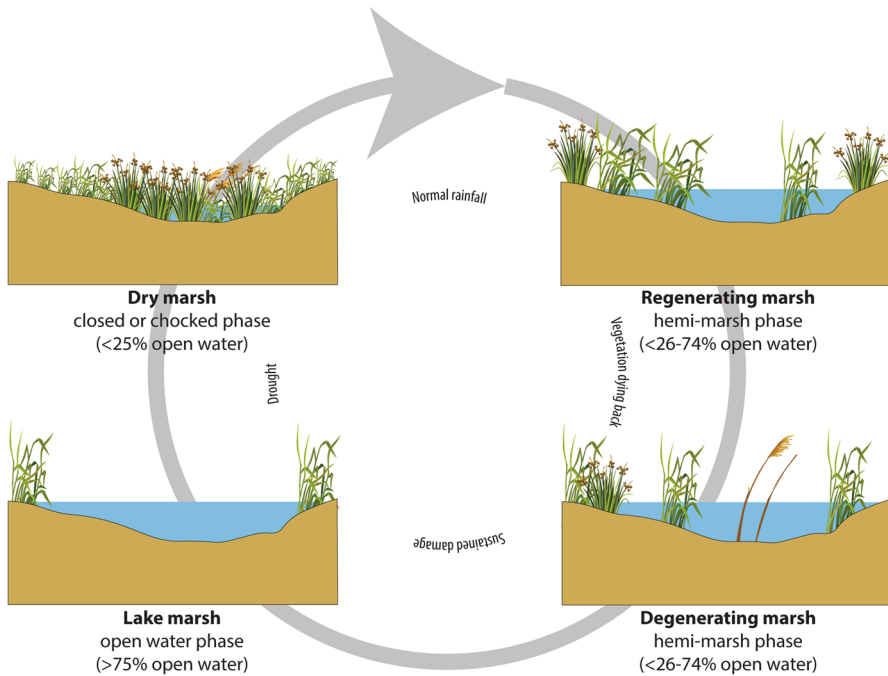
Fig. 11 Cover cycle of semi-permanent wetlands (based on Wermer et al., 2013, Fig. 3) with protracted periods of high water flooding out the vegetation resulting in lake marsh conditions or extended drought cycles leading to dry marsh conditions. Ideal breeding environment for waterfowl is during the hemi-marsh phases. This model, created for the Prairie Pothole region, demonstrates that external stimuli are needed to maintain a healthy wetland environment—these can be a combination of the natural fluctuations of precipitations, and the active removal of the emergent vegetation

On the contrary, in the "choking phase", an increase in benthic invertebrates that live in the sediment and that are tolerant of poor water quality will result in waterfowl numbers *reducing*, at least for some species, because of a contraction in the diversity of food sources as well as the lack of cover. Furthermore, if water levels change dramatically over the breeding season, nests can be flooded or left exposed to predators (Ma et al., 2010). Whilst fluctuating water levels are one method to maintain a healthy wetland environment, harvesting of emergent vegetation is an alternative method. Humans managing wetlands that have a relatively stable water level allows the vegetation to undergo cycles of regrowth and create areas of water suitable for waterfowl to forage. Macrophyte cover of around 20–40% provides good habitats for benthic invertebrates in the water, and these are known to benefit success of breeding ducks in a range of species (Broyer & Curtet, 2010). In Sweden, wetland restoration projects involved cutting or removal of emergent vegetation to increase the amount of open water surface and open up shorelines as well as hydrological modifications to restore spring/autumn flooding regimes. The effect on numbers of

breeding birds before and after demonstrated that both shallow and deep-water foragers benefited from these conservation efforts (Kačergytė et al., 2022). Although this is a very different ecological setting, it shows the importance of external stimuli to refresh the wetland environment. Whilst seasonal and yearly variation in rainfall in the wadi systems may also have been a factor, the deliberate management of wetland vegetation to promote breeding of waterfowl is well documented (Kantrud, 1986). The modern ecological data reviewed above highlights that management of Levantine wetlands created conditions that increased the breeding populations of waterfowl (Ashkenazi, 2004).

Mutual Human and Avian Ecologies in Past Wetland Environments

Whilst the climate in the past likely encouraged more consistent wetland environments which attracted waterfowl and breeding populations, this environment existed within the mutual ecologies of humans and animals. Given the complex ecology of wetlands and the well-documented presence of human and non-human animals' activities in the landscape of the Qa'Shubayqa at the transition between Pleistocene and Holocene, we consider our data on waterfowl breeding within the framework of mutual ecologies and Niche Construction Theory. Niche Construction Theory recognises that organisms modify natural selection processes in a way that influences their own evolution as well as that of other species (Laland & O'Brien, 2010). Multispecies perspectives destabilise the duality between humans, non-human animals and other living beings and proposes a world created by hybrid more-than-human communities whose "becoming-with" produces each other's realities (Haraway, 2008; Tsing, 2015). This process of "world-making" is always the result of historically situated, entangled and co-dependent relationships between humans and non-human animals (Haraway, 2008; Kirksey & Helmreich, 2010). Below, we explore a number of threads which illustrate how the Qa' Shubayqa landscape could have been co-created within this multi-species framework (Fig. 12). Human agency at Late Pleistocene Shubayqa wetlands is entangled with various ecosystem processes.

At the beginning of the Holocene human transformation of the wetland coincided with transformation of the terrestrial landscape (Colledge et al., 2018) as the practice of crop cultivation could have altered the biodiversity and species distribution in the wider ecosystem. A tantalising indication of the extent of such impacts may have been recorded by the avifaunal assemblage: quail (*Coturnix coturnix*), a species that is well adapted to managed agricultural environments (Németh et al., 2019; Šálek et al., 2022) suddenly increased in frequency at Shubayqa 6 in the LPPNA (Table 1). This may reflect a practice documented by Emslie (1981), who notes how Pima Indians of southern Arizona snare Gambel's quail (*Callipepla gambelii*) in their fields exploiting the bird's attraction to wild and cultivated seeds. Cultivated crops also encourage certain wetland bird species: Puebloan farmers in thirteenth century Albuquerque intentionally left some grain in the fields to attract migratory birds
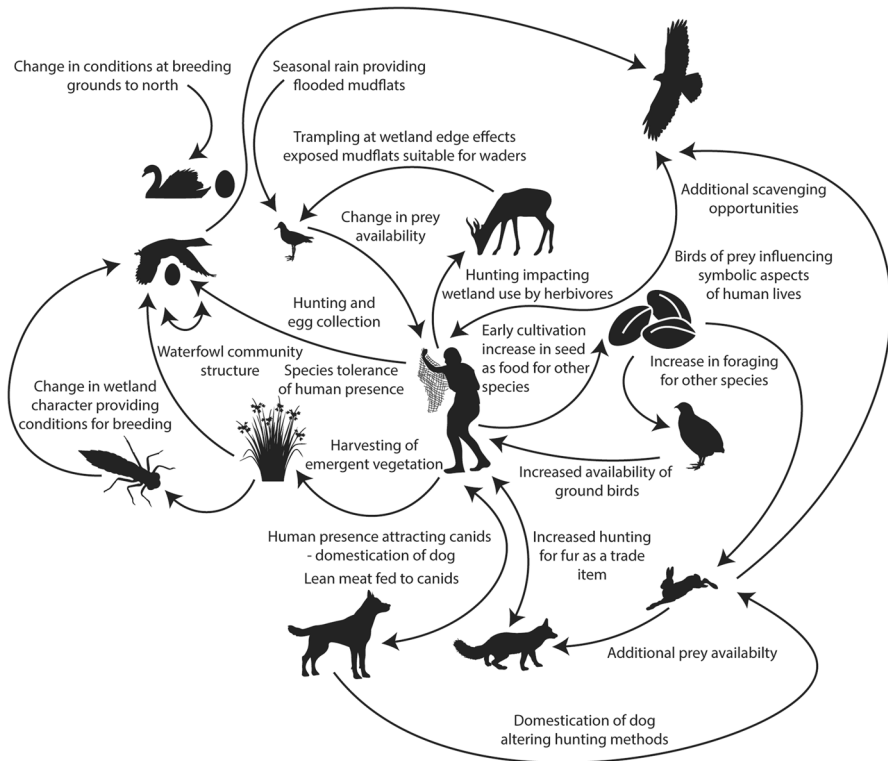
Fig. 12 Tanglegram (following Fuller et al., 2016; Hodder, 2012; Hodder & Mol, 2015; Hussain et al., 2022) of some human-animal-plant interaction envisioned for a wetland at Shubayqa in the Bølling-Allerød. The full range of interactions is impossible to cover in the figure, but the illustration highlights the complexity within a mutual-ecologies system and includes the presence of dogs (Yeomans et al. 2019)

enticing these flocks to overwinter in the area rather than continue south to Mexico; cranes and geese feeding on this grain provided the farmers in the Rio Grande Valley a valuable winter resource (Cordero, 2018). At Shubayqa, we will examine these possibilities upon integration with forthcoming results of archaeobotanical analyses.

Humans at Shubayqa gathered tubers from emergent vegetation for food as well as reeds to be used as the raw material for roofing/bedding/basketry (Ramsey & Rosen, 2016). Given that these would have been basic needs throughout occupation of the site, these materials would have been consistently harvested and would have prevented vegetation stands becoming too dense, pausing the wetland cover cycle within the hemi-marsh phase, favourable for wetland birds. A similar argument has been made by Ramsey et al. (2018), in their discussion of the phytolith evidence from the nearby site Khareneh IV, an Early Epipaleolithic site near Azraq. They note how sedge and reed resources responded favourably to anthropogenic disturbance and propose that their intentional collection enhanced the ecological productivity of the wetland.

Wild animals also have similar impacts on vegetation regeneration in wetland ecosystems: for example, grazing animals can control the growth of emergent vegetation around the edges of marshes. Indeed, the exclusion of grazing animals at the Azraq wetland in 1995 resulted in the uncontrolled growth of *Phragmites*, eliminating the open pools and exposed mud areas which were key habitats for waterbirds (Disi et al., 2004). Water buffalo have since been reintroduced to the wetland reserve with positive results (Biró et al., 2019). Mute swans also engage in many of the same niche constructing activities associated with humans in wetland ecosystems. Their grazing, trampling and harvesting behaviours can influence vegetation structure, which in-turn, alongside the swan's aggressive nature can impact community structure of the ecosystem (Guillaume et al., 2014). Human interactions with wild terrestrial and aquatic animals, then, can have diverse impacts on local ecosystems beyond that of the immediate relationship between the human and animal.

Human activities may also disrupt the nesting behaviour of birds. Recent studies by Cherkaoui et al. (2017) on Anatidae at 25 wetlands in Morocco found that human activity, such as distance to nearest road or human settlement, did not seem to have a negative impact on the breeding of mallards, whilst other species of ducks (ruddy shelduck, gadwall, marbled duck, red-crested pochard, common pochard, ferruginous duck and white-headed duck) were negatively influenced by human presence. At Shubayqa, zooarchaeological data indicate long-term stability in the gazelle hunted by the inhabitants, which suggests that overall human population densities were low and their activities sustainable. Nonetheless, hunting may have changed the behaviour of grazing animals (gazelle, wild sheep, onager and aurochs), which would have become wary of people, or of the predators (hyena, leopard, wolf), which would have been competing with people for prey. Human hunting may have reduced the overall herbivore biomass, but this may be considered a positive factor, as it would have kept the animal population in check.

Overall, the documented and inferred multi-species interactions at the Qa' Shubayqa point towards a situation of long-term balance of the wetland, with human and non-human activities such as grazing, foraging and hunting likely contributing to the productivity of the system. This is in line with our novel finding of waterfowl breeding in the area, which implies that birds were finding a productive environment, enabling them to reside year-round or at least to sustain their young through the dry season even in the Younger Dryas. The documented taxonomic diversity of the water birds, based on bone remains (including juvenile waterbirds) and eggshell hints at the presence of open water and emergent vegetation. As we are working towards a more refined way to separate eggshell taxa within the same clade, using palaeoproteomics and micromorphology, we will be able in the future to consider the requirements of each tribe (Table 3) and build a higher-resolution picture of the wetlands. Additional analysis of the stratigraphic data and further radiocarbon dates will further refine the picture of the wetland environment from the Bølling-Allerød to the Early Holocene.

Here, we draw from ethnographic and archaeological examples to hypothesise that the high biodiversity and stability over time of the wetlands at the Qa' Shubayqa were accentuated by human management, which may have promoted species diversity and biomass within the avifaunal community. Were these activities intentional?

Proving intentionality drawing from the archaeological record is very difficult, but ecologically attuned hunter-gatherers would have perceived that harvesting emergent vegetation could create open-water habitats for feeding activities and take-off space of waterfowl, which in turn provided other sources of food in the form of birds and eggs. Positive feedback and niche construction is evident in other geographical and temporal areas:

1) Wetland management associated with early rice paddies at Tianluoshan in the Lower Yangtze region of China (7,000–6,100 cal BP) had the effect of promoting growth of *Typha*. The presence of *Typha* pollen in coprolites suggests humans used it as a food source (Zhang et al., 2020). The avifaunal remains also indicate that the large numbers of wetland birds, including ducks, rails and geese were exploited (Hsu et al., 2021) with the later managed by humans (Eda et al., 2022). The impact of management of the rice paddies might have promoted the suitability of the wetland to the birdlife and ultimately provided the necessary conditions for goose management.

2) In the Nile Valley, the paleoenvironmental evidence from Wadi Kubbaniya (19–17,000 cal BP) is similar to the wetland setting of Shubayqa, with evidence for exploitation of Cyperaceae tubers (Hillman, 1989) and frequent waterfowl bones and eggshell (Gautier & Van Neer, 1989). It has been postulated that aeolian sands from the western desert overran the Blue Nile leading to the creation of dams, behind which lakes formed (Vermeersch & Van Neer, 2015) thus sustaining human presence. Hillman (1989) showed that the humans extensively exploited wetland vegetation at sites like Wadi Kubbaniya, effectively maintaining the wetland and encouraging the use of the lakes by waterfowl.

3) In the wetlands of Australia, Fitzsimmons et al. (2014) noted that there was increased evidence of human occupation at Lake Mungo when the lake levels were fluctuating, reinforcing what we know about the increased productivity of wetlands during phases of regeneration. In southwestern Victoria, hunter-gatherers actively managed swamps: Lourandos (1987: 299) notes how "controlled burning replaced forest with savannah, encouraged annual species, exposed feed for birds and animals and rejuvenated swamplands by removing growth in dry months". Humans acted as "environmental modifiers" building complex fish traps as well as constructing protected areas for the fish to grow.

4) Perhaps, the most striking and well-documented example of human management of wetlands comes from Mesoamerica. Prior to the historical development of Mexico City, the high altitude, semi-arid Basin of Mexico housed a large system of interconnected lakes, whose mix of saline, brackish and freshwater ecosystems supported massive populations of North American winter migratory birds as part of the Central Flyway migratory route. Exploitation of lake resources intensified with the development of cities and eventually the Aztec empire, whose capital was situated on an island within the largest of the five lakes, Texcoco. Ethnographic and historical records document the heavy reliance by the Aztecs on aquatic plants, algae, insects, fish, amphibians and waterfowl for food production, craft production or market exchange (Parsons, 2010). They also extensively modified the wetland ecosystem for agriculture and water management. The lakeshore and

shallow freshwater lake beds were locations for constructing *chinampas*, highly productive and self-watering raised platforms made of rich lacustrine soil for agricultural production, separated by canals dug into the lakebed for transport of goods (Armillas, 1971). They also modified the lake system through systems of canals, dykes and causeways to control flooding and water-levels (Rojas Rabiela et al., 2009), in addition to use of more perishable barriers evident in a sixteenth century map, which Parsons (2005) suggests illustrates control over water depth specifically for the exploitation and management of various plant and animal resources. Whilst earlier settlements in this region canalised springs and rivers to feed agricultural fields (Nichols, 2015), waterlogged deposits from Terremote demonstrate that residents harvested a wide range of plant and animal aquatic products and employed similar construction techniques later seen in the development of the chinampas (Serra Puche, 1988). Despite the lack of archaeological evidence for extensive wetland modification at this time, they likely employed various techniques documented by colonial period sources to attract and harvest aquatic animals in later periods (summarised in Parsons, 2005). Insect eggs, for example, could be acquired by partially submerging bundles of reeds in water to attract insects to lay their eggs, which could then be dried and shook loose from the reeds. Besides the use of freestanding nets to catch waterfowl, gourds could be cast into the lake to desensitise waterfowl, allowing hunters to wear gourds as disguise in order to take fowl by hand.

5) In South America, extensive evidence human transformation of aquatic environments of Amazonia has been reviewed by Prestes-Carneiro et al. (2021), demonstrating the variety of ways that the waterscapes have been influenced by humans to increase productivity enabling the storage of freshwater turtles as well as fish corrals.

These few examples show the complex relationship between humans and wetlands. Humans are drawn to these locations and the effort taken to alter the physical characteristics of these locations pays dividends in terms of the improved foraging opportunities afforded. Examples of increased productivity of wetland vegetation under human management are well documented archaeologically (e.g. Hoffmann et al., 2016; Zhang et al., 2020), and many cases shown how fish stocks can be beneficially influenced, but the effect on avifaunal communities has not been previously discussed. Overall, the importance of waterbirds and wetlands throughout history emerges clearly from these examples. Wetlands were very important ecosystems for various human groups (Nicholas, 1998) and their distribution often crucial for migration into new regions globally (e.g. Ellis et al., 2011; Latorre et al., 2013). Smith (2007) applied Niche Construction Theory to explain *how* humans transitioned to agricultural practices through the increasing manipulation of targeted resources and their environments. Humans altering the productivity of the wetlands during the Late Pleistocene of the Levant are part of this process of gradually increasing ecological manipulation. This provides humans with water birds for hunting and eggs for gathering and in other settings seems to have led to the domestication of waterfowl.

Conclusions and Perspectives

This study stems from our novel finding of Anatidae eggshell from Early Natufian and Final Natufian at Shubayqa 1 and juvenile waterbird remains from Shubayqa 6. Reflecting on the significance of our pilot study, we highlight intertwined lines of enquiry that are worth pursuing further:

i)   The presence of eggshell and juvenile bones indicates that the wetland at Shubayqa in the Southern Levant could sustain breeding populations of water birds. Were these birds all-year residents? Did this pattern shift with changing global conditions, as the Bølling-Allerød turned into the cooler and dryer Younger Dryas and then with the beginning of the Holocene? Initial results suggest that water was available through much of the year during the Younger Dryas. However, this will be clarified through denser sampling of eggshell and avian bones throughout the archaeological sequence, as well as additional radiocarbon dates, allowing subdivision of the Final Natufian to PPNA phase. Our results are in line with a growing body of evidence suggesting that the cooler temperature and less seasonal rainfall of the Younger Dryas might have resulted in higher water levels (Hartman et al., 2016; Langgut et al., 2021; Liu et al., 2013; Orland et al., 2012).

ii)   Improved taxonomic resolution within Anatidae is paramount for obtaining high-resolution reconstruction of wetland conditions. As shown in Table 3, different duck tribes display very different ecological requirements. Ongoing work on perfecting biomolecular approaches will enable us to identify the presence of breeding dabbling / diving / grazing ducks. Using their ecological traits, we will reconstruct habitats diachronically.

iii)   Water birds, people and wetlands are entangled in complex socio-economical webs. Here, we have begun to sketch some of the key relationships and how these might have contributed to construction of the shared niche. Green and Elmberg (2014) have summarised the range of ecosystem services that water birds provide, beyond the provisioning of meat, feathers and eggs, including maintaining diversity in other species and pest control, as well as contributing to human well-being (Gaston, 2022). With more fined grained chronological and taxonomic information for Shubayqa, we can begin to trace the human-wetland entanglement diachronically, revealing how wetlands and the waterfowl populations changed with both human and environmental inputs, and how these in turn might have encouraged intentional management of the wetland.

By drawing on archaeological and ethnographic examples, we have highlighted the potential that intentional management of the Qa' Shubayqa wetland could have increased productivity of the environment. We suggest that such activities may have been another example of the intensification process that led to the domestication of plants and animals (Zeder & Lemoine, 2022), and perhaps the productivity of the environment was sufficient that it contributed to the fact that waterfowl remained to breed. This fits in the third category of hunter-gatherer niche construction of enhancing and/or expanding the geographic range of specific animal species, as

defined by Nikulina et al. (2022) and is supported by recent discussion of habitat modification in the Levantine Epipalaeolithic wetlands based on phytolith evidence (Ramsey, 2023). The importance of wetlands as settings for niche construction activities and centers for innovation in human subsistence across the Pleistocene/Holocene boundary is increasingly apparent. Feedback from promoting wetland productivity had implications for water bird activity, and this may have further encouraged human occupation. This paper has combined Niche Construction Theory and Mutual Ecologies to develop a detailed reconstruction of the wetland environment at Shubayqa and the co-dependencies of a multitude of species that were drawn to this location. The Natufian and Pre-Pottery Neolithic A were periods when humans were on the cusp of developing agriculture. There is a growing range of studies and theoretical arguments that consider the evolution of habitat modification activities as an important driver in this process (Zeder & Lemoine, 2022). Considering the known outcome of agriculture, we argue that intentional management of wetlands was a stage in this process and that such locations were ideal places for human innovation (Ramsey, 2023). The presence of eggshell supports the idea that human activity gradually influences these resources more extensively through the Late Pleistocene and Early Holocene. By the PPNB, human management of water was taking place on a considerably larger scale as evidenced by surface water barrages at Jafr Basin sites of Wadi Abu Tulayha and Wadi Ruweishis ash-Sharqi designed to collect surface runoff (Fujii, 2011).

The novel finding of eggshells of breeding waterfowl at Shubayqa has allowed us to demonstrate the year-round presence of water at the wetland through the Late Pleistocene and Early Holocene. This has encouraged us to think about the multispecies interactions in this context and consider the agency of humans and other species in modifying the environment. As Rowley-Conwy and Layton (2011) note, the actions of niche construction activities carried out by forager societies improved the productivity of food systems. Future work will help us advance our understanding of how human and non-human species contributed to shaping the ecology of wetlands and to enhancing their potential as loci for the emergence of agriculture.

Declarations

Competing Interests The authors declare no competing interests.

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