



Distinct modes and intensity of bird exploitation at the dawn of agriculture in the Upper Euphrates and Tigris River basins

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Abstract

Early Neolithic avifaunas excavated at the sites of Göbekli Tepe and Gusir Höyük illustrate two entirely different modes of bird exploitation in south-eastern Anatolia during the 10th and 9th millennia BCE, which prompted us the re-evaluation of other substantial bird bone assemblages from contemporaneous sites in the upper basins of the Euphrates and Tigris rivers. We thus compared the range and diversity of species captured, seasonal aspects of bird hunting, and types of habitats exploited by Near Eastern communities of foragers at the dawn of agriculture. Fowling practices in the Upper Euphrates catchment aimed at multiple avifaunal resources in varied habitats explaining high taxonomic diversity in the respective assemblages. Overall, the proportions of birds, mammals and fish in the diet were similar in all sites. In contrast, meat diet in the Upper Tigris River basin proved less culturally uniform. The contribution of birds, fish and mammals to the diet varied significantly between sites. Our study also showed that avifaunal diversity was very low at some sites in the Tigris basin suggesting an overall limited interest and time commitment to this economic activity there. An intensification of bird hunting in autumn and winter was observed in both areas.

Keywords Early Neolithic · Göbekli Tepe · Gusir Höyük · Bird exploitation · Upper Mesopotamia

Introduction

Since the late 1960s, the ‘Broad Spectrum Revolution’ coined by Flannery (1969) has become a widely accepted hypothesis when addressing faunal exploitation by Epipalaeolithic and early Neolithic human communities inhabiting SW Asia. It refers to a broadening of the diet of foragers at the transition of the Pleistocene to the Holocene and is illustrated in the faunal record by a significant increase in the consumption of smaller-sized prey (Stiner et al. 2000; Stutz et al. 2009). Within the small prey category, birds are generally considered more challenging since they are quick and therefore more difficult to catch (Stiner et al. 2000). The diversification within the fast prey category, however,

necessitates more specialised and diversified foraging techniques and a thorough knowledge of the ecology and the behavioural traits of the pursued prey (Munro et al. 2021).

In the southern Levant, quite diverse avifaunas have been reported in Epipalaeolithic archaeofaunas (e.g. Ohalo II: Simmon and Nadel 1998; Steiner et al. 2022; Nahal Ein Gev II: Munro et al. 2021; Shubayqa 1: Yeomans and Richter 2018). Faunal analyses from contemporaneous sites in Upper Mesopotamia, however, are rare and show divergent trends. Avifaunal assemblages from Natufian/Khiamian Mureybet in the western part of Upper Mesopotamia are substantial and comparably rich in species (Gourichon 2004). Conversely, in the Zarzian levels at Palegawra Cave in the eastern part of Upper Mesopotamia birds are rather scarce, becoming even less important during site occupation (Asouti et al. 2020). Published avifaunas from subsequent early Neolithic PPNA sites in the Southern Levant (e.g. Netiv Hagdud: Tchernov 1994; Gilgal: Horwitz et al. 2010) as well as in Upper Mesopotamia (e.g. Tell Mureybet: Gourichon 2004; Göbekli Tepe: Peters et al. 2005; Hallan Çemi: Zeder and Spitzer 2016; Körtik Tepe: Emra et al. 2022) seem to be similarly rich in species and diverse as at Epipalaeolithic/Natufian

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sites in the southern Levant and the western part of Upper Mesopotamia.

Unpublished substantial avifaunal assemblages from Göbekli Tepe and new data from Gusir Höyük stimulate a re-evaluation of the role of birds in PPNA Upper Mesopotamia. This study thus addresses the modes of exploitation of avian resources at these sites as regards taxonomic composition, species diversity and patterns of seasonal exploitation. In order to evaluate these findings in a broader cultural context, we compared our results with those obtained from broadly contemporaneous avifaunas originating from other sites located in the upper basins of the Euphrates and Tigris rivers.

Material

Göbekli Tepe (Upper Euphrates basin, SE Anatolia, Turkey)

The site of Göbekli Tepe (GT), famous for its megalithic architecture and rich animal iconography (Peters and Schmidt 2004; Peters et al. 2005; Schmidt 2006), is located some 18 km northeast of the modern town of Şanlıurfa (Prov. Şanlıurfa) on one of the southernmost hills of the Germuş mountain range fringing the northern margin of the Harran plain (Fig. 1). The site's catchment area is crossed by several seasonal watercourses that are part of the headwaters of the Balikh River (Nykamp et al. 2020), an important tributary discharging into the Euphrates in N Syria. Excavations at Göbekli Tepe started in 1995 and unearthed a complex, multi-layered site with two main architectural phases, more precisely an earlier phase with megalithic round to oval structures and a later phase characterized by

smaller rectangular buildings (Fig. 2). Their relationship to a third architectural feature consisting of small round buildings is not yet completely understood, but contemporaneity with at least some of the monumental buildings seems possible, if not even representing a preceding occupation phase, at least partly (Kinzel and Clare 2020). Building and repair activities started early in the Pre-Pottery Neolithic A (PPNA; c. 9600–8700 BCE) and continued into the early Middle Pre-Pottery Neolithic B (Middle PPNB; c. 8200 BCE), site use thus lasting at least 1400 years (Dietrich et al. 2013). From their material culture, however, it can be concluded that the aforementioned small round buildings date to the PPNA (Kinzel and Clare 2020).

For the moment, the chronological relationship of the subsequent architectural phases and their associated material culture is still under investigation. Largely composed of relocated materials, the fills of the initial round monumental or the subsequent rectangular buildings cannot be assigned to either architectural phase. Consequently, avifaunal remains retrieved from undisturbed PPNA contexts, and those collected in units of mixed origin must be dealt with separately (Table 1).

Bird remains unequivocally assigned to PPNA occupation levels originate from three locations situated respectively in squares K10-13/23, L9-78 and L9-97 (Fig. 2). They were collected in the deep trenches dug down to bedrock to fix the posts for the roof shelter. As such, the material culture of square K10-13/23 has been interpreted as domestic refuse based on the layout of the architecture, composed of small round structures and open spaces. Excavations in square L9-78 unearthed the vestiges of a small round structure attached to Building D containing fine ashy layers and a significant accumulation of bird bones. The situation in square L9-97 is less clear since only a small trench has been excavated so far. From the excavation notes, however, we know that accumulations of bird bones also occurred in thin layers immediately outside the walls of Building C. While the contents of these three in situ PPNA contexts have been sieved systematically (mesh sizes: 10 mm and 2 mm), sampling of the relocated debris (termed “mixed” in the tables) excavated inside the monumental and rectangular buildings usually involved hand-collecting, with occasional instances of sieving. For the moment, published information on the avifaunas is only available for the fills (Peters and Schmidt 2004; Peters et al. 2005). Based on the analysis of archaeobotanical remains, the early Holocene vegetation in the Göbekli Tepe hinterland belongs to the Irano-Turanian zone, characterized by vast grasslands and scattered stands of pistachio and almond trees (Neef 2003).

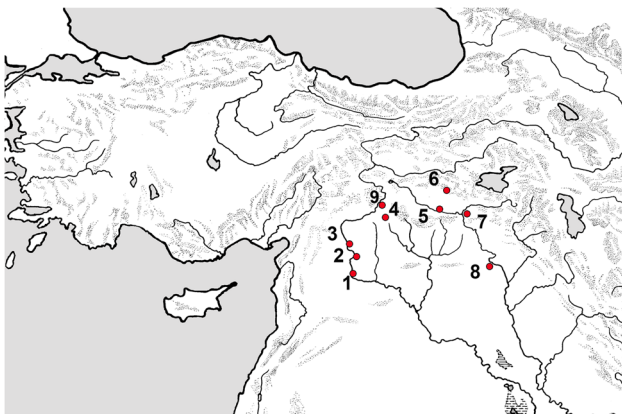


Fig. 1 Map of SW Asia showing (1) Tell Mureybet (TM); (2) Jerf el Ahmar (JA); (3) Dja'de el-Mughara (DM); (4) Göbekli Tepe (GT); (5) Körtik Tepe (KT); (6) Hallan Çemi Tepesi (HÇ); (7) Gusir Höyük (GH); (8) Qermez Dere (QD); (9) Nevalı Çori (NC)

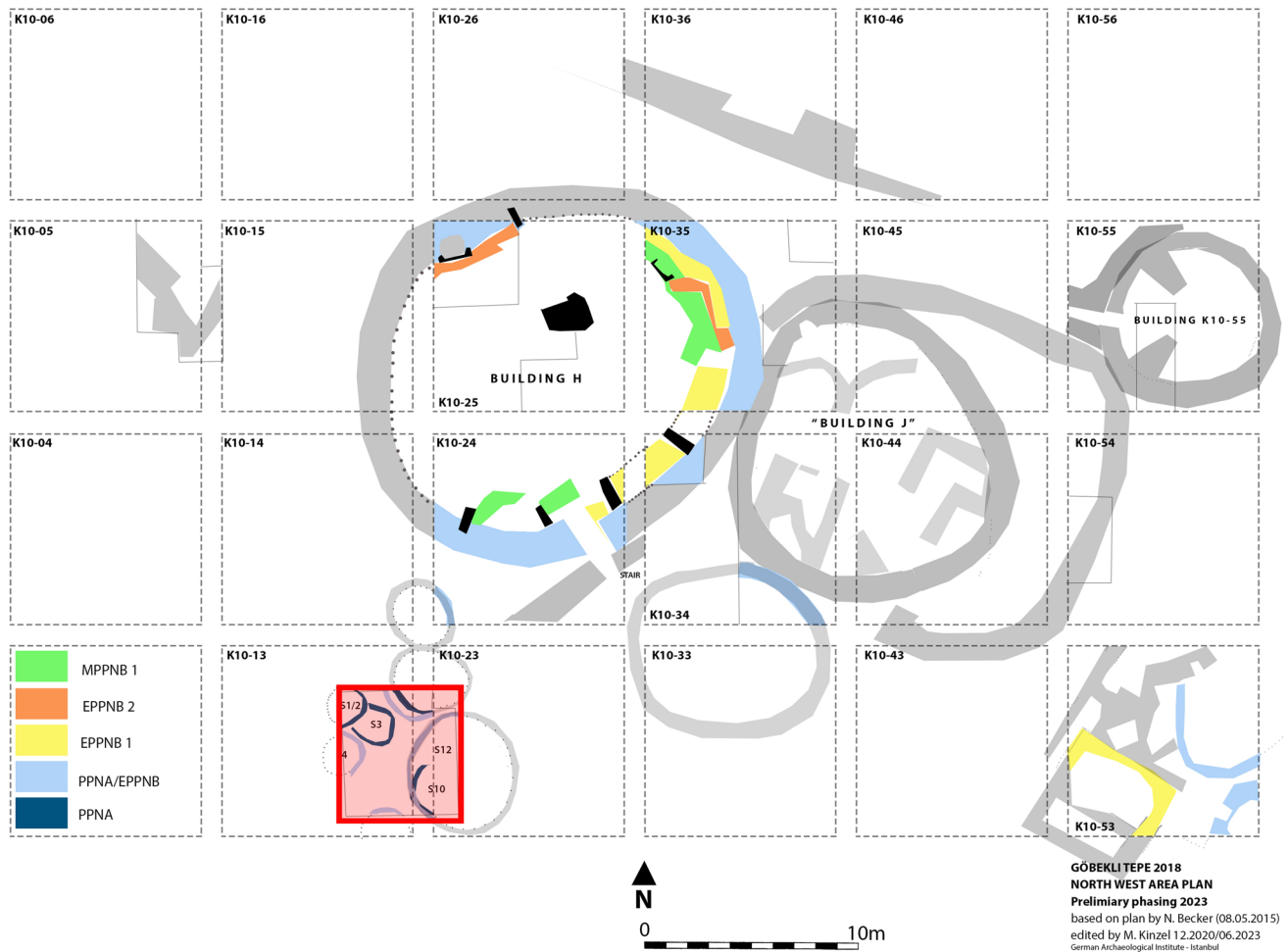


Fig. 2 Göbekli Tepe. **a** NW area with K10-13/23 marked in dark red (© Nico Becker, edited by Moritz Kinzel, DAI-Istanbul); **b** SE area with L9-78 and L9-97 marked in dark red (© based on plans by D.

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Gusir Höyük (Tigris basin, SE Anatolia, Turkey)

Gusir Höyük (GH) is an Early Neolithic site located at the shore of Lake Gusir, about 40 km south of the provincial capital of Siirt (Prov. Siirt) and immediately south of the confluence of the Tigris and Botan Rivers (Fig. 1; Karul 2011). The site was excavated between 2009 and 2014 in the frame of salvage excavations necessary due to the Ilisu dam building project. A series of radiocarbon dates suggest that human occupation at Gusir Höyük lasted from c. 9750 until 8300 BCE, which corresponds to the PPNA and early PPNB (Karul 2011; Kabukcu et al. 2021). Faunal recovery was done by dry-sieving (mesh size 5 mm). Information regarding taxonomic composition of a representative subsample was published recently (Kabukcu et al. 2021). The faunal remains were recovered primarily from a midden (square 21G) and a special building (square 21L) (Fig. 3).

Archaeobotanical analyses revealed that the immediate surroundings of Gusir Höyük featured a woodland vegetation dominated by almond and pistachio trees and complemented by hackberry, oak and acer trees; it thus belongs to the Kurdo-Zagrosian oak and pistachio-almond steppe forest zone (Zohary 1973; Kabukcu et al. 2021). Additional botanical evidence points to the exploitation of riparian woodlands along the aforementioned rivers and extensive grasslands.

Comparative datasets

Representative avifaunal assemblages from contemporaneous sites located in the Upper Euphrates and Tigris River catchments will be used for comparison (Table 1 with references). Besides GT, this concerns three sites situated in the western part of the northern Fertile Crescent, i.e. Jerf el-Ahmar, Dja'de el-Mughara and Tell Mureybet. Contrary to GT, however, these sites are located on the riverbanks of

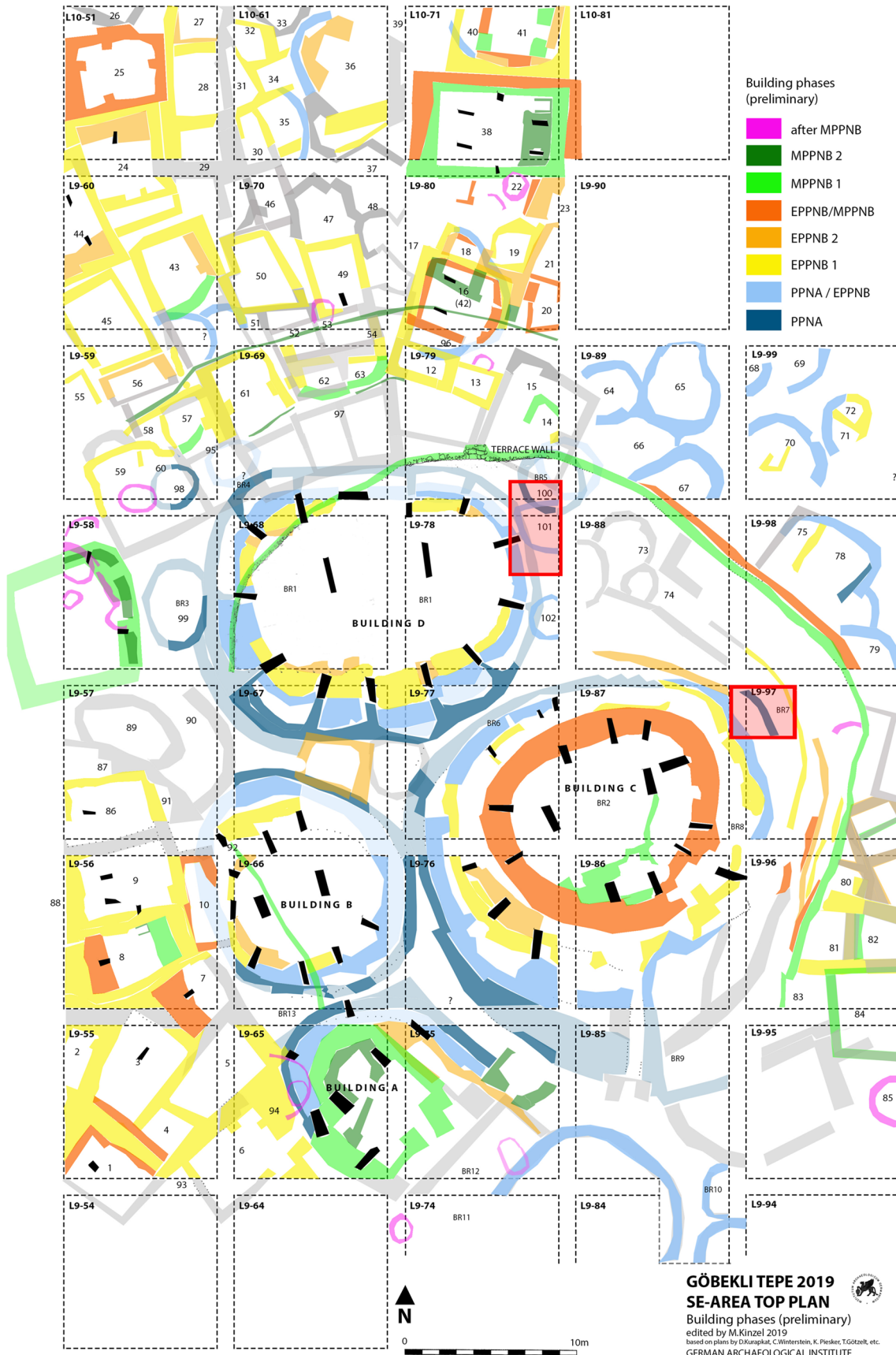


Fig. 2 (continued)

Table 1 Overview of the avifaunas reported from Early Neolithic Upper Mesopotamia, supplemented by information on the seasonality of fowling, habitats exploited, recovery methods and authors of the individual studies

	Euphrates Basin										Tigris Basin						
	Tell Mureybet		Jerf el Ahmar		Dja' de el-Mughara		Göbekli Tepe		Körtük Tepe		Hallan Çemi		Gusir Höyük		Qermez Dere		
	PPN A	PPN A	PPN A	PPN B	PPN A domestic (K10-13/23)	PPN A 'special' (L9-78)	PPN A 'special' (L9-97)	PPNA total	Mixed	Total	PPN A	PPN A	PPN A	PPN A	PPN A	PPN A	
Chronology (BCE)	9200–8550	9500–8700	8808–8290	9600–8700	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200	9600–8200
Birds species (min.)	36	49	29	46	49	21	74	45	84	16	53	4	16	16	16	16	16
Bird NISP	605	1526	351	350	359	196	892	442	1155	241	1151	442	378	442	378	442	378
Bird aD	3.9	5.6	5.6	5.6	5.6	5.6	9.4	8.3	8.3	3.0	6.8	1.1	2.4	1.1	2.4	1.1	2.4
%Ungulates	86	-	84.7	-	-	-	72.8	-	-	56.6	87.3	90.9	42.3	87.3	42.3	90.9	42.3
%Small mammals	2.8	-	1.5	-	-	-	17.8	-	-	1.1	4.9	1.1	49.4	4.9	1.1	1.1	49.4
%Birds	11.1	-	13.9	-	-	-	9.2	-	-	10.4	5.1	6.2	8.4	5.1	6.2	6.2	8.4
%Fish	0.1	-	-	-	-	-	0.2	-	-	32.0	2.6	1.8	-	2.6	1.8	1.8	-
%NISP	58.8	35.1	17.4	2.1	10.1	1.0	5.1	3.4	4.8	57.2	25.3	0	0	25.3	0	0	0
Aquatic birds	2.3	18.0	1.1	4.4	2.0	2.0	2.9	5.0	4.1	1.8	5.9	0.2	7.3	5.9	0.2	0.2	7.3
Large waders	20.5	24.1	65.0	37.8	12.3	6.6	19.6	9.1	16.0	34.3	47.4	99.1	80.1	47.4	99.1	99.1	80.1
Gamebirds	14.4	17.2	8.1	5.9	4.8	5.1	5.3	9.2	7.3	6.0	17.4	0.5	9.1	17.4	0.5	0.5	9.1
Raptors	3.6	5.3	7.3	19.2	29.4	49.5	30.0	52.0	38.5	0.6	4.0	0.2	2.8	4.0	0.2	0.2	2.8
Corvids	0.3	0.4	1.1	30.7	41.5	35.7	37.2	21.2	29.2	0	0	0	0.8	0	0	0	0.8
%Average live weight	62.6	24.2	9.3	6.2	12.7	6.2	6.2	29.7	29.7	29.7	20.9	0	0	20.9	0	0	0
Aquatic birds	6.6	18.6	0.6	12.7	12.7	12.7	12.7	12.7	12.7	1.2	6.9	1.8	20.8	6.9	1.8	1.8	20.8
Large waders	8.7	17.8	85.9	57.1	57.1	57.1	57.1	57.1	57.1	65.7	56.3	95.1	59.3	56.3	95.1	95.1	59.3
Gamebirds	20.6	38.5	3.3	6.6	6.6	6.6	6.6	6.6	6.6	3.3	15.3	2.6	19.1	15.3	2.6	2.6	19.1
Raptors	1.5	0.8	0.9	14.6	14.6	14.6	14.6	14.6	14.6	0.03	0.6	0.5	0.8	0.6	0.5	0.5	0.8
Corvids	0	0	0	2.8	2.8	2.8	2.8	2.8	2.8	0	0	0	0	0	0	0	0
Small birds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1 (continued)

	Euphrates Basin				Tigris Basin			
	Tell Mureybet	Jerf el Almar	Dja de el-Mughara	Göbekli Tepe	Körtik Tepe	Hallan Çemi	Gusir Höyük	Qermez Dere
	PPN A	PPN A	PPN B	PPN A domestic (K10-13/23)	PPN A 'special' (L9-78)	PPN A 'special' (L9-97)	PPN A	PPN A
					total			
Seasonality of fowling	Year round, intensified autumn/winter	Year round, intensified autumn/winter	Year round	Year round, intensified autumn/winter		Year round, intensified autumn/winter	Year round, intensified autumn/winter	Year round
Habitat exploitation	Mainly wetland	Grassland, wetland	Mainly grassland	Grassland, wooded steppe		Wetland, grassland	Grassland	Grassland
Recovery method(s)	Sieved (10 mm, 2 mm), flotation	Sieved (10 mm, 2 mm), flotation	Sieved (10 mm, 2 mm), flotation	Sieved 10 mm, 2 mm	Hand-picked/sieved 10 mm	Hand-picked, some sieving (7–8 mm; 3.5 mm), flotation	Sieved (5 mm)	Sieved (4 mm); wet-sieved (3 and 1 mm)
References	Gourichon 2004	This report	This report	Emra et al. 2022	Rosenberg et al. 1998; Starkovich and Stiner 2009; Zeder and Spitzer 2016	Dobney et al. 1999	This report	Dobney et al. 1999



Fig. 3 Gusir Höyük. Map of the site showing the location of (1) the special building in square 21L and (2) the midden in square 21G (both marked in red) (© N. Karul, Istanbul University)

the Euphrates. Another three sites situated in the eastern part of the northern Fertile Crescent, i.e. Hallan Çemi, Kör-tik Tepe and Qermez Dere complement the dataset for the Upper Tigris River basin. While the Kör-tik Tepe inhabitants settled on the banks of the Tigris River, Hallan Çemi and Qermez Dere are situated further away from the Tigris in tributary valleys.

Methods

Anatomical and taxonomic classification of Göbekli Tepe and Gusir Höyük birds

Bird remains recovered at both sites were separated when analysing the archaeofaunal assemblages in the respective material depots. Using modern comparative skeletons borrowed from the reference collection of the State Collection of Palaeoanatomy Munich (SPM), we were able to identify the majority of GT bird bones on the spot. The remainder of the specimens was exported to Munich on loan and identified with the aid of the modern reference collection of the SPM. With respect to the avian remains from GH, most specimens could be identified in the field without the use of reference skeletons. Only few specimens were taken on loan and determined with the aid of the SPM reference collection.

We identified all skeletal elements to the lowest taxonomic rank possible. Bones that could not be identified to the family level were assigned to size classes, i.e. small, medium and large. In this respect, small birds comprise all taxa the size of thrushes and smaller. Bustards, cranes, geese and large raptors like vultures belong to the large bird category, while birds of in-between size, such as partridges, doves, sandgrouses, ducks, small raptors, lapwings and corvids, were classified as medium-sized.

Quantification

Quantification of the avifauna is primarily based on Number of Identified Specimens (NISP) counts, the most widely used method in archaeozoology (Table 1; for the detailed record see Table SI 1). To these, we added the minimum number of bird taxa for each site. Additionally, diversity of avifaunas was estimated by means of Shannon entropy (H'). We converted the Shannon entropy into the effective number of taxa (${}^1D = \exp(H')$), which is more intuitive to interpret, since increasing effective number of taxa will result in an increase in diversity, while the opposite is the case for Shannon entropy (Jost 2006). Contrary to biological field studies, archaeozoological analyses are difficult to base on species data since many specimens can only be identified to higher taxonomic levels, e.g. family. Therefore, for archaeozoological data, the index is based on

NISP counts at the family level, which we correspondingly named archaeobiodiversity index (aD) to emphasize the difference (Pöllath et al. 2008).

As simple fragment counts do by no means reflect the real dietary significance of a given taxon, different approaches have been proposed to modify the dataset accordingly, without reaching consensus in the archaeozoological community so far, though (see the discussion in Darlington 2018). While in the following we decided to use NISPs to compare the assemblages regarding taxonomic abundancy, ecology and seasonality, we relied on the average live weight of each taxon multiplied with their NISP counts in order to approximate the relative dietary contribution of each bird group following the approach proposed by Gourichon (2004, pp. 159–160) (Table SI 2). Although the live weight approach does not circumvent existing methodological flaws, we would nonetheless argue that it allows a more meaningful appreciation of the role in the diet of each bird taxon in relation to the others. The birds' average live weights were taken from Del Hoyo et al. (1992, 1994, 1996, 1997, 1999, 2004, 2005, 2009, 2010).

Bird data and categories

Understanding past relationships between humans and birds necessitates insight into key avian behavioural traits, such as habitat choice, seasonality and migration patterns, food preferences and breeding behaviour. Relevant information has been extracted from Kirwan et al. (2008), Shirihai and Svensson (2018) and Del Hoyo et al. (1992, 1994, 1996, 1997, 1999, 2004, 2005, 2009, 2010). Addressing seasonal exploitation relies on migratory behaviour recorded in modern literature. Following standard ornithological practice (e.g. Curry-Lindahl 1981), birds can be classified into four groups according to their migratory behaviour, i.e. residents, migrants, summer visitors and winter visitors. Finally, another useful criterion for evaluating possible techniques for trapping birds is a species' sociability, since some taxa basically remain solitary throughout the year, while others aggregate in smaller or larger flocks, eventually also seasonally (see also Gourichon 2004). For our analysis of habitat use by hunters, we relied only on species showing a strong preference for a particular habitat. Ubiquitous species were excluded here. Relevant data for the different taxa identified at GT and GH can be found in Table SI 2.

For inter-site comparison, bird taxa have been classified into six groups following the approach proposed by Zeder and Spitzer (2016), with slight modifications (Table 1 and Table SI 1): Birds still pursued for their meat by present-day fowling (and therefore likely for similar reasons in ancient times) can be divided into two groups, i.e. aquatic birds (= ducks, geese, and rails) and terrestrial game birds (= bustards, doves, sandgrouses, partridges and other phasianids). Though taxonomically representing distinct groups, we nonetheless merged diurnal and nocturnal raptors into a

single category based on their comparable dietary behaviour. Large non-raptor carnivorous or piscivorous birds including cranes, storks and herons have been classified into a single category named 'large waders' due to their high-legged habitus and overlapping feeding niches. The species-rich order Passeriformes is subdivided into the group of corvids, encompassing all members of the family Corvidae, and of numerous other, usually smaller birds, mainly comprising passerine taxa (and as the only exception one bone of a plover at GT, see Table SI 1).

All statistical calculations and graphs were created in R, version 4.2.2 (R Core Team 2022).

Other animal groups

For comparisons between the sites, other taxonomic entities considered by us are ungulates (*Bos*, *Ovis*, *Capra*, *Gazella*, *Cervus*, *Dama*, *Capreolus*, *Equus*, *Sus*), small mammals (*Vulpes*, *Lepus*) and fish. For quantification, we relied on NISP data. Although important at some sites, tortoise remains were excluded as raw data were not available for all sites.

Taphonomy

Taphonomy is particularly important when interpreting bird bone assemblages, which might have been accumulated by agents other than human fowling. This is particularly true for small passerines, since their remains may well come from decomposed pellets of raptors deposited in (abandoned) buildings, for example. We therefore examined the bone surfaces for traces of digestion, gnawing and butchering. The presence of small bones and in general bones of small species such as passerines also depends on the recovery methods (handpicking, sieving, flotation), which are noted in Table 1. Although we documented skeletal element representation for each taxon, we decided not to elaborate in much detail on the results here, simply because we noted that the methods used for comparing skeletal distributions definitely need a critical re-appraisal that would go far beyond the scope of this study and will therefore be published separately. Nonetheless, we will refer to the results of our taphonomic analysis of the respective assemblages in case necessary.

Results

Göbekli Tepe

Taphonomy Traces of animal gnawing from rodents and small carnivores are very rare (< 1%). Cut marks are present but rare as well. They are mainly associated with the manufacturing of bone tools and/or instruments (cutting off

articulations from wing bones), while traces of butchering number very few. No traces of digestion typical for bones from pellets could be identified. PPNA assemblages were sieved using mesh sizes of 10 mm and 2 mm, resulting in a large number of bones of small passerine birds.

Overall taxonomic composition At GT, a surprisingly rich avifauna comprising at least 84 taxa can be evidenced (Table 1 and Table SI 1). Considering the grand total, corvids (38.5%) represent the numerically most important group. Among these, larger species including the rook (*Corvus frugilegus*) and the hooded crow (*C. cornix*) predominate, which we merged into a single category because in fragmented specimens identification to the species level was often impossible. Jackdaws (*C. monedula*) rank second, while the remaining corvid species only occurred in much smaller numbers. Due to its appearance and its crow-like chorus, we also placed the European roller (*Coracias garrulus*) into this group.

With 29.2% of the total assemblage, the small-sized birds form the second largest group. It encompasses passerine birds the size of sparrows to thrushes as well as a single small wader species, the greater sand plover (*Charadrius leschenaultii*). The most abundant taxon in this group is the starling (*Sturnus vulgaris*); buntings (Emberizidae) rank second, followed by larks (Alaudidae), thrushes (Turdidae) and finches (Fringillidae).

‘Classic’ gamebirds (16.0%) rank third. Chukar partridges (*Alectoris chukar*), great bustards (*Otis tarda*) and two species of sandgrouses (*Pterocles alchata*, *P. orientalis*) are the most numerous in descending order of importance. Few bone specimens each come from different species of doves (*Columba livia*, *C. palumbus*, *C. oenas*, *Streptopelia turtur*) and lapwings (*Vanellus spinosus*, *V. vanellus*) as well as the corncrake (*Crex crex*), the quail (*Coturnix coturnix*), MacQueen’s bustard (*Chlamydotis macqueenii*) and two cuckoos, the great spotted (*Clamator glandarius*) and the common cuckoo (*Cuculus canorus*).

The remaining bird groups include raptors (7.3%), aquatic birds (4.8%) and large waders (4.1%); they are all of less numerical importance. Despite contributing little in terms of absolute numbers, the raptor category is surprisingly diverse comprising at least 21 species of diurnal and nocturnal birds

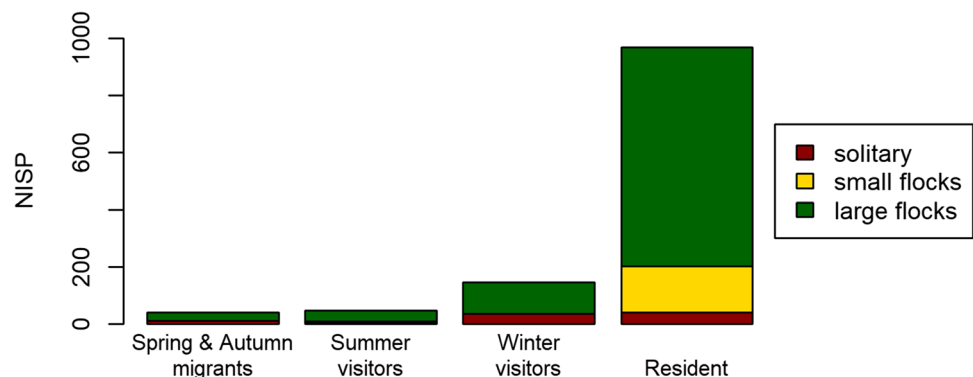
of prey. Buzzards (*Buteo buteo*, *B. rufinus*) are most prominent in this assemblage, followed by vultures (*Aegypius monachus*, *Gyps fulvus*, *Neophron percnopterus*), with the griffon vulture (*Gyps fulvus*) predominating. We also identified three eagle species, i.e. Bonelli’s eagle (*Aquila fasciata*), eastern imperial eagle (*A. heliaca*) and booted eagle (*Hieraetus pennatus*) as well as two species each of hawks (*Accipiter gentilis*, *A. nisus*) and harriers (*Circus cyaneus*, *C. pygargus*). To these, we can add the black kite (*Milvus migrans*), several species of falcons (*Falco cherrug*, *F. peregrinus*, *F. tinnunculus* and a small falcon *F. columbarius* or *F. naumanni*) and three species of owls (*Bubo bubo*, *Asio otus*, *Strix aluco*).

In the group termed ‘large waders’ in this study, remains of cranes predominate and represent either the common crane (*Grus grus*) or demoiselle crane (*Anthropoides virgo*). Other taxa pertaining to this group are the white stork (*Ciconia ciconia*) and two species of heron, i.e. grey heron (*Ardea cinerea*) and black-crowned night heron (*Nycticorax nycticorax*).

Dabbling ducks prevail in the ‘aquatic birds’ category, with the mallard, *Anas platyrhynchos*, being most frequently targeted. Diving ducks (*Aythya fuligula*, *Netta rufina*), shelducks (*Tadorna tadorna*, *T. ferruginea*), geese (*Anser albifrons*, *A. anser*) and the Eurasian coot (*Fulica atra*) have been identified as well, but in significantly smaller numbers.

Contextual taxonomic composition In the three distinct archaeological units described above, avifaunal composition varies considerably (Table 1, Table SI 1). As explained above, these numbers are largely influenced by the techniques of recovery applied and the fact that we are partly dealing with avifaunas from relocated middens, the so-called mixed units. Obviously, destruction or even loss of the more fragile bones of smaller taxa during relocation and bone recovery through handpicking likely reduced their abundance significantly. Expectedly, the vast majority of bones of small passerine birds was retrieved using sieving. Conversely, in the handpicked mixed units, passerines were mainly represented by larger-sized taxa, such as thrushes and starlings. We also noted that bones of vultures were restricted to such mixed units, with not a single specimen being found in the three PPNA contexts. In one of these,

Fig. 4 Göbekli Tepe. Bar plot illustrating the sociability and seasonality of its avifauna. Data see Tables SI 1 and SI 2



notably, the domestic unit (K10-13/23), gamebirds (37.8%) predominate. Sub-unit L9-78 with its ashy deposits shows a heavy preponderance of small birds amounting to 41.5%, followed by corvids (29.4%). Half of the avian assemblage collected in sub-unit L9-97 and in the mixed units were corvids (49.5% and 52.0% respectively), followed by small passerine birds (35.7% and 21.2% respectively). Despite immanent recovery bias, the preponderance of corvids and small passerine birds underlines the importance of both avian categories even in mixed units.

Seasonality With respect to seasonal exploitation, our results indicate that the inhabitants of Göbekli Tepe mainly targeted resident birds (80.6%), first and foremost chukar partridges, great bustards, crows, jackdaws and starlings (Table 1, Table SI 2; Fig. 4). The griffon vulture seems the most pursued resident raptor species. Winter visitors form the second largest category of birds persecuted by humans (12.1%). Most numerous herein are ducks, geese and the common crane. Many raptor species, such as the Northern goshawk (*Accipiter gentilis*), the European sparrowhawk (*Accipiter nisus*), the peregrine falcon (*Falco peregrinus*) and the hen harrier (*Circus cyaneus*), visit Southeast Anatolia in winter as well, as do passerine birds like the songthrush (*Turdus philomelos*), the fieldfare (*T. pilaris*), the ring ouzel (*T. torquatus*) and the two chough species (*Pyrrhocorax pyrrhocorax*, *P. graculus*). Birds crossing the southern Anti-Taurus piedmont on migration, such as the white stork and the demoiselle crane, are quite abundant too. Typical summer visitors number few. They include taxa such as the black-headed bunting (*Emberiza melanocephala*) and played a very minor role in the site's economy.

Regardless of their availability during the year, fowling activities seem to have been particularly successful when dealing with gregarious taxa, such as crows and jackdaws, or those that aggregate in flocks in the post-breeding season, such as starlings, black-headed buntings, calandra larks (*Melanocorypha calandra*) and chukar partridges. Since birds living in flocks promise a higher yield per catch effort,

it can be reasonably assumed that the site inhabitants intensified fowling once birds aggregated. To sum up, in view of the relative abundance of resident birds, fowling may have been a year-round activity, but exploitation of birds was likely intensified in early autumn and winter, when the catching of flock birds was particularly efficient and therefore profitable.

Bird habitats The habitats illustrated by the avifauna fit the landscape features and archaeobotanical record from GT (Table 2; Table SI 2; Neef 2003). The analysis of the plant remains illustrated that the vegetation covering the rocky calcareous hills of the Germuş mountain range in early Holocene times comprised grasslands interspersed with shrubs and areas wooded with almonds and pistachio trees. This clearly contrasts with the present-day vegetation cover characterized by the almost complete absence of natural tree vegetation. More than 80% of the birds identified at GT prefer these habitats. Moreover, some 10 to 20 km south and southeast of GT in the wider source area of the Balikh River in the Harran plain, wetlands and gallery forests bordering the watercourses constituted the biotope where riverine woodland-adapted species (3.5%), waterfowl and the large waders (totalling 11.4%) could be encountered in numbers.

The Anti-Taurus piedmont north of GT as well as the Karacadağ range located further east offered suitable mountainous habitat for the large vultures and the chough species. The hunters did not have to track them down in their nesting and breeding habitats in steep rocky terrain, as these scavenging taxa may well have been attracted by the waste from hunting activities and outdoor carcass processing at GT. In addition, when food becomes scarce at higher altitudes, choughs will frequent lowlands during wintertime. That said, their scarcity in the faunal assemblage (1.9%) suggests that suitable breeding and nesting habitats were located at some distance of GT.

Gusir Höyük

Taphonomic traces on bird bones are even fewer than at GT, with only a single bone specimen exhibiting cut marks. There are also no indications of animal gnawing or the digestion of bird bones by predators. The presence of smaller skeletal elements in the assemblage, like the anterior phalanges of partridges or the vertebrae of small fishes (not reported here), render confident that sieving with a mesh size of 5 mm was effective for bird bone recovery.

Compared to GT, avifaunal composition at contemporaneous Gusir Höyük (GH) could not be more different (Table 1, Table SI 1). The species spectrum is not only extremely poor, but also very lopsided in terms of numbers. Gamebirds account for 99.1% of the assemblage and consist

Table 2 Göbekli Tepe and Gusir Höyük. Habitats reflected in the avifaunal record. For habitat data see Table S2

	Göbekli Tepe		Gusir Höyük	
	NISP	%NISP	NISP	%NISP
Mountains	26	2.2		
Rocky hills	151	12.5	215	94.7
Wooded steppe	699	57.9		
Woodland	42	3.5		
Grassland	151	12.5	10	4.4
Wetlands	138	11.4	2	0.9
Total	1207		227	

of two species, namely the chukar partridge (*Alectoris chukar*) and the grey partridge (*Perdix perdix*). Differences in absolute bone size allow classifying the majority of complete bones as chukar and only few specimens as grey partridge. Most of the damaged specimens had to be classified as *Alectoris/Perdix*, though.

Besides this very dominant group, single bone specimens could be assigned to the common crane (*Grus grus*), the white-tailed eagle (*Haliaeetus albicilla*), the eagle owl (*Bubo bubo*) and the common raven (*Corvus corax*). Regarding seasonality of fowling, chukar and grey partridges are resident birds and can therefore be caught year-round. However, as they gather in larger flocks in late summer after breeding (Alkon 2015), autumn and winter may have been ideal for fowling. As no other gregarious winter visitors were detected at GH apart from the crane, however, confirmation that bird hunting took place mainly in winter is still pending. The other three species are resident birds that rarely, if ever, flock together; they thus add little colour to the seasonal picture of bird exploitation.

Since the two partridge species inhabit grassland habitats, we conclude that the GH site inhabitants hardly exerted efforts to pursue birds in other ecological settings (Table 2; Table SI 2), despite the fact that extensive wetlands and gallery forest habitat along the Tigris and Botan Rivers must have covered major areas within the site catchment. In this respect, the peculiarity of the avian record has a parallel in the archaeobotanical inventory, which illustrates a focus on the exploitation of dry grassland species and an evident lack of interest in riparian plant taxa (Kabukcu et al. 2021). While the lack of avian taxa populating wetland and gallery forest habitat illustrates that bird hunters did not claim these riparian zones, human exploitation of aquatic resources is nonetheless evident from the remains of fish and edible clams in the faunal assemblage. Besides an indeterminate species of catfish, we identified two barbel species that can reach considerable sizes, i.e. mangar (*Luciobarbus esocinus*) and shabout (*Arabibarbus grypus*), besides numerous shells of *Unio* mussels. With sizes surpassing 100 cm, some mangar individuals would imply adequate fishing technology for accessing such individuals in the main riverbed, where they prefer to stay. Having said that, with only 126 specimens out of more than 17,000 animal remains analysed so far, fish obviously did not play a major role in the human diet, and fishing was probably an opportunistic rather than a qualified activity.

Discussion

Taxonomic composition, diversity, seasonality and habitat exploitation

While GT and GH seem to be in agreement regarding the seasonality of fowling, they disagree in all other aspects. As

such, the inhabitants of GT obviously targeted almost the entire range of native and migratory avifauna, whereas the GH community essentially focussed on two, closely related taxa. The Göbekli Tepe inhabitants exploited all major habitat types within the site's catchment and even visited the waterbodies in the Harran plain to access aquatic birds. Conversely, although the GH inhabitants definitely exploited riverine resources including fishes and clams, bird taxa populating the adjacent wetland and riverine habitats are virtually absent. Instead, fowling was restricted to two phasianid species, the grey and the chukar partridge, accessible year-round in the extensive dry grasslands and vegetated rocky hills characterizing the immediate environs of the site. Since these partridge species aggregate into flocks in late summer, hunting efficiency likely increased in the second half of the year. As such, the observed discrepancy in taxonomic richness between Göbekli Tepe and Gusir Höyük seems not rooted in a permanent (GT) versus a seasonal occupation (GH). Rather, fowling at GH may have been a spatially and/or temporary restricted activity, targeting those species that promised maximum hunting success with minimum effort. In contrast, fishing may have taken place year-round based on the presence of barbels of all size classes, but probably intensified in spring as suggested by the considerable number of bones of large individuals. Larger fish such as the mangar are much easier to catch when adult individuals leave the main Tigris channel in April and May to spawn in more shallow waters (Ali and Tomas 2009; Özgür et al. 2016).

Broadening our perspective by considering other avifaunal studies from PPN Upper Mesopotamia, indicators of seasonal fowling turn out rather uniform: the significant contribution of winter visitors and the preference for species aggregating in flocks after breeding indicate that fowling was generally intensified in autumn and winter (Table 1). Such human behaviour, in which fowling gained importance in wintertime, seems already common in the wider region since the Epipalaeolithic, as illustrated by findings from the southern Levant, e.g. at Ohalo II (Steiner et al. 2022), Wadi Jilat 22 (Martin et al. 2013), Shubayqa 1 (Yeomans and Richter 2018) and in the subsequent PPNA, for instance at Netiv Hagdud (Tchernov 1994) and Gilgal I (Horwitz et al. 2010).

PPN sites in Upper Mesopotamia also show clear parallels in the way birds were exploited. Obviously, habitats where sizeable flocks could be expected were the preferred hunting grounds. Correspondingly, early Neolithic communities settling on the riverbanks of larger permanent waterbodies, such as Tell Mureybet, Jerf el-Ahmar and Körtek Tepe, mainly exploited gregarious ducks, geese and waders adapted to riverine habitats in numbers during winter (Gourichon 2004; Emra et al. 2022). Expectedly, the inhabitants of sites situated away from major waterbodies, such as GT, GH

and Qermez Dere, mainly targeted terrestrial taxa populating the predominant vegetation types in the respective ecological settings, e.g. dry grasslands and wooded steppes. As mentioned before, consumption of aquatic birds at GT indicates that fowling also occurred at some distance of this hilltop site, for instance in downhill wetland habitat along the Culpay Suyu river and its tributaries and/or near the Urfa-Harran springs (Nykamp et al. 2020). At Hallan Çemi, both the archaeobotanical and avian records indicate that grasslands and wooded steppe habitats shaped the Early Neolithic site catchment (Zeder and Spitzer 2016). At that time, however, the Sason river, a tributary of the Batman river originating in the high Anti-Taurus, likely carried sufficient water to feed and maintain (seasonally) extensive wetland biotopes, thus explaining the relative abundance of waterfowl and waders in that particular assemblage. A parallel situation has been noted at Körtik Tepe, where the onset of the Holocene climatic optimum caused the establishment of more extensive water areas and alluvial floodplains increasingly frequented by waterfowl, most prominently geese (Emra et al. 2022).

The abundance of small passerine birds at Göbekli Tepe is singular considering their extreme rareness at contemporaneous archaeological sites (Table 1). Taphonomic reasons are rather unlikely responsible for the absence of small passerines from the other sites since dry- or wet-sieving or even flotation was practised at all sites for at least a representative amount of sediment. At some sites, mesh sizes were even smaller than at GT. The near absence of small passerines from contemporaneous avifaunal records strongly suggests that this category of birds was not targeted as intensely by the respective communities as has been the case at GT.

While most of the aforementioned Neolithic sites are characterized by marked avifaunal diversity indicative of fowling in varied ecological settings, two sites definitely buck the trend. One is GH with its strong focus on

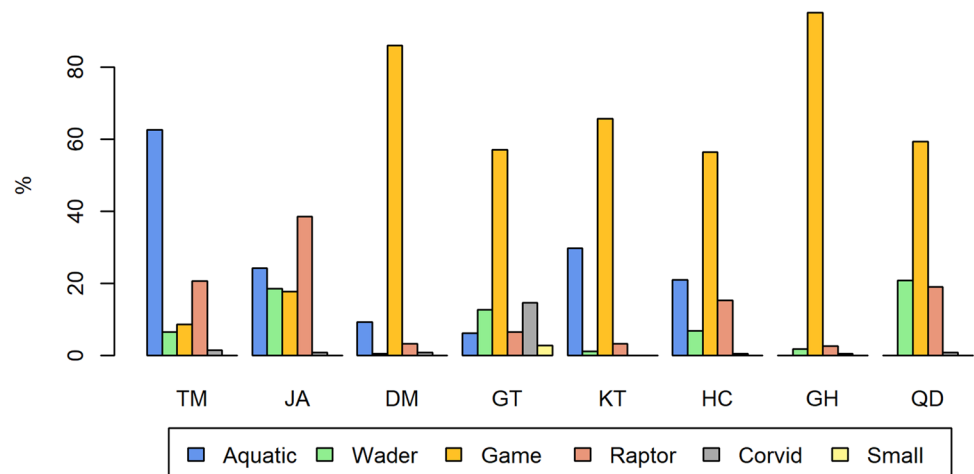
partridges. Similar to GH, a single taxon, more precisely the sandgrouse family (Pteroclididae), largely predominates the Qermez Dere avifauna. Although some sandgrouse species are reported migrating in northern Iraq, the pin-tailed sandgrouse (*Pterocles alchata*), the most abundant species at QD, is a resident bird in the area (Del Hoyo et al. 1997). Interestingly, flocks of sandgrouse daily visit watering places to drink, a predictable behaviour making them vulnerable to targeted bird hunting, especially during the dry season.

Finally, turning to taxonomic diversity (aD) of the avifaunas, the values for GT are the highest, which can be explained by the taxonomically rich assemblage of passerine birds (Table 1). Expectedly, the lowest value was calculated for the extremely skewed and species-poor avifauna of GH. Taken together, the available data illustrate a clear divide, with the lowest values being calculated for sites in the Tigris basin and the higher ones for sites in the Euphrates basin — with HÇ being a notable exception, since exhibiting a high aD value as well, actually the second highest after the GT assemblages.

Birds as food

Despite the fact that some bird taxa may have been caught essentially for reasons other than food supply, such as feathers, skins and bone tool production or for decorative, symbolic or ritual purposes, we nevertheless assume that all taxa contributed to the human diet in some way. Different options also become apparent in the varied skeletal element distribution patterns, where certain elements seem to be over-represented, for example wing bones in cranes and talon bones in raptors, or heavily underrepresented, such as foot bones in passerines. However, since the vast majority of the contextually assignable bones have been found associated with domestic structures, we suspect that the meat of most birds was also consumed, probably even that of the raptors.

Fig. 5 Contribution of the five avian groups defined by us to the bird meat diet, based on the average live weight per species. Data see Tables 1, SI 1 and SI 2



While most modern societies would not regard raptors' meat suitable for human consumption, this may well have been different in prehistoric societies.

The surprising abundance of passerine birds at GT raises questions if their accumulation is caused by agents other than human beings, such as mammalian or avian predators benefitting from abandoned buildings. Our observations contradict such interpretation, though, since traces of digestion usually found on bones from pellets (Laroulandie 2002) or beak or gnawing marks were not observed on any of the specimens. The underrepresentation or even complete absence of small passerine birds at all sites except GT is certainly not due to methods of recovery, since at all sites sieving or even flotation was performed, at least for representative samples (Table 1). If passerines had been pursued and consumed with the same intensity, their bones would certainly have been recovered.

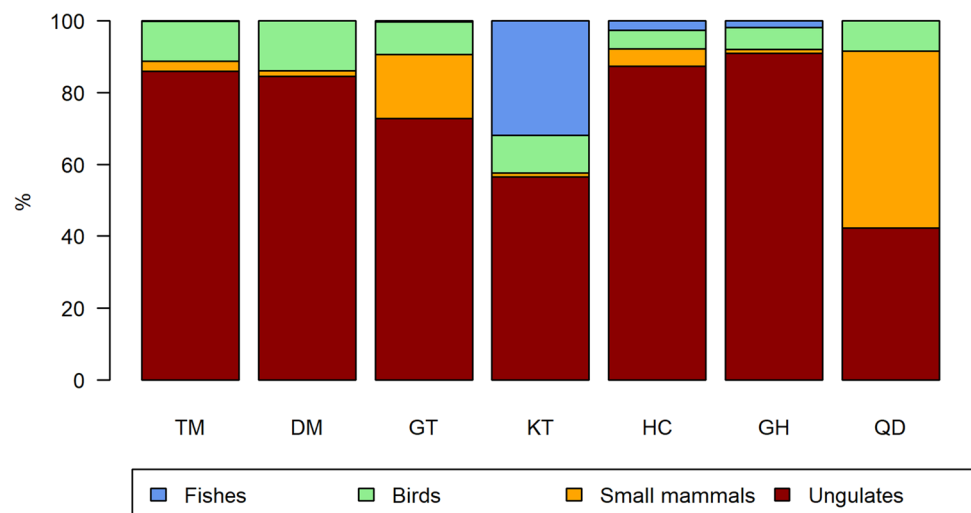
Taking into account bird size and hence live weight (Table SI 2), it becomes clear that NISP counts do not necessarily reflect a taxon's contribution to the human diet. By evaluating the relative importance of taxa based on live weight, a shift in relative proportions becomes visible, though rankings stay more or less the same, with few exceptions (Table 1; Fig. 5). The most striking difference is found in the PPNA assemblages at GT, where the importance of small passerine birds drops dramatically from 37.2% (NISP counts) to 2.8% (average live weight). Another change occurs at JA: Assuming that the meat of raptors was eaten, they move from fourth (NISP counts) to first rank (average live weight), relegating aquatic birds from first to second place. Of course, if we exclude raptors, aquatic taxa remain the prime source of bird meat. Overall, terrestrial game birds were by far the most important source of meat across the study area (Fig. 5). This can be explained on the one hand by the heavy weight of the great bustard, a key food taxon found in numbers at DM, GT and HÇ, and the almost exclusive

reliance on partridges at GH and sandgrouses at QD. The only exception to this is the Euphrates river bank sites of TM and JA, where aquatic birds (and raptors) dominate.

If we compare the meat yield of the heaviest bird, the great bustard weighing *c.* 10 kg, with the live weight of a single aurochs (between *c.* 700 and 1000 kg depending on the sex of the animal), birds only contributed marginally to the human diet. So even at those sites where bird frequencies surpassed 10% of the total identified vertebrate assemblage, fowling appears not very essential in the meat supply of early Neolithic foragers inhabiting the northern Fertile Crescent. The expenditure of time for fowling, however, must have been significant, which raises the question how fowling was organised. Because of the overall low meat yield, ethnographic evidence suggests that consumption of wild birds happened at the level of the individual household (e.g. Peters et al. 2009). Arguably, hunting and consumption of birds would have been organised differently compared to that of medium-sized to larger mammals (from gazelles to aurochs). Particularly the latter involved larger groups of hunters or even most of the community (Pöllath et al. 2018), while fowling was probably undertaken by single (young) individuals, as noted in recent hunter-gatherers (Peters et al. 2009). Meat consumption of collectively hunted larger game species was also a communal activity, while smaller prey such as birds was prepared individually.

The rich taxonomic spectra identified in SW Asian Neolithic contexts also imply multiple techniques for catching birds. Historic and ethnographic studies list varied techniques that can be grouped into five main categories based on the methods: (1) snares and traps, (2) nets, (3) falconry, (4) missiles (e.g. arrows, throwing sticks, slingshots) and (5) lime applied to twigs or strings (Macpherson 1897; Shrubbs 2013). Their exertion, however, is difficult to prove in the archaeofaunal record — probably with the exception of lime twigs (or strings) for smaller birds: we observed that the

Fig. 6 Importance of birds compared to other animal categories during the Early Neolithic in Upper Mesopotamia. Data see Table 1



bones of the feet (tarsometatarsals and phalanges) are heavily underrepresented in passerine birds at GT. A most likely explanation, therefore, is that they were caught using lime twigs and that the glued feet were separated from the legs when ‘harvesting’ the birds from the twigs. Catching small- and medium-sized birds with snares, traps, slingshots and lime twigs was probably an occupation mainly of children and young adolescents, as suggested by historic and ethnographic sources (Macpherson 1897; Peters et al. 2009). For species gathering in flocks, such as ducks, partridges and many passerine birds, the use of nets would be the most economical way to catch large numbers with minimum effort (Shrubb 2013). Bird hunting was probably essential for young people to apprehend and improve hunting skills in preparation for tracking, pursuing and killing larger game later in adulthood.

Birds are, however, only one of several animal groups exploited by PPN foragers (Table 1; Fig. 6). In the Fertile Crescent, the inclusion of small game taxa, more precisely small mammals, birds, fish and tortoises into the diet at the expense of ungulate game was noted before by Flannery (1969), who termed this phenomenon ‘Broad Spectrum Revolution’ (BSR). The emergence of this human behaviour in the Upper Palaeolithic has been explained by resource stress due to overhunting of high-return ungulates, forcing communities to incorporate low-return taxa in their diets as well (Stiner et al. 1999, 2000; Stutz et al. 2009). The review of Epipalaeolithic and PPN assemblages from the Southern Levant revealed that together with other indices, the small game index peaked in the Natufian and the PPNA periods, but began tapering off in the course of the PPNB (Munro et al. 2018). Developments in Upper Mesopotamia seem paralleling those reported from the Southern Levant given the significant proportions of small game animals in the Natufian and Khiamian assemblages at TM (Gourichon 2004) and Zarzian contexts at Palegawra cave (Asouti et al. 2020).

Zooming in on Upper Mesopotamia, subsistence strategies developed differently in the Euphrates and the Tigris basins: In the Euphrates basin, fish was a negligible source of protein already in the Epipalaeolithic, while the avifauna was substantial and diverse (Gourichon 2004). PPNA sites in the same region (TM, DM, GT) exhibit a rather uniform pattern with small variations largely owing to the environmental conditions characterizing the site catchment (Fig. 6): Ungulates are more important at TM and DM, conceivably because they were easier to hunt when frequenting the river banks to water. Further away from permanent waters, GT hunters had to target more small mammals to meet their demand for meat. The other small game taxa, birds and fishes, were taken in similar quantities at all three sites. Being located away from perennial water courses, the scarcity of fish remains at GT

is not surprising. The small number of fish bones at sites located on river banks, however, is indeed noteworthy. The inhabitants of TM and DM intensively exploited aquatic birds but ignored fish as a food resource suggesting that they deliberately avoided it.

Turning to the eastern part of Upper Mesopotamia, the situation seems to be more complex already in the Epipalaeolithic. Tortoise was an important food resource at Zarzian Palegawra cave, while fishes and birds were of minor importance (Asouti et al. 2020). At KT, fishing and fowling contributed considerably to the human diet during the Epipalaeolithic, with tortoises being far less important (Emra et al. 2022). In the subsequent PPNA, hunting preferences appear even more multifaceted (Fig. 6): Ungulates are decidedly more important at HÇ and GH but less so at KT and QD. Fish was a relevant source of meat at KT, while it was negligible at the other sites. The absence of fish at QD can be explained by the site’s distance to larger waterbodies. HÇ and GH, however, are situated on riverbanks. Obviously, their inhabitants largely disregarded fish, although not to the extent the inhabitants of TM and DM did. Interestingly, the archaeofaunas at GH and TM show contrasting patterns regarding the exploitation of aquatic birds and fish. At QD, hunters compensated the rather low proportion of ungulates by an increased number of small mammals. Despite the aforementioned differences between these eastern sites, the proportions of birds seem rather similar. As demonstrated above, however, differences become apparent in the taxonomic composition of the avifaunal assemblages.

Altogether, PPNA sites in the Upper Euphrates basin appear rather uniform regarding their subsistence strategies in general and also regarding fowling. This is in contrast with sites in the Upper Tigris basin, which differ from the aforementioned as well as among themselves in almost every aspect of hunting and fowling. The Upper Tigris sites clearly exhibit a cultural independence and distinctiveness from the sites in the Upper Euphrates basin, which is also mirrored in their architecture and material culture (Goring-Morris and Belfer-Cohen 2016).

With the onset of farming, fowling obviously became increasingly unattractive for human food supply. This can be deduced from the faunal remains from Nevali Çori, an early and middle PPNB site on the Euphrates located c. 50 km north of Göbekli Tepe (Fig. 1) (von den Driessch and Peters 2001). Based on NISP counts of bird and ungulate remains, only 1% of the bones can be attributed to birds. Obviously, the proportionately time-consuming hunting of birds had become unprofitable, in particular since adults had attended to the various new tasks in agriculture. If young people guarding the fields or herding livestock still had the time to pursue smaller birds, they possibly hunted and consumed them while away from the settlements.

Conclusions

The avifaunas from the sites of Göbekli Tepe and Gusir Höyük presented in this study complement and diversify at the same time the picture of bird exploitation during the PPN in the catchments of the Upper Euphrates and Tigris Rivers. While passerine birds unexpectedly dominate the Göbekli Tepe assemblage numerically, their low respective live weights rendered them nonetheless of limited value in overall meat supply. The Göbekli Tepe findings nevertheless illustrate systematic exploitation of varied kinds of habitat and seasonal fowling that fit well into the picture known from slightly earlier as well as contemporaneous sites in the wider region. Interestingly, the GT findings are in marked contrast to those from Gusir Höyük, characterized by an avian assemblage extremely poor in species, the vast majority of remains (> 99%) pertaining to partridges. When practicing fowling, people seemingly ignored major landscape-defining features, such as alluvial wetlands, gallery forests and water bodies, but instead focussed on very few taxa inhabiting the hilly to rocky grasslands characterizing the immediate surroundings of the site. A good opportunity was provided by the birds that came to drink at the small freshwater lake on whose shores Gusir Höyük lays. Like elsewhere in the early Neolithic northern Fertile Crescent, fowling at Gusir Höyük likely benefited from seasonal post-breeding aggregations of birds resulting in large flocks.

Overall, Upper Mesopotamian communities exploited avian resources for meat supply within their catchment area in broadly similar ways, focussing on the seasonally most abundant species in the corresponding habitats. Expectedly, aquatic birds and waders dominate in settlements characterized by extensive riverine habitat in their vicinity (e.g. Tell Mureybet, Jerf el-Ahmar). In sites located away from major waterbodies, species populating dry grasslands and steppe environments prevail (e.g. Göbekli Tepe, Qermez Dere). Besides, fowling by the GT inhabitants also occurred at a distance of the settlement. The avian record from Gusir Höyük is a notable exception to this. So far, it is the only early Neolithic community in Upper Mesopotamia that deliberately neglected wetland and riverine habitat when fowling, despite immediate access to such habitat nearby and the rich avifaunal potential of riparian landscapes. All in all, bird hunting does not seem to have been conducted to fill major gaps in the supply of animal protein, since it was most intensely practised in autumn and wintertime, when plenty of other plant and animal resources were available (e.g. gazelles: Lang et al. 2013; aurochs: Pöllath et al. 2018; plants: Dietrich et al. 2019).

Although the PPN avifaunal dataset is still patchy, our findings nonetheless suggest a possible geo-cultural divide

in the modes of bird exploitation between the western and eastern parts of Upper Mesopotamia. Birds' meat was a small but not negligible resource for foraging communities in the Upper Euphrates River basin, while in the Upper Tigris River basin, its importance varied from very minor to insignificant. Correspondingly, archaeobiodiversity in avifaunal assemblages is significantly higher in western compared to eastern sites, with the notable exception of Hallan Çemi. Interestingly, western and eastern sites also differ in the relative importance of other animal groups, with the western sites exhibiting a rather uniform pattern while the eastern sites differ from the western but also among themselves. This apparent East–West divide corresponds to the cultural provinces of the “Middle Euphrates PPN” and the “Roundhouse Horizon”, as defined by Goring-Morris and Belfer-Cohen (2016).

Finally, the presence and abundance of bird taxa known for their symbolic value, such as cranes and raptors, strongly suggest that in Neolithic Southwest Asia, birds not only stood on the menu, but that certain taxa also provided objects for ritual and ornamental purposes (e.g., Russell and McGowan 2003). As stated earlier, addressing the socio-cultural aspects of early Neolithic human behaviour is beyond the scope of this paper and will be discussed in a forthcoming study.

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Code availability Not applicable.

Declarations

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Consent to participate Not applicable.

Consent for publication Not applicable.

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