



Seasonality, duration of the hominin occupations and hunting grounds at Middle Pleistocene Qesem Cave (Israel)

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Abstract

The behaviour and mobility of hominins are dependent on the availability of biotic and abiotic resources, which, in temperate ecosystems, are strongly related to seasonality. The objective of this study is to establish evidence of seasonality and duration of occupation(s) of specific archaeological contexts at late Lower Palaeolithic Qesem Cave based on the study of ungulate teeth. Combining individual ageing using dental eruption and replacement with variability measurement of tooth microwear, we estimated the seasonality of occupations at different levels of the site and their relative duration. Information about the diet of the ungulates and the habitats where they were hunted was also derived from tooth mesowear and microwear analyses. In the different tooth assemblages analysed, where the fallow deer was the most abundant herbivorous species, animals were selectively hunted in specific habitats. For example, the fallow deer individuals brought back to the Hearth area had a different diet than those found in other parts of the cave. The Hearth area seems to have been used seasonally, probably during short-term events and more than once a year. The other areas of the cave show different seasons of game procurement and different patterns of occupation of the site, possibly more than once a year or, alternatively, for a longer period. The data suggest that Qesem Cave was inhabited by human groups for a long period, perhaps not continuously, and their knowledge of the environment surrounding the cave allowed them to allocate specific game, most probably from distinct hunting grounds, to designated activity areas at the cave. We hypothesise that the difference in feeding locations might have been related to specific needs of the cave inhabitants (food, hide and marrow extraction), and thus, animals from different hunting grounds were wisely used to maximise the potential of specific habitats in the environment. This study is an additional testimony to the ingenuity of the cave inhabitants that allowed them to persistently use the cave for a prolonged period in a year.

Keywords Qesem Cave · Middle Pleistocene · Tooth microwear · Tooth mesowear · Seasonality · Ageing · Ungulates · Dietary traits

Introduction

Hominin behaviour and mobility, including settlement system dynamics, are strongly related to the availability of biotic and abiotic resources (Kelly, 1995, 2013). The

availability of the biotic resources, both vegetal and animal, is dependent on the phenology of each species, i.e. related to the seasonal and interannual events that occur in the biological life cycles. The plants and animal's phenology are controlled by climate, mainly by temperature, and also by parameters of the habitat (e.g. altitude and orientation). Depending on the availability of resources, Palaeolithic populations adapted their behavioural strategies related to food management to the local conditions (Binford, 1980). Based on the archaeological record, different types of sites were identified — long-term residential camps, short-term regular hunting camps, brief stopover camps — depending, among other things, on the duration of the settlement and the type of activities that were performed. Among these, residential base camps were occupied for a relatively long period and exhibited evidence of various activities performed. Such

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types of sites can be identified through multidisciplinary studies, as is the case for Qesem Cave. While it is assumed the cave served as a residential base camp (Barkai et al., 2017a, 2017b; Blasco et al., 2016a), it is unknown as to what extent and also what period of the year it was used.

The objective of this study is to establish evidence of seasonality and duration of occupation(s) of specific archaeological contexts at Qesem Cave and to infer related human preferences and behaviours. For this purpose, we used tooth micro- and mesowear analyses combined with dental eruption and replacement on ungulates.

Mesowear analysis is a method of categorising the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the relative amounts of attritive and abrasive dental wear (Fortelius and Solounias, 2000; Ackermans, 2020). A diet with low levels of abrasion (high attrition) maintains sharpened apices on the cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, result in more rounded and blunted cusp apices. Mesowear represents a long-term dietary signal averaging diet over several years (Ackermans et al., 2020).

Microwear analysis is a technique that allows to reconstruct the diet of individuals and populations based on the microscopic features recorded on the enamel. Several methods were developed in the past decades using different types of microscopes, such as the SEM (Rensberger, 1978; Walker et al., 1978), the stereomicroscope (Solounias and Semprebon, 2002; Semprebon et al., 2004) or the confocal microscope (Scott et al., 2005). Microwear is known to have a high turnover that reflects a short-term dietary signal (Grine, 1986) but the actual duration indicated by microwear in ungulates is still under investigation (Ackermans et al. 2021).

Dental eruption and replacement in ungulates allow for the estimation of the age at death of the young individuals by using known patterns in extant relatives (e.g. Klein et al., 1981; Reitz and Wing, 2008; Bowen et al., 2016). Knowing the annual reproductive cycles (and timing of birth) of ungulates leads us to establish schedules that are used as a guide for determining the seasonality in archaeological sites. For the youngest individuals, before 5 months, the method can provide ages with an accuracy of 2 months (e.g. Brown and Chapman, 1991a; Bowen et al., 2016).

From a methodological perspective, the advantage of combining tooth micro- and mesowear analyses with dental eruption and replacement is that it considers the entire population of ungulates, i.e. the young individuals studied through dental eruption and the adults and young adults analysed via tooth microwear and mesowear (for a discussion on the advantages, see Rivals et al., 2020). Additionally, the combination of tooth micro- and mesowear and two proxies reflecting diet on different time scales allows for a better

estimation of seasonality in archaeological sites (Rivals et al., 2009a; Sánchez-Hernández et al., 2016). Finally, due to its high turnover rates (Grine, 1986), tooth microwear indicates the ungulates' diet and the vegetal characteristics of their environment at the time of death. The variability of the microwear pattern is known to be correlated to the duration of accumulation of an assemblage (Rivals et al., 2009a; 2015a). All three non-destructive methods may provide a reliable estimation of the seasonality at Qesem Cave.

Qesem Cave

Qesem Cave is located 90 m above present-day sea level in the western foothills of the Samaria Hills, about 12 km east of Tel Aviv, Israel. Anthropogenic sediments are > 11 m deep, while bedrock had not been reached yet. The stratigraphic sequence is subdivided into two parts: the upper part comprises 4.5 m of mostly cemented sediment formed by calcite precipitated from dripping waters with a large ash component and the lower part comprises a > 6.5 m accumulation of sediments with clastic content and gravel, indicating a more closed karst environment (Karkanias et al., 2007). The speleothems from the cave were dated by U–Th to be from about 420 to 200 ka (Barkai et al., 2003; Gopher et al., 2010) and a similar date range was obtained by thermoluminescence (TL) and electron spin resonance (ESR), as well as by new ESR/U-series (Mercier et al., 2013; Falguères et al., 2016).

All strata are assigned to the Acheuleo-Yabrudian Cultural Complex (AYCC) of the late Lower Palaeolithic Levant. Although the predominant lithic industry is the Amudian blade-dominated industry, the scraper-dominated Yabrudian industry is also detected in three stratigraphically and spatially distinct areas of the site (Barkai et al., 2009; Parush et al., 2015). Hand axes are rare in the sequence, and only a few were retrieved within Amudian and Yabrudian contexts (Barkai et al., 2013; Agam et al., 2020). Lithic recycling is a recurrent phenomenon in the cave and is present in all the archaeological contexts. An important sample of recycled items shows wear and residue from meat cutting as well as from working vegetal material (Parush et al., 2015; Assaf et al., 2015; Lemorini et al., 2015; Venditti et al., 2019). Bone fragments were also occasionally recycled and used for shaping stone tools, and they show the typical morphological and functional features observed in similar or later periods (Blasco et al., 2013; Rosell et al., 2015).

The habitual use of fire is registered in the form of wood ash remnants, moderately heated soil lumps and large quantities of burnt flint and bone (Karkanias et al., 2007). The micromorphology and Fourier transform infrared (FTIR) microspectroscopy analyses indicated a combustion feature covering ~4 m², dated to ca. 300 ka and comprised two

superimposed use cycles, each comprised shorter episodes in the central part of the cave (Shahack-Gross et al., 2014). Burned material is also widely registered in the deepest sediments of the cave, indicating that the controlled use of fire has been used since the earliest occupation at Qesem.

The systematic excavations at the site have yielded, to date, a significant set of hominin permanent and deciduous teeth. According to Hershkovitz et al. (2016), the Qesem hominids show no affinities with *Homo erectus*; rather, they are more similar to later Middle Palaeolithic populations of this region, including Neanderthal affinities.

The large mammal record comprises exclusively Palaeo-arctic taxa with no African influences and is extremely rich along the stratigraphy. The sequence is mainly dominated by fallow deer (*Dama cf. mesopotamica*), supplemented by red deer (*Cervus cf. elaphus*), horses (*Equus ferus*), aurochs (*Bos primigenius*), wild ass (*Equus hydruntinus*) and wild boar (*Sus scrofa*). Small ungulates, such as goat (*Capra aegagrus*) and roe deer (cf. *Capreolus capreolus*), and small prey, such as birds and tortoises, are also present (Stiner et al., 2009, 2011; Blasco et al., 2014, 2016a, b, 2019a; Sánchez-Marco et al., 2016). The taphonomic studies on faunal specimens showed that assemblages were produced by the human groups occupying the cave and were primarily affected by their food-processing activities. The ungulate skeletal profile is biased towards the highest-nutritional value elements (mainly limb bones), indicating transport of selected body parts to the site (Stiner et al., 2009, 2011; Blasco et al., 2014, 2016a, 2019b). The ungulate mortality pattern is characterised by adult-aged individuals, although in the case of fallow deer, the incidence of infants and young individuals could be linked to cooperative hunting strategies or episodes of incipient multiple predation (Stiner et al., 2009, 2011; Blasco et al., 2014). Zooarchaeological analyses also provided evidence of complex behaviours, such as bone marrow storage and its delayed consumption (Blasco et al., 2019b) and the presumable use of feathers in the case of a swan specimen (Blasco et al., 2019a). Other bird taxa (*Columba* sp., *Corvus ruficollis* and *Sturnus* sp.) and small animals, such as tortoises, served as backup resources or supplements in the Qesem hominin diet (Blasco et al., 2016b, 2019a). Another main characteristic of the faunal record is the extremely rare presence of carnivores. The incidence of carnivore-induced damage does not exceed in any case 0.3% in all units (Barkai et al., 2017a for details).

All archaeological contexts investigated in this study originate from the lower part of the stratigraphic sequence of the cave and are thus 300 ka or earlier (Fig. 1A–E). Results are obtained from the contexts that underwent detailed faunal analysis, while the rest of the excavated assemblages still awaits analysis. Generally speaking, the analysed assemblages could be regarded as representing three distinct contexts in the cave: (1) a horizontally spread spatial-activity

area dated to ca. 300 ka (including the Hearth, the Shelf Yabrudian and the South East Yabrudian); (2) the stratigraphic sequence below the rock shelf (including the following contexts: large stones in brown sediments; soft/cemented sediments close to the cave wall; and dark brown sediments). All these contexts are earlier than 300 ka. Actually, the Shelf Yabrudian mentioned above is at the top of the stratigraphic sequence under the rock shelf and should be regarded in this diachronic perspective as well; and (3) the South Western Spheroid assemblage. The South Western Yabrudian assemblage mentioned above is stratigraphically positioned directly above the Spheroid assemblage. Our ongoing explorations at the cave indicate that in many cases, it appears that the different archaeological contexts of the cave represent distinct activity areas in which spatial and stratigraphical sets of tasks were performed, and thus, the designation of the different contexts is not only technical but also bears behavioural implications (mostly in the cases of the Hearth and Spheroid contexts and also regarding the differentiation between Amudian versus Yabrudian contexts. All contexts not specified as Yabrudian are Amudian.).

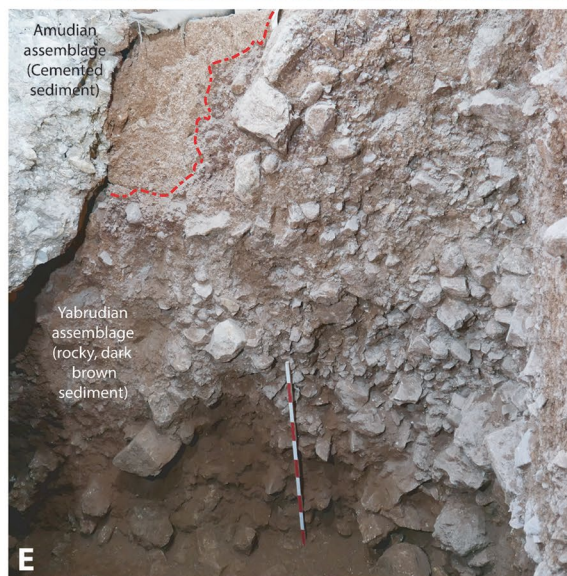
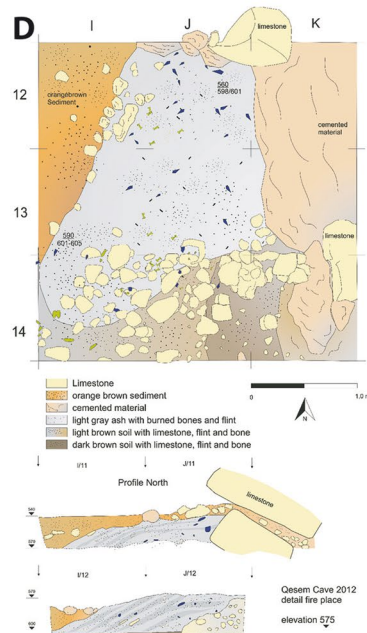
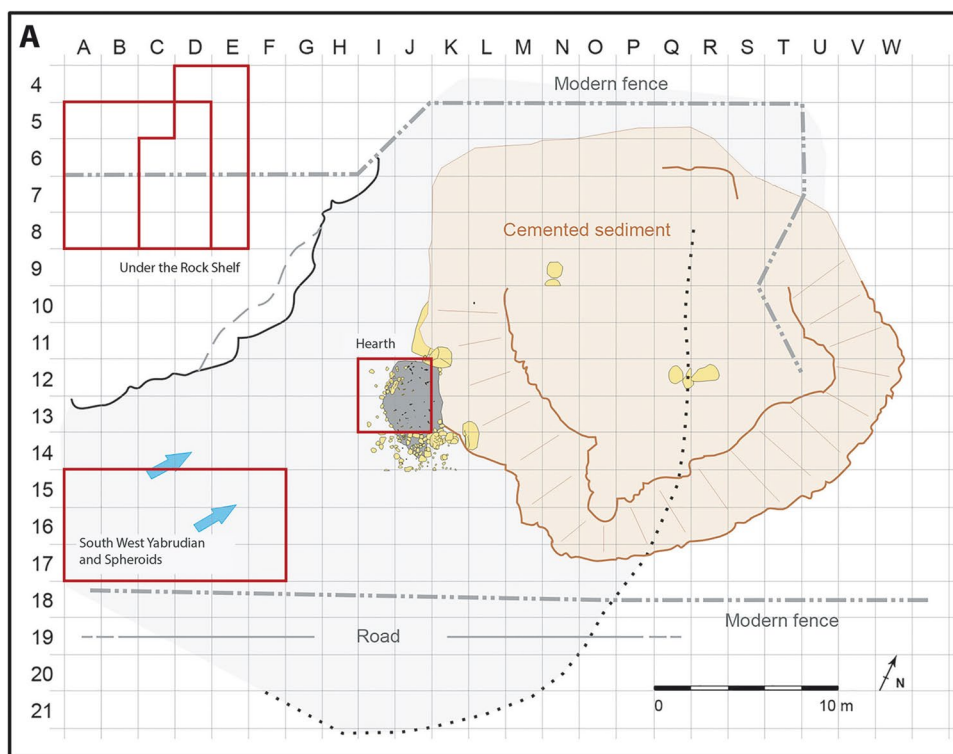
Below is a short description of the different archaeological contexts represented in this study:

- The Hearth: (squares I–J/12–13 of the cave's grid, Figs. 1B–D) comprises the central Hearth feature. Sediments are mostly grey in colour and spread over 4 m² at elevations 540 and 605 cm below datum. The feature is covered by a 10 cm layer of brown sediment, overlain by large boulders attributed to a roof collapse (Frumkin et al., 2009; Karkanas et al., 2007). The assemblage of the Hearth is assigned to the Amudian industry. It is dated to ca. 300 ka.

The Hearth feature comprises two superimposed use phases, identified based on mineralogical and microscopic criteria (Shahack-Gross et al., 2014). Each use phase comprised macroscopic and microscopic, shorter episodes of use. A vertical analysis conducted on the lithic assemblage allowed the division of the area to at least three levels (levels I–III). Level III represents sediments directly on top of the Hearth, which might be related to the final use of the Hearth. Level II explicitly aligns with the activity of the Hearth feature itself and was further divided into two sub-levels (IIa–b), each correlating with one of the two micro-archaeological use phases: sub-level IIa aligns with an early use phase of the Hearth and sub-level IIb with a late use phase. Level I represents the earliest excavated use cycle of the Hearth, while the lowermost phases of the Hearth were not yet fully excavated.

- Shelf Yabrudian: (squares C–E/4–8 of the cave's grid, elevation 520–700 below datum). A scraper-dominated assemblage found within brown-orange sediments. It was published and analysed thoroughly (Parush et al., 2015; Venditti et al., 2019). It is located under an inner karstic shelf. All 6.5 m of sediments under the shelf are older than

Fig. 1 **A** General plan of the cave showing the location of the studied archaeological contexts. **B** The Hearth in its archaeological contexts. The Hearth was excavated in half, and the unexcavated part is behind the stick. **C** Close-up at the unexcavated half of the Hearth. **D** Drawing of the Hearth at elevation 590 cm below datum. **E** Field relations between the SCW and DBS contexts under the rock shelf. The lowermost red line marks the division between the two contexts at elevation 1000 cm below datum. Part of the cave wall can be noticed at the left-hand side



300 ka, and the Shelf Yabrudian is below the rock shelf and thus is the youngest assemblage in this context.

- Large stone in brown sediment (LSBS): (squares E–F/9 of the cave’s grid, elevation 655–770 below datum). An Amudian assemblage recovered in soft sediments below massive stones. It is located underneath the Shelf Yabrudian context, and a swan bone with cut marks was recovered from this context (Blasco et al., 2019a, b).

- Soft/cemented sediments close to the wall (SCW): (squares A–D/6–7 of the cave’s grid, elevation 870–1050 below datum). An Amudian assemblage recovered within a combination of soft and cemented sediments nearby the northern and western walls of the cave in these elevations. Stratigraphically, this unit is found directly below the LSBS context. This unit comprises sediments inclined to the west and north with absolute top and bottom elevations that are parallel to the ones of the DBS context directly below it (Fig. 1E). The dividing line between the two contexts is rather clear, indicating that the DBS context is earlier than the SCW (Fig. 1E).

- Dark brown sediment (DBS): (squares C–E/6–8 of the cave’s grid, elevation 835–1050 below datum). This is part of the lowest layer excavated thus far at the cave that currently extended to elevation of 1200 below datum (and it continues to depths not yet excavated). It is designated as Yabrudian due to the ubiquitous presence of scrapers within the tool category; however, blades are common as well. Ongoing lithic analysis will elucidate these interesting aspects in the future, while unpublished ESR dates indicate that the lower excavated parts of this context are older than 400 ka (Falgüères et al., pers. comm. 06/2021). Moreover, this context is inclined, most probably due to post-depositional processes, and is clearly below, and thus earlier than the SCW context.

- South West Yabrudian: (squares A–D/15–17 of the cave’s grid, elevation 545–635 below datum). This excavation area is located in the south-western part of the cave and is adjacent to the highway, which is south of the cave. The upper elevations of this area yielded a Yabrudian assemblage recovered from brown-orange sediments, which is similar to the Shelf Yabrudian. It is plausible that these two excavation areas are part of a single Yabrudian layer; however, a physical connection between the two areas has not yet been established.

- South West Spheroid: (squares E–F/15–17 of the cave’s grid, elevation 660–715 below datum). This Amudian archaeological context is positioned directly below the SW Yabrudian and is extended through squares A–F/15–17; however, faunal analysis included only the squares rich in Spheroids, and only this part of the context is included in this analysis. A concentration of shaped stone balls was recovered from this context (Barkai and Gopher, 2016), and a techno-functional analysis indicated

that the stone balls were used in marrow extraction (Assaf et al., 2020).

Materials and methods

Materials

All the teeth available from the following contexts were screened: Hearth (subdivided in the four sub-levels HI, HIIa, HIIb and HIII), LSBS, DBS, SCW, Shelf Yabrudian, SW Yabrudian and SW Spheroids. We selected those that were identified at the species level and that occlusal surfaces presented wear facets.

Tooth mesowear analysis

Mesowear is scored macroscopically from the buccal or lingual side of upper and lower molars, respectively. Unworn (and marginally worn) teeth, extremely worn teeth and those with broken or damaged cusp apices were omitted from mesowear analysis. Cusp sharpness is sensitive to ontogenetic age among young individuals (which have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, mesowear is found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007) and, therefore, suitable for dietary reconstruction. The method is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6) (Mihlbachler et al., 2011). The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or MWS (Mihlbachler et al., 2011). The mesowear was scored on the upper and lower teeth except for the horse where only the lower teeth were analysed. To reduce inter-observer error, dental mesowear analysis was conducted by a single experienced researcher (FR).

Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleaning, moulding, casting and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). All the data were collected by a single experienced observer (FR). The occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was moulded using high-resolution silicone (vinylpolysiloxane), and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with poorly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh

features made during the collecting process or during storage) were removed from the analysis, following King et al. (1999). Casts were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at 35× magnification, using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e. elongated scratches and rounded pits) were quantified on the paracone of the upper teeth and the protoconid of the lower teeth in a square area of 0.16 mm² using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004), which distinguished pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that have straight and parallel sides. The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002; Rivals et al., 2010).

Finally, following Rivals et al. (2015a), two measurements of the variability of scratch density, the standard deviation (SD) and the coefficient of variation (CV), were used to estimate the seasonality of human occupation and accumulation of faunal assemblages at the sites. As seasonal changes in diet are recorded by microwear, the variability of the microwear signal allows for the detection of seasonality. The combination of the two measurements of variability permits the classification of assemblages into one of the following categories: (A) seasonal events or shorter time windows, (B) events longer than a season (i.e. two or more contiguous seasons) and (C) separate events that occurred in different non-contiguous seasons. As some of the samples used here are too small to detect the true CV and SD values of the larger population that they represent, we applied a joint bootstrapped function of CV and SD ($n = 500$, with replacement) using the R code by Domínguez-Rodrigo et al. (2019).

Age at death: dental eruption and replacement

The ungulate mortality pattern was analysed from states of dental eruption and wear on mandibles and isolated teeth (e.g. Greenfield and Arnold, 2008; Azorit, 2011; Greenfield et al., 2015; Bowen et al., 2016). Our analyses were focused on the fallow deer as it is the predominant species in all the Qesem assemblages and shows the highest proportion of the youngest individuals. In addition to the tooth eruption patterns, the crown height measurements were also considered when teeth were fully erupted (Bowen et al., 2016). By applying a tested system based on collections of known-age fallow deer, we assumed a birth period set at the end of March or beginning of April (e.g. Chapman and Chapman, 1975; Brown and Chapman, 1991b; Werner et al., 2015). Season of death was therefore established for the young individuals of fallow deer from the four sub-levels of the Hearth unit and for SCW and Shelf Yabrudian. Fallow

deer was also integrated with the rest of taxa and grouped into different categories with the objective of assessing the general ungulate mortality profile at the site. Stiner et al. (2009, 2011) divided the mortality profile at Qesem Cave into three age classes, regardless of taxon: juvenile (prior to first wear on mandibular P4), prime (erupted P4 and in wear) and old age (> 50% of P4 crown worn away). Here, we added a fourth category for initial stages of development, as proposed in Blasco et al. (2014): infantile (ungulates with deciduous teeth and M1 visible in crypt or about halfway to full occlusal height), young or sub-adult (lightly to moderately worn deciduous teeth, erupted M1 and M2 erupting through the bone), adult (all erupted permanent teeth with no or moderate wear in M3) and old or senile (very advanced wear on most of the crown). The repetition of dental pieces and reconstruction of dental series according to the age at death of individuals were used to calculate the minimum number of individuals (MNI)

Results

Dietary traits of the ungulates

The mesowear and microwear data were analysed for each level (assemblage) separately, including the sub-levels of the Hearth (Table 1), but in some cases, the sample size is small ($N < 8$). For these small samples, the interpretations should be taken with caution.

The fallow deer shows relatively low mesowear values ($MWS \leq 2$) for all the assemblages (Fig. 2), indicating a diet with low abrasion. These values correspond to extant leaf browsers and browse-dominated mixed feeders. For the large samples (with $N > 8$), the values are very similar to the mesowear scores of the extant fallow deer, *Dama dama* (DD on Fig. 2). The microwear pattern supports this interpretation, with enamel surfaces showing a low number of scratches and a very variable number of pits. All the samples fit within the confidence ellipse for the extant leaf browsers (Fig. 3A). Considering that extant fallow deer are mixed feeders (i.e. feeding on both browse and grass on a seasonal basis), all these animals died at a time when they were mainly feeding on low abrasive resources. There are some relevant differences among the samples throughout the sequence. The samples from the Hearth show a microwear pattern different from that of the other levels. In the four sub-levels belonging to the Hearth (HI, HIIa, HIIb and HIII), the percentage of gouges is lower (between 18.8 and 31.3%) than the values observed in the other levels of the sequence (from 40 to 82.5%). In the Hearth, the percentage of hypercoarse scratches is very low (between 1.7 and 6.3%) compared to the values reported for the other levels (from 20 to 57.5%). Considering that the other microwear features (numbers of

Table 1 Summary results of the mesowear and microwear analyses on the ungulates from Qesem Cave. Abbreviations: *N*, number of specimens; *MWS*, mesowear score; *NP*, mean number of pits; *NS*, mean number of scratches; *SD*, standard deviation; *CV*, coefficient ofvariation; *%LP*, percentage of individuals with large pits; *%G*, percentage of individuals with gouges; *SWS*, scratch width score; *%XS*, percentage of individuals with cross scratches; *%HC*, percentage of individuals with hypercoarse scratches

Context	Species	Mesowear		Microwear										
		<i>N</i>	<i>MWS</i>	<i>N</i>	<i>NP</i>	<i>SD</i>	<i>NS</i>	<i>SD</i>	<i>CV</i>	<i>%LP</i>	<i>%G</i>	<i>SWS</i>	<i>%XS</i>	<i>%HC</i>
DBS	<i>D. cf. mesopotamica</i>	21	1.57	19	22.3	6.7	14.2	2.32	0.16	100	36.8	1.2	0	31.6
	<i>E. ferus</i>	2	4.00	4	13.1	3.3	19.6	4.13	0.21	25	25.0	1.0	0	0.0
	<i>B. primigenius</i>	5	2.20	8	22.7	13.2	16.7	4.98	0.30	62.5	25.0	0.9	0	12.5
LSBS	<i>D. cf. mesopotamica</i>	9	1.44	8	45.7	12.3	12.1	1.37	0.11	100	50.0	1.5	0	25.0
SCW	<i>D. cf. mesopotamica</i>	14	1.67	18	37.8	12.8	12.3	3.64	0.30	76.1	56.7	1.4	0	32.8
Shelf Yabrudian	<i>D. cf. mesopotamica</i>	22	1.73	23	34.8	11.7	12.6	4.05	0.32	65.2	52.2	1.3	0	34.8
SW Yabrudian	<i>D. cf. mesopotamica</i>	5	1.20	5	28.5	9.1	12.2	1.82	0.15	60.0	40.0	1.0	0	20.0
HI	<i>D. cf. mesopotamica</i>	4	1.00	5	23.5	7.5	15.1	4.40	0.29	75.0	31.3	1.3	0	6.3
IIIa	<i>D. cf. mesopotamica</i>	10	1.76	15	21.7	6.8	13.9	4.20	0.30	52.1	18.8	1.3	2.1	2.1
IIIb	<i>D. cf. mesopotamica</i>	4	2.00	7	23.1	7.1	13.6	4.19	0.31	58.0	20.0	1.3	0	2.0
III	<i>D. cf. mesopotamica</i>	29	1.72	29	23.1	7.0	13.7	4.19	0.31	65.0	26.7	1.3	0	1.7
	<i>E. ferus</i>	-	-	8	14.9	4.4	14.4	3.64	0.25	38.5	7.7	1.1	7.7	0
IIIa + IIb	<i>D. cf. mesopotamica</i>	14	1.78	22	23.1	7.1	13.6	4.19	0.31	58.0	20.0	1.3	0	2.0
	<i>E. ferus</i>	3	3.33	5	18.2	3.1	13.3	1.25	0.09	40.0	20.0	1.0	0	0.0
H all sub-levels	<i>D. cf. mesopotamica</i>	47	1.72	56	23.1	7.0	13.7	4.19	0.31	65.0	26.7	1.3	0	1.7
	<i>E. ferus</i>	3	3.33	13	14.9	4.4	14.4	3.64	0.25	38.5	7.7	1.1	7.7	0
SW Spheroids	<i>B. primigenius</i>	2	2.00	2	19.0	-	18.8	-	-	-	-	-	-	-
	<i>C. cf. elaphus</i>	4	2.25	3	26.0	6.1	13.3	-	-	100	33.3	1.3	0	33.3
	<i>D. cf. mesopotamica</i>	62	1.71	40	26.6	4.2	11.7	2.17	0.19	100	82.5	1.6	0	57.5
	<i>E. ferus</i>	9	4.44	14	18.4	3.8	20.3	1.89	0.09	71.4	28.6	1.1	0	21.4
All Qesem Cave	<i>B. primigenius</i>	12	2.16	16	23.1	12.5	17.0	4.68	-	62.5	12.5	0.9	0	6.3
	<i>C. cf. elaphus</i>	8	1.75	7	24.1	5.9	15.9	4.98	-	100.0	42.9	1.3	0	14.3
	<i>E. ferus</i>	14	4.14	34	16.4	4.4	18.0	4.09	-	47.1	17.6	1.1	2.9	11.8

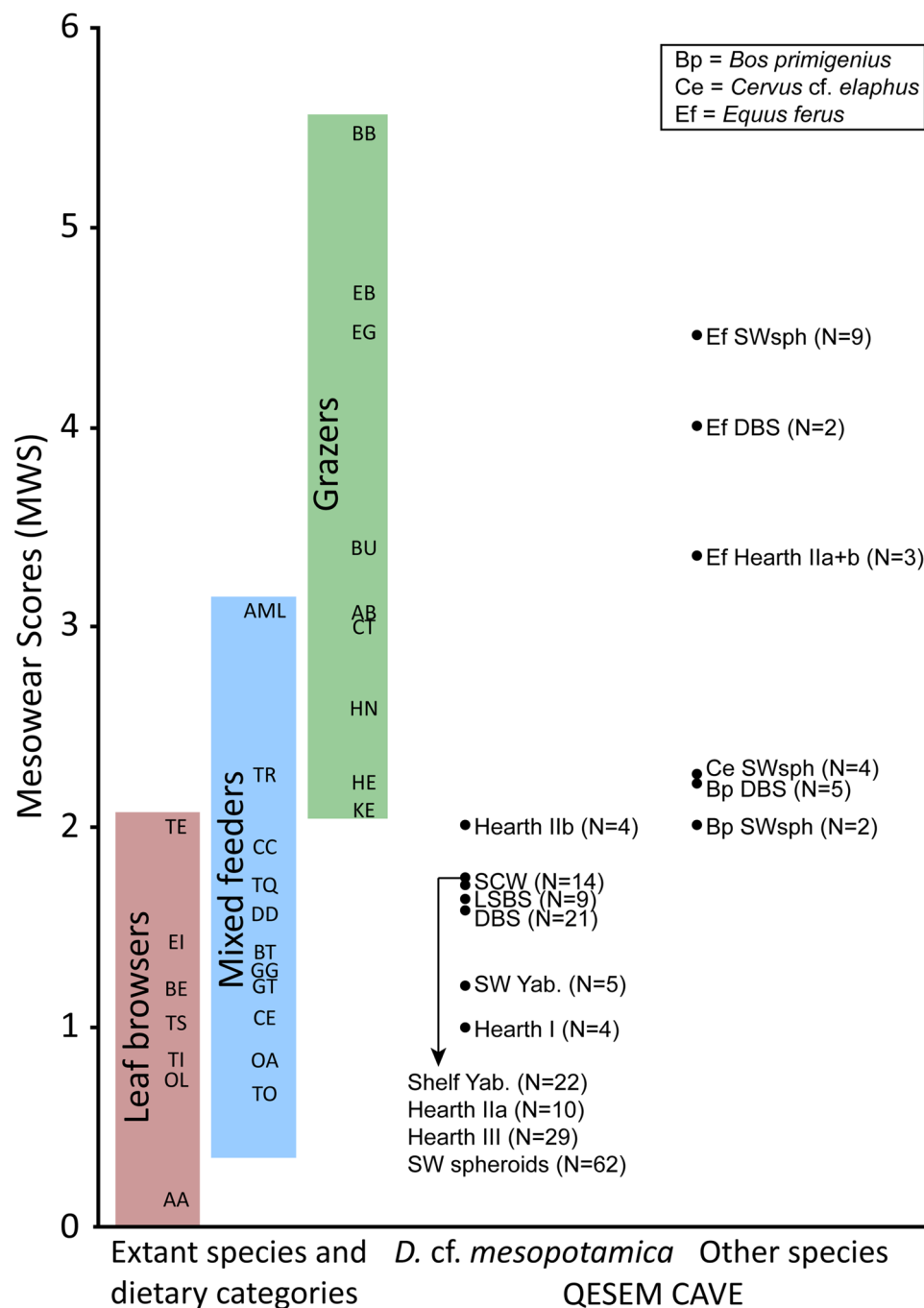
pits and scratches, large pits, cross scratches) do not vary throughout the sequence, it indicates that the fallow deer always fed on browse (i.e. low abrasive resources), such as dicots and leaves from bushes or trees. However, the differences observed in the gouges and hypercoarse scratches would indicate that fallow deer from the other levels than the Hearth, besides the leaves, included some bark in their diet, probably from feeding on twigs or very small branches. The animals that were found to be associated with the Hearth sub-levels did not include any (or low proportions) bark and were fed exclusively on leaves. Besides these differences in consumed plant parts, fallow deer from all the contexts analysed from Qesem Cave were pure browsers.

The red deer is represented by only a few individuals. The largest sample, from the SW Spheroids, is still very small and results should be taken with caution. We also provided the data for the individuals from all the levels lumped together (Table 1). The red deer showed a pattern similar to that of the fallow deer (except those from the Hearth), both regarding meso- and microwear (Figs. 2 and 3B). The low mesowear score fits within the range of extant mixed feeders.

The microwear pattern is characteristic of leaf browsers. The number of scratches, however, has more variability than in fallow deer, suggesting more variable dietary habits. Additionally, it has a high percentage of individuals with large pits, an intermediate percentage of gouges and a low proportion of hypercoarse scratches.

The aurochs show mesowear values similar to that of the red deer and the fallow deer from the Hearth sub-level IIb (Fig. 2). The mesowear score is above the limit between extant browsers and grazers, suggesting a diet categorised as grass-dominated mixed feeders. The microwear signal from DBS, with relatively low number of scratches (Fig. 3B), high percentage of large pits, finer scratches than the deer, indicates a browse-dominated mixed feeding diet. The microwear pattern from the Hearth, with a higher number of scratches than the other sample, plots among the extant grazers (Fig. 3B). The slight discrepancy between the mesowear and microwear signals suggests that these aurochs were mixed feeders.

The horses, with high mesowear values ($MWS = 3.3$ to 4.4), plot among the extant grazers (Fig. 2). The largest



sample, from the SW Spheroids, shows values similar to those reported for the two extant zebra species, *Equus grevyi* and *E. quagga* (EG and EB, respectively on Fig. 2). The other samples show lower mesowear scores, indicating a less abrasive diet, as the sample from the Hearth sub-level II shows the lowest value. The microwear pattern, however, showed lower values in the number of scratches (Fig. 3B). The samples from DBS and the SW Spheroids plot on the limit between grazers and mixed feeders. In the SW Spheroids, the number of pits is higher than in DBS; however, the

number of scratches fits within the range of extant grazers. The samples from the Hearth unit (HI, HIIa, HIIb and HIII) are plotted among the extant leaf browsers (Fig. 3B). As also observed previously through mesowear, the horses from the Hearth are those with the lowest level of abrasiveness.

It is important to report that both mesowear and microwear analyses show consistent results that indicate the same gradient of increasing abrasiveness from *D. cf. mesopotamica*, *C. cf. elaphus*, *B. primigenius* and finally *E. ferus*. Furthermore, while mesowear and microwear are in agreement

Fig. 2 Mesowear scores for the samples of *Dama cf. mesopotamica*, *Bos primigenius*, *Cervus cf. elaphus* and *Equus ferus* from Qesem Cave compared to extant ungulates. List of abbreviations for the extant species: **Grazers.** AB, *Alcelaphus buselaphus*; AL, *Sigmoceros lichtensteini*; BBB, *Bison bison bison*; BBO, *Bison bonasus*; BU, *Bubalus mindorensis*; CS, *Ceratotherium simum*; CT, *Connochaetes taurinus*; DL, *Damaliscus lunatus*; EB, *Equus quagga*; EG, *Equus grevyi*; HH, *Hemitragus hyllocrius*; HE, *Hippotragus equinus*; HN, *Hippotragus niger*; KE, *Kobus ellipsiprymnus*; OO, *Ourebia ourebi*; PCC, *Procavia capensis capensis*; RR, *Redunca redunca*; RCD, *Rucervus duvaucelii*. **Leaf browsers.** AA, *Alces alces*; AM, *Antilocapra americana*; BE, *Tragelaphus eurycerus*; CB, *Camelus bactrianus*; CEE, *Cervus elaphus*; CL, *Camelus dromedarius*; DB, *Diceros bicornis*; DS, *Dicerorhinus sumatrensis*; EI, *Ammodorcas clarkei*; GC, *Giraffa camelopardalis*; LGU, *Lama guanicoe*; LW, *Litocranius walleri*; OH, *Odocoileus hemionus*; OJ, *Okapia johnstoni*; OL, *Capreolus capreolus*; OV, *Odocoileus virginianus*; RS, *Rhinoceros sondaicus*; TE, *Tragelaphus strepsiceros*; TI, *Tragelaphus imberbis*; TS, *Tragelaphus scriptus*. **Mixed feeders:** AML, *Ammotragus lervia*; AP, *Axis porcinus*; AX, *Axis axis*; BBA, *Bison bison athabasca*; BT, *Budorcas taxicolor*; CA, *Capricornis sumatraensis*; CC, *Capra caucasica*; CEC, *Cervus elaphus canadensis*; CI, *Capra ibex*; CN, *Cervus nippon*; CP, *Capra pyrenaica*; CU, *Rusa unicolor*; DD, *Dama dama*; GG, *Nager granti*; GT, *Eudorcas thomsonii*; HB, *Heterohyrax brucei*; HJ, *Hemitragus jemlahicus*; LGL, *Lama glama*; LGU, *Lama guanicoe*; MA, *Antidorcas marsupialis*; ME, *Aepyceros melampus*; MR, *Muntiacus reevesi*; MU, *Muntiacus muntjak*; OA, *Oreamnos americanus*; OC, *Ovis canadensis*; OD, *Ovis ammon darwini*; OM, *Ovibos moschatus*; OP, *Ovis ammon polii*; PA, *Pantholops hodgsoni*; PR, *Procapra gutturosa*; RA, *Rupicapra rupicapra*; RF, *Redunca fulvorufula*; RU, *Rhinoceros unicornis*; SC, *Syncerus caffer aequinoctialis*; ST, *Saiga tatarica*; TA, *Tragelaphus angasi*; TO, *Taurotragus oryx*; TQ, *Tetracerus quadricornis*; TR, *Boselaphus tragocamelus*; VV, *Vicugna vicugna*. Data from Fortelius and Solounias (2000), Rivals et al. (2010, 2013, 2014)

for the diet of the fallow deer, the red deer, aurochs and horse, the discrepancy between the two proxies suggests a mixed feeding diet (mesowear) that shifted towards browsing near the time of death (microwear).

When the minimum number of individuals for each taxon (Table 2) is considered, in each assemblage, the community of species that was analysed is always largely dominated by the leaf browsers, which represent between 70 and 100% of the individuals (Table 3). This result is directly related to the dominance of fallow deer in all the assemblages studied.

Seasonality of game procurement at Qesem Cave

The variability of the microwear signal was used to establish seasonality in the procurement of the prey. The model established by Rivals et al. (2015a, b) allowed us to characterise (1) accumulation(s) resulting from seasonal (or shorter) events or (2) accumulations that lasted longer than a season

(i.e. two or more consecutive seasons) or repeated accumulations at different seasons of the year. The CV and SD values were computed when the sample size was at least $N=5$, in the four sub-levels of the Hearth and in the other levels of the sequence.

The microwear pattern for the fallow deer from the four sub-levels of the Hearth unit (HI, HIIa, HIIb and HIII) shows a high variability regarding both SD and CV values. All the samples plot within zone B of the heat map (Fig. 4A), corresponding to accumulation of remains that lasted longer than a single season. The same pattern of high microwear variability is observed for the horse from HIII (Fig. 4B). However, in HIIa+HIIb, the horse sample plots in area [A], i.e. in the area corresponding to a seasonal procurement (3 months or less). Regarding the seasonality established from dental eruption and replacement (Fig. 5), in HI, the main peak occurred from late autumn to late winter (MNI young individuals = 8) and a small peak corresponded to a single individual hunted in late spring. In level IIa, the pattern is similar but shifted with a main peak from late winter to late spring ($NMI=6$) and a small one in autumn ($NMI=2$). Sub-levels HIIb and HIII showed the same pattern with three peaks in late summer, late winter and late spring. Only the number of individuals is different between these two levels.

Samples from other levels at the site showed more diverse patterns. The fallow deer assemblages from the Shelf Yabrudian and SCW showed high variability of the microwear patterns and correspond to accumulations during occupations that lasted longer than a single season, similar to what was reported for the fallow deer from the Hearth (Fig. 4B). The season of death established from tooth eruption and replacement (Fig. 5) showed death scattered through half of the year. In the Shelf Yabrudian, it occurred during two periods: late summer and autumn and from late winter to late spring. In SCW, three periods were evidenced: late summer and autumn (as in the Shelf Yabrudian), winter, and spring (Fig. 5).

In contrast, in the SW Spheroid assemblage, where fallow deer and horse are present, the variability of the microwear signal is low and suggests seasonal or shorter procurement events related to the accumulation of these two species (Figs. 4A–B). This pattern of shorter events is also observed for the fallow deer from the LSBS assemblage (Fig. 4A).

In the DBS assemblage, the fallow deer sample with low CV and SD values plots in area [A] corresponding to duration of one season or shorter (Fig. 4A). Conversely, the horse sample showed higher variability values and plots in area [B] corresponding to duration longer than one season (Fig. 4B). In DBS, the occupation probably lasted longer than one season with a regular procurement of horses and a more seasonal hunting focused on fallow deer.

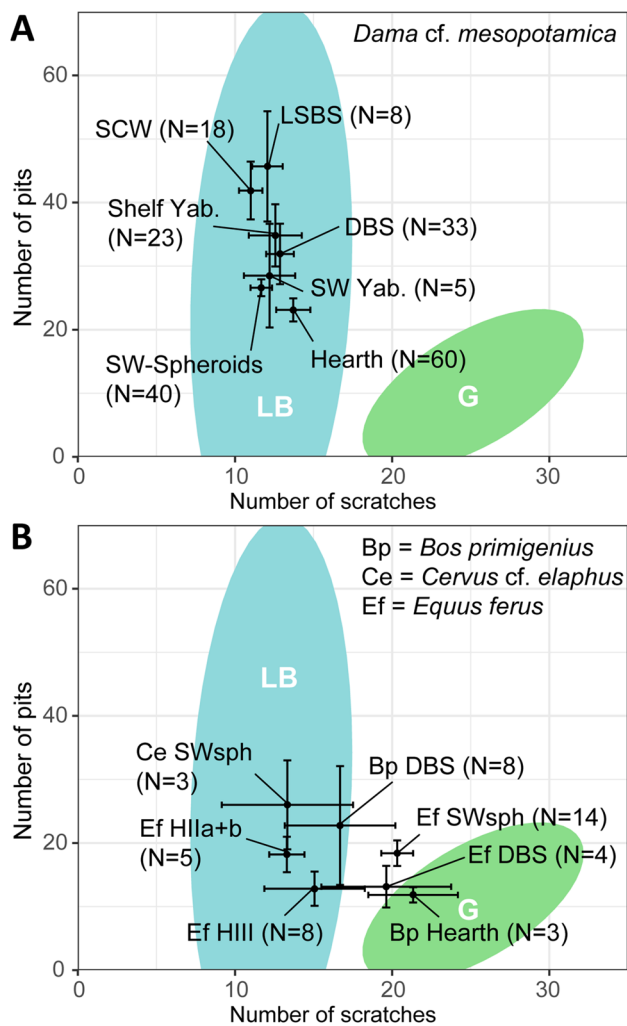


Fig. 3 Bivariate plot of the number of pits and scratches for the ungulates from Qesem Cave. **A** *Dama cf. mesopotamica*. **B** *Bos primigenius*, *Cervus cf. elaphus* and *Equus ferus*. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. Plain ellipses correspond to the Gaussian confidence ellipses ($p=0.95$) on the centroid for the extant leaf browsers (LB) and grazers (G) based on the reference database from Solounias and Sempredon (2002)

Discussion

Dietary traits, habitats and niche partitioning among ungulates

The dietary traits, interpreted from the tooth mesowear and microwear analyses, are summarised in Table 4.

The fallow deer shows mesowear and microwear patterns similar to that of the extant leaf browsers and browse-dominated mixed feeders. In all assemblages, the fallow deer fed mostly on browse (i.e. low abrasive plants), such as dicots and leaves from bushes or trees. However, some differences related to the plant parts consumed were identified throughout the sequence. The samples from the Hearth

show a microwear pattern different from that of the other levels. In the other levels, the differences observed in some microwear variables would indicate that fallow deer, besides the leaves, included some bark in their diet, probably from feeding on twigs or very small branches. The dietary traits of the fallow deer from the Hearth — which, unlike the hunted individuals from the other contexts, ate only leaves and no bark or twigs at all — may hold a potential for quite interesting suggestions, even if speculative. For example, the fallow deer brought repeatedly to the Hearth were either animals selected for their special qualities or animals hunted in selected hunting grounds. The Shelf Yabrudian and the SW Yabrudian assemblages — which are roughly contemporaneous with the Hearth area (i.e. at the top of the lower sequence sometime around 300 kya) — show various diets for the hunted fallow deer. As opposed to the case of the Hearth, where we cautiously suggested that the hunted fallow deer may represent either fallow deer hunted in specific habitats or individual fallow deer hunted during specific seasonal episodes, in the other parts of the cave, fallow deer from other habitats were consumed. The fact that the same microwear pattern is reflected in the different use cycles of the Hearth might indicate that this is a recurrent pattern and that some selectivity characterised the fallow deer that was brought back to be consumed in the Hearth area. A detailed consideration of other sets of data from the Hearth area would indicate that it differs, to some degree, from other assemblages of the cave. For the lithics assigned to the Amudian, this is expressed in density measures (higher at the Hearth than in any other part of the cave) and frequencies of lithic categories of both debitage (e.g. cores) and shaped tool categories (Venditti et al., 2019; Assaf et al., 2020). For the fauna, the Hearth unit as a whole showed the highest concentration regarding density, which also includes the smallest bone fragments (Blasco et al., 2016a). It seems that Hearth-centred activities included particular human behaviours; however, it is difficult to decipher why fallow deer with a different diet than the diet of fallow deer from assemblages of other parts of the cave are related to the Hearth. As we have already noted, the reasons for the difference may be related to hunting season or specifically timed preferences or to hunting in selected different habitats. While we obviously cannot delve deep into interpreting such results, we may speculate about the different diet consumed by the fallow deer brought to the Hearth. As such, we may say that this might most probably relate to one of two elements, or both, namely, the qualities of the meat (and/or marrow) or the nature and role of the Hearth for the inhabitants of the cave. Meat quality and its taste are eventually affected by the seasonally available diet of the hunted animals and vary accordingly. The refined selection of resources by humans, clearly food resources, has been documented in ethnographical studies (e.g. Koster et al., 2010). There is no reason to deny

Table 2 Minimum number of individuals (MNI) in the different assemblages from Qesem Cave

Taxa/size body class	HI	HIIa	HIIb	HIII	LSBS	DBS	SCW	Shelf Yabr	SW Yabr	SW Spher
Carnivora			1					1		
<i>Stephanorhinus hemitoechus</i>		1	1	2	1	1	1	1	1	2
<i>Equus ferus</i>	2	2	2	4	1	1	1	1	2	5
<i>Equus hydruntinus</i>	1	1	2	1						
<i>Sus scrofa</i>				3	1	1	1	1	2	2
Cervidae indet		1	2	1						1
<i>Dama cf. mesopotamica</i>	9	15	19	23	7	7	9	14	8	28
<i>Cervus cf. elaphus</i>	2	2	5	4	2	2	3	4	2	4
cf. <i>Capreolus capreolus</i>	1	2	1	1	1	1		1	1	
<i>Bos primigenius</i>	2	2	2	2	4	2	3	4	1	3
<i>Capra aegagrus</i>		1			1	1		1	1	1
<i>Testudo</i> sp.	1	2	2	1	5	2	1	4	2	2
Large bird				1						
<i>Cygnus</i> sp.					1					
<i>Corvus ruficollis</i>		1	1	1				1		
<i>Columba</i> sp.				1				1		
Aves, indet					1		1			
Total	18	30	38	45	25	18	20	34	20	48

Table 3 Minimum number of individuals for each dietary group, total and percentage of leaf browsers in each assemblage of Qesem Cave

	Leaf browsers	Mixed feeders	Grazers	Total	% Leaf browsers
HI	9	2		11	81.8
HIIa	15	2	2	19	78.9
HIIb	19	4	2	25	76.0
HIII	23		2	25	92.0
LSBS	7			7	100
DBS	7	2	1	10	70.0
SCW	9			9	100
Shelf Yabrudian	14			14	100
SW Yabrudian	8			8	100
SW Spheroids	28	4	1	33	84.8

Palaeolithic hunters of this behavioural pattern, and there is good reason to believe that choices of prey animals and, as a result, the place and time of hunting them would be deeply ingrained in their quality and taste.

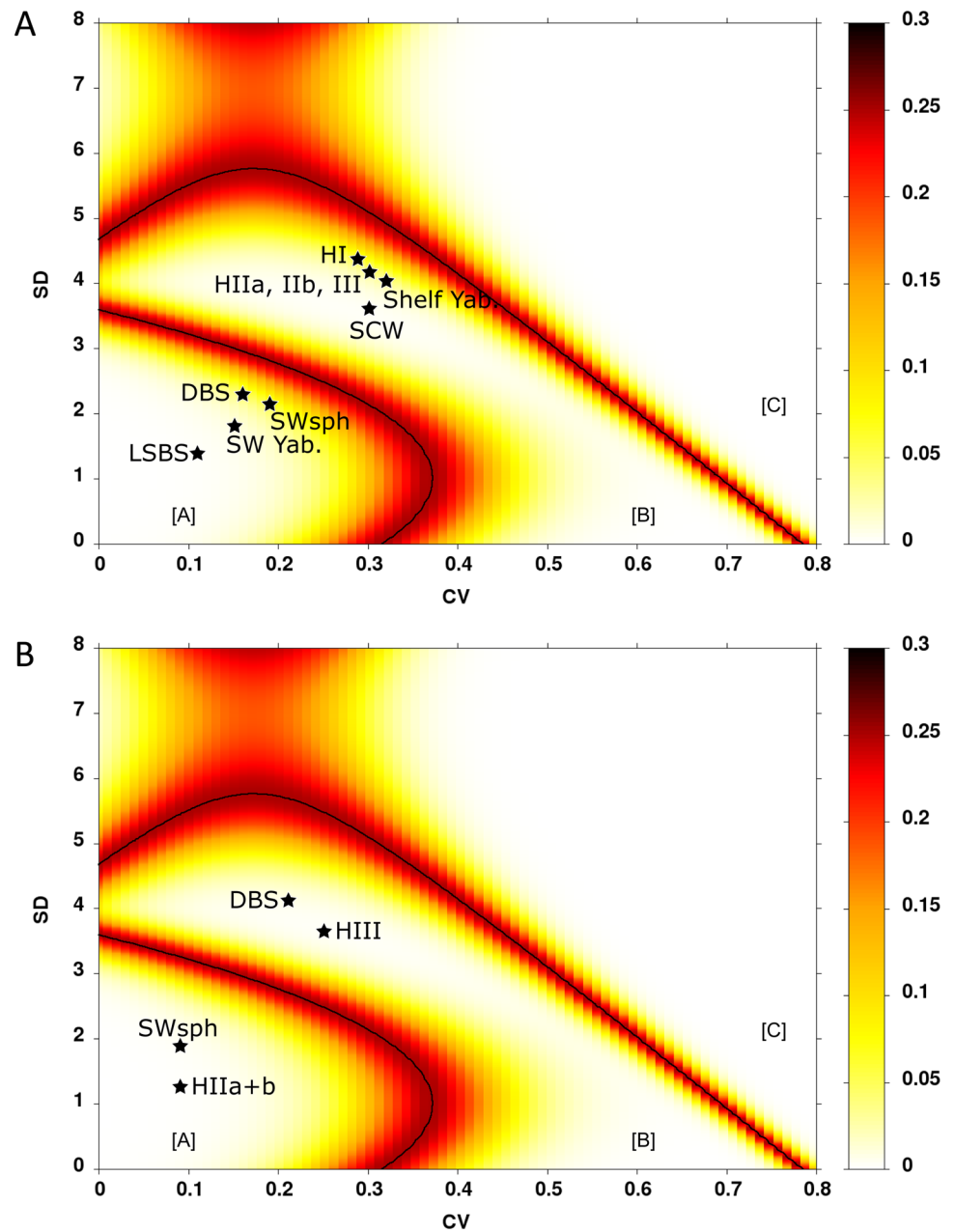
For the red deer, the sample size is small. However, the broad meso- and microwear patterns are similar to that of the fallow deer. Red deer was a mixed feeder (mesowear) that died at a time it was mainly feeding on browse resources (microwear), especially on dicots and leaves from bushes or trees. The dietary traits of the red and fallow deer are similar; the two species probably occupied habitats with similar resources (i.e. mainly shrubs and/or trees). However, due to resource partitioning among species, they certainly occupied different ecological niches. It could be either two different habitats around the cave or the same habitat used alternatively at different seasons throughout the year. Niche

partitioning allowed these two browsing cervids to coexist in the area occupying different ecological niches. The two species could have been hunted along similar hunting trips in similar landscapes.

The aurochs had a general mixed feeding diet (as indicated by mesowear) and the microwear signal is shifted either towards browsing or grazing. This suggests that the animals died at different seasons in the different assemblages analysed. Some died during a season they were mainly feeding on browse, while others died during a season they were grazing. These differences are certainly an indication of cave usage at different seasons of the year rather than only at a specific season.

The long-term dietary signal (mesowear) of the horses from the different assemblages analysed shows grazing dietary habits, and the short-term signal (microwear) indicates

Fig. 4 Boundary lines with the error probability (heat map) based on standard deviations (SD) and coefficient of variation (CV) values of microwear data used for the classification of Qesem Cave samples into short events (region A), long-term events (region B) or two separate short events (region C). **A** *Dama cf. mesopotamica*. **B** *Equus ferus*



diversity of diets, including grazing, mixed feeding and leaf browsing. Regarding microwear, a diet based on highly abrasive plants corresponding to definite grazing traits would be expected for the horse. However, this result is not surprising since other populations of Pleistocene horses have been reported to be mixed feeders or even leaf browsers (Rivals et al., 2009b, 2015b; Uzunidis, 2020). The discrepancy between the mesowear and microwear results indicates a strong seasonal signal (Sánchez-Hernández et al., 2016). The annual (average) diet of the horse is that of a typical grazer, as indicated by mesowear. However, the microwear signal suggested the horse had a diet shifted towards mixed feeding and the inclusion of more browse at the time of

death. In these cases, it indicated that these animals died at a time when a high amount of leaves from trees, bushes or herbaceous plants were available. In the case of the Hearth, both mesowear and microwear provided consistent results suggesting horses were hunted in specific habitats, as previously observed for fallow deer and red deer. Interestingly, the horse sample from the Spheroid area showed a different diet, being mostly grazers. Bone marrow extraction activities using Spheroids were pronounced in that area and probably aimed to some extent at horse mandibles and bones (Assaf et al., 2020). Hence, the human groups probably brought horses from specific habitats to be processed for marrow extraction.

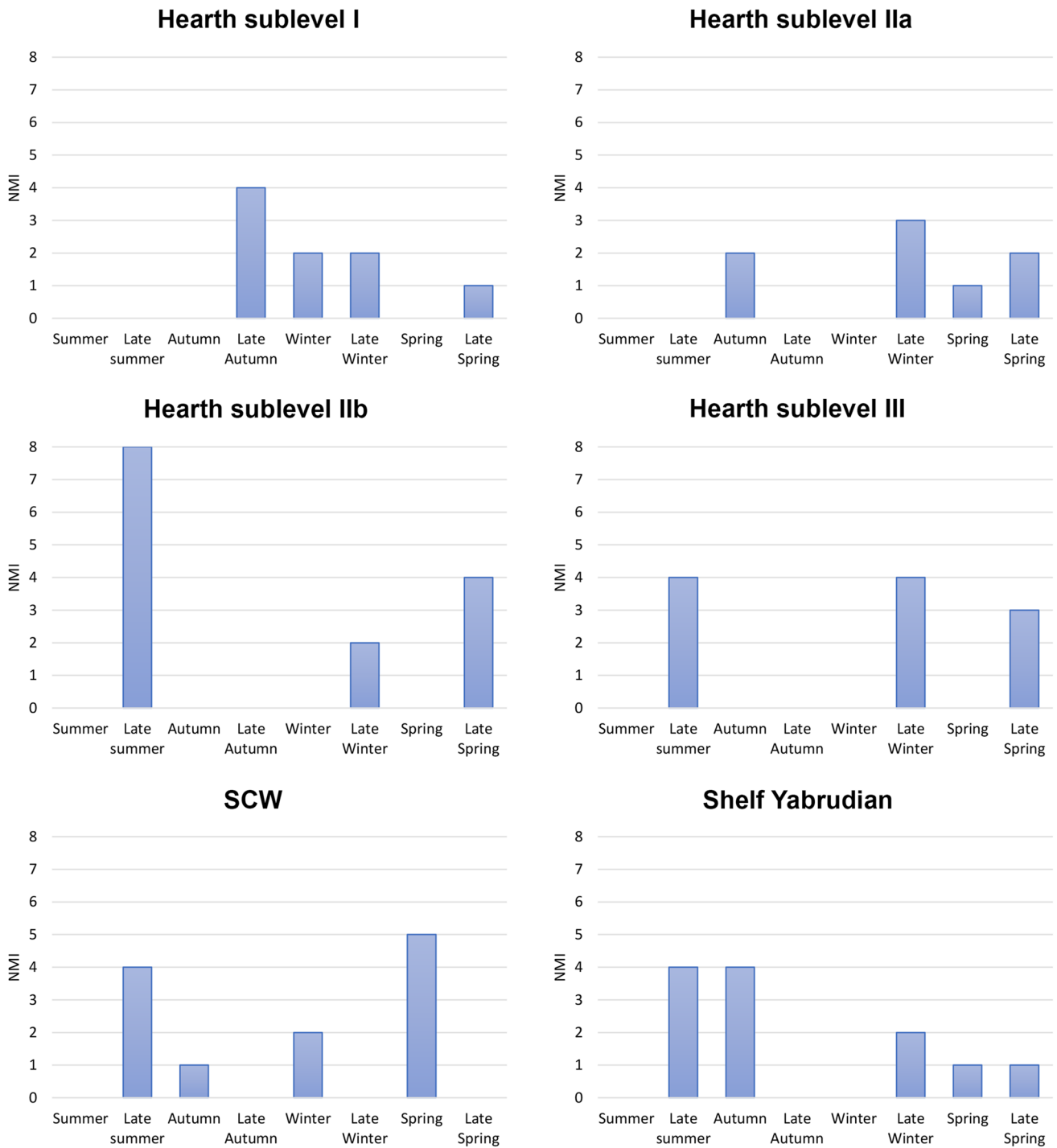


Fig. 5 Seasonality of fallow deer (*Dama cf. mesopotamica*) procurement at Qesem Cave based on tooth eruption and replacement patterns

In all levels of Qesem Cave, the assemblages were clearly dominated by browsers, as they represent between 70 and 100% of the individuals hunted. It showed the availability of low abrasive plants like forbs or leaves from bushes and trees were available to these taxa. The vegetal associations in the region are such that winter is rich in green plants,

such as grasses and trees, most of which do not lose their leaves, while summer is poor in grasses or contains only dry grasses. For all species hunted and brought back to Qesem Cave, we can report patterns in specific activity areas (Hearth, Spheroids/SW) that are different from in other areas of the cave. There is a clear relation between these specific

Table 4 Summary of the interpretations made from mesowear, microwear and dental eruption and replacement on the ungulates from Qesem Cave in terms of dietary traits and seasonality. *Seasonality is classified as (1) short, i.e. one season or shorter, or (2) long, i.e. longer than one season

Context	Species	Dietary trait	Seasonality*
HI	<i>D. cf. mesopotamica</i>	Browser	Long
HIIa	<i>D. cf. mesopotamica</i>	Browser	Long
HIIb	<i>D. cf. mesopotamica</i>	Browser	Long
HIII	<i>D. cf. mesopotamica</i>	Browser	Long
	<i>E. ferus</i>	Grazer	Long
LSBS	<i>D. cf. mesopotamica</i>	Browser	Short
DBS	<i>D. cf. mesopotamica</i>	Browser	Short
	<i>E. ferus</i>	Grazer	Long
	<i>B. primigenius</i>	Mixed feeder	–
SCW	<i>D. cf. mesopotamica</i>	Browser	Long
Shelf Yabrudian	<i>D. cf. mesopotamica</i>	Browser	Long
SW Yabrudian	<i>D. cf. mesopotamica</i>	Browser	Short
SW Spheroids	<i>D. cf. mesopotamica</i>	Browser	Short
	<i>E. ferus</i>	Grazer	Short
	<i>B. primigenius</i>	Mixed feeder	–
	<i>C. cf. elaphus</i>	Mixed feeder	–

activity areas and the animals hunted in particular habitats, i.e. with a distinct diet. There is a high diversity of habitats available around the cave, corresponding to a mosaic of open landscapes with sparse vegetation, shrub land, Mediterranean forest, rocky areas and riverbanks (Maul et al., 2016; Sánchez-Marco et al., 2016). Nevertheless, it seems that certain habitats were exploited for precise and well-targeted activities. Interestingly, horses and aurochs were probably hunted seasonally, while the fallow deer was hunted all year round. It may indicate that at the time of death, lower abrasive plants like forbs and leaves from bushes and trees were available to these taxa. Browse was probably available all year round, and only grasses would change in quality, from green to dry during the dry season. If animals avoided dry grasses, they may have increased browsing during the dry season. This was probably what occurred in the case of the red deer, aurochs and horse.

Seasonality of game procurement at Qesem Cave

The combination of tooth microwear analysis and tooth eruption and wear, two independent techniques, allowed for precise estimations of the seasonality of game procurement at Qesem Cave. The main interpretations for each context are summarised in Table 4.

In the Hearth unit, considering there is no difference among the microwear results observed for the fallow deer from the four sub-levels, the data suggest the same dynamic from HI to HIII. This indicates that the fallow deer was

hunted and brought back to the cave at various seasons of the year in all four sub-levels of the Hearth. However, it is not possible to differentiate whether it was hunted during a long (year round) occupation of the cave or during a succession of few and shorter visits in different seasons of the year (covering a few or all seasons). In any case, our microwear results point to a prolonged use of the cave, either year round or during different seasons. The study of tooth eruption and replacement in the fallow deer allowed us to detect some evidence for seasonal procurement at Qesem (Stiner et al., 2011; Blasco et al., 2014). A more detailed analysis of the remains from each of the sub-levels of the Hearth allowed us to identify some differences with two or three periods of hunting (Fig. 5). It is important to report that the results on the seasonality of the fallow deer are based on the study of dental eruption and replacement in young individuals, while the results from microwear are mostly based on young adults and adults. Possibly, these two age cohorts of the population were hunted differentially throughout the year (or part of the year). The adults were probably hunted during more episodes throughout the year when the cave was inhabited, and other minor hunting events took place when they hunted the young individuals. For fallow deer, we can also include storage and delayed food consumption (Blasco et al., 2019b) and argue for longer occupations of the cave. For the horse, the same pattern as for the fallow deer is observed in HIII; however, in HIIa and HIIb, the accumulation of horse remains lasted a single season or less, according to microwear. All the results indicate the occupation of the cave at different times of the year for hunting.

In the Shelf Yabrudian and SCW, microwear suggested that the fallow deer assemblages correspond to accumulations during occupations that lasted longer than a single season, similarly to what was reported for the fallow deer from the Hearth. The season of death established from tooth eruption and replacement (Fig. 5) shows scattered death throughout the year. The Shelf Yabrudian and the Hearth belong to the same occupation horizon from a stratigraphic perspective and roughly also from a chronological perspective (Falguères et al., 2016). From a functional perspective, they correspond to two nearby activity areas where similar activities were performed (Venditti et al., 2019). Hence, it is relevant that the two adjacent and perhaps contemporaneous activity areas show longer occupations. However, the fallow deer from these two areas were leaf browsers; they fed on different types of plants. There might have been a preferred selection of fallow deer from specific habitats to be brought to each activity area and this took place repeatedly throughout the prolonged human occupation of these areas.

For the SW Spheroid assemblage, seasonal or shorter procurement events are related to the accumulation of fallow deer and horse, according to microwear analysis. The SW Spheroid area seems to be a distinct activity area at a specific

location of the cave with a high concentration of Spheroids and might have been used seasonally, while other areas of the cave could be used for longer durations (Hearth and Shelf Yabrudian). Moreover, the horses from this area were grazers, as opposed to the horses from the Hearth, and this could also point to a more specific human use of this area for specific purposes like marrow extraction from horses hunted in different habitats.

In LSBS, microwear indicates that the hunting events of the fallow deer lasted for one season, or even less, a duration similar to what was reported for the SW Spheroid assemblage. However, there are no data on the season of death of the fallow deer for these two assemblages to confirm the interpretation from tooth microwear.

In the DBS area, the occupation probably lasted longer than one season with a regular procurement of aurochs and horses and a more seasonal hunting focused on fallow deer. However, aurochs and horses are not more abundant than fallow deer in this assemblage.

In conclusion, despite the limitations of the two methods and their resolution and the small sample sizes in some cases, the detailed study of archaeological context in the cave (such as the Hearth), the detailed analyses of faunal and lithic assemblages around the Hearth and in other parts of the cave and the results presented in this study, we may summarise that the assemblages of large mammals from Qesem Cave were accumulated in almost every season. Thus, if even cautiously, it is likely that hominins inhabited the cave for a long period.

Conclusions

The combination of dental eruption and tooth micro- and mesowear analyses allowed us to establish the seasonality and the duration of occupation of various levels from Qesem Cave. The fallow deer is the dominant species in all assemblages; hence, the seasonality established for this species is highly significant regarding meat procurement. However, since other species, such as aurochs and horses, are much lower in number, they indicate other hunting events that are significant in behavioural terms. Human groups inhabited Qesem Cave for a long period, probably not continuously. The diverse microwear patterns observed in the different species suggest that the animals were living in different habitats and that human groups exploited large game selectively and in specific habitats. Some assemblages from Qesem Cave show unique patterns, such as roasting meat at the Hearth or extracting marrow at the Spheroids' area. There is a clear relationship between specific traits of human behaviour and the particular selection of animals that were brought to these locations of the cave from different habitats. It was evidenced that the animals brought back to the Hearth area were coming from a different habitat than those from

the other units of the cave. The Hearth area was used seasonally, probably during short-term events, and it was related to the consumption of selected animals from specific habitats around the cave. The differences in habitats exploited for hunting were probably related to specific needs of the cave inhabitants for meat, marrow or hide. The assemblages from Qesem Cave reflect complex human behavioural strategies regarding game procurement and the occupation of the cave.

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