



Seasonality of the Final Natufian occupation at Eynan/Ain Mallaha (Israel): an approach combining dental ageing, mesowear and microwear

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Abstract

The Final Natufian level Ib from Eynan/Ain Mallaha provided a large and diversified assemblage of ungulates used here to study the seasonality of game procurement. The objective of this study was to evaluate the advantage of combining two methods, dental eruption and wear, and tooth microwear. Tooth microwear results allowed us to confirm the seasonality of procurement of red and roe deer and to narrow down its duration for the gazelle and the fallow deer. Game procurement occurred throughout the year for the roe deer. Red deer were hunted in spring and summer, and gazelle in late autumn–early winter. This approach allowed us to improve the accuracy of seasonality estimates and to increase sample size by using the entire population (young and adult individuals) for each species. The few individuals that were analysed with the two methods also permitted us to characterize the diet of the population at the time of death.

Keywords Archaeozoology · Tooth eruption · Dental wear · Diet

Introduction

Ain Mallaha/Eynan (Eynan hereafter) was one of the main hamlets in the Levant to be intermittently inhabited by groups

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of hunters-fishers-gatherers for several millennia at the end of the Pleistocene (e.g. Valla et al. 2017). The presence of numerous built structures and heavy basalt pounding tools as well as the evidence of commensal species and anthropogenic niche formation before the domestication of plants and animals has cast doubt on the degree of mobility of the site occupants (e.g. Tchernov 1984; Bridault et al. 2008; Weissbrod et al. 2017; Valla et al. 2017; Valla 2018). The site is located in the Northern Jordan Valley (Israel), on a slope overlooking the Eynan spring (Fig. 1). The Eynan people settled in the vicinity of the Hula Lake and the vast adjacent wetland area, and exploited a wide array of resources and habitats, as reflected by the plant and faunal remains at the site (Bridault et al. 2008; Rosen 2010; Askhenazi 2013; Simmons 2013; Borvon et al. 2018; Bridault 2019). The local availability of water and grass made this area attractive to herbivore populations. Nonetheless, it remains to be documented if the inhabitants of Eynan hunted large and medium game throughout the year or only during certain seasons. Investigating hunting seasons is a means of estimating the season(s) of occupation of the site and Natufian mobility patterns, which are crucial issues still debated for the period.

Davis (1983) established the mountain gazelle (*Gazella gazella*) mortality profile at several prehistoric sites, based on dental eruption stages for the juveniles and wear stages

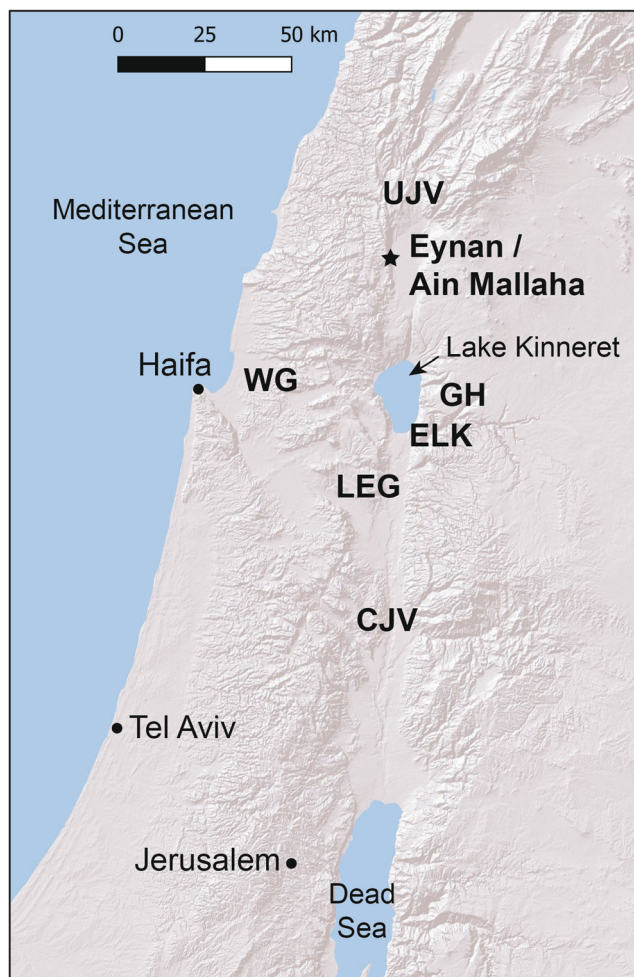


Fig. 1 Map showing the location of Eynan/Ain Mallaha and the areas of provenance of the modern samples of mountain gazelles, fallow deer and wild boar. Abbreviations: GH = Golan Heights; CJV = Central Jordan Valley; LEG = Lower Eastern Galilee; ELK = Eastern Lake Kinneret; UJV = Upper Jordan Valley; WG = Western Galilee

(measuring crown height of the lower third molar) for young adults and adults. The results indicated a slight increase in juvenile gazelles culled during the Natufian. He argued that this might result from a change in the Natufians' lifestyle, from seasonal mobility to sedentism.

This question was tackled later on by focusing on the mountain gazelle, the predominant game during the Epipalaeolithic (Lieberman et al. 1990; Lieberman 1993, 1998). He estimated the season of death of the hunted animals by analysing seasonal bands in the dental cementum of the teeth sampled from several sites. Results showed that in the majority of Natufian sites studied, including Eynan, the gazelles were hunted during several seasons (Lieberman 1993 table 1, 1998 table 1). From these data, the author hypothesized that Natufian sites were occupied for more than one season. By examining the thin sections and the impregnated blocks analysed by Lieberman, however, we found that this sample was composed of dental remains of gazelle from the Early and Late Natufian layers,

although the results were published as coming from a single set (Lieberman 1993 table 1, 1998 table 1).

The site was discovered in 1954 after construction work that caused severe damage to some of its structures. Ten excavation seasons, in which more than 200 m² were excavated, were conducted at the site by Jean Perrot, Monique Lechevallier and Francois Valla of the French National Centre of Scientific Research (CNRS). They distinguished three main phases of occupation: Early Natufian (layers IV and III), Late Natufian (layers II, Ic) and Final Natufian (layer Ib). None of the previous analyses were carried out on dental material from the Final Natufian occupation (excavated by F. Valla and H. Khalaily; Valla et al. 2017). The objective of this paper is to evaluate the combination of two methods—tooth mesowear and microwear techniques with ageing by tooth eruption and wear stages—to investigate the seasonality of game procurement at the site. Each method has its own limitation. Tooth eruption and wear stages have higher accuracy until permanent dentition is established while tooth mesowear and microwear can be applied mostly to subadults and adults with well-developed occlusal wear facets on their permanent dentition. By combining these two methods, we increased the sample size to include the entire population (both young and adults) and thus improved the accuracy of the seasonality estimate from the archaeological perspective.

Environment and climate during the Final Natufian in the Jordan Valley

The southern Levant is influenced by a combination of global and local phenomena. Its terrain is varied, and substantial changes occur along the east-west and north-south geographical axes. The source of the rain and its frequency and rate are under continuous study and debate, and it appears that fluctuations occurred on a regular basis, and were not necessarily reflected in the larger paleoclimatic frame (e.g. Ben Dor et al. 2019; Lev et al. 2019). When focusing on a specific area, there are several methods used to reconstruct the habitats. One is a comprehensive summary viewed from an ecological perspective, such as Askhenazi's (2013) reconstruction of the habitats in the Eynan ecosystem, based on the site's flora and fauna, coupled with recent conditions. Actually, the Eynan inhabitants had numerous sources of food for foraging. In the vicinity to the east, Lake Hula, a shallow lake with marshes (that was drained in the mid-twentieth century), had submerged and floating vegetation, and muddy, stony and sandy shores. In its marshy areas, there was slow running water with stony and sandy bottoms and swamps with reeds and Cyperaceae. The springs near the site have a constant year-round temperature of 21–22 °C, and in the past created an open pond and a short river about 3 km long before it entered the lake (Dimentman et al. 1992). These shores and river banks were populated with

reed and grass. To the west of the site, dense or open Mediterranean woodland covered the hill slopes. Moderate slopes with dry grass land with rocky fields prevailed towards the south (Askhenazi 2013).

It seems that slight fluctuations in the track, depth and frequency of mid-latitude eastern Mediterranean cyclones, resulting in wetter and drier regional climatic episodes, were observed during the late Pleistocene (Ben Dor et al. 2018). One should also be aware of the evaporation factor that was enhanced during the Holocene as seen from Lake Kinneret (20 km southern to Eynan; Lev et al. 2019). The severity of the fluctuations during the Younger Dryas, which was broadly the time interval of the Final Natufian of Eynan, is a question of debate. Global data clearly shows a phase of major change; however, its representation on the local scale might vary. Could the magnitude of these changes be observed in the archaeological record? Were human behavioural patterns, mode of prey procurement, seasonality and foraging methods influenced as a result? Some studies have pointed out the relative stability of the environmental conditions at Eynan (Askhenazi 2013; Biton et al. 2016), while others support the existence of a somewhat cooler climate compared to the present (Bar-Matthews et al. 1997, 1999; Hartman et al. 2016; Valla et al. 2007; Borvon et al. 2018).

Based on the analysis of the phytoliths from Abu Hureyra (Syrian Euphrates), Rosen and Rivera-Collazo (2012) suggest that Late Natufians exploited a broad range of grass species and sedges in other sites as well, Eynan, el-Wad and Hilazon Tachtit (Northern Israel), that suggests a shift away from woodland products in the Early Natufian to heavier emphasis on small-grained grasses as well as wild cereals. They argue that ‘hunter–gatherer subsistence systems in the Near East were highly adaptable, and climatic fluctuations leading to major restructuring of vegetation only resulted in a shift in resource focus rather than forcing a collapse of foraging economies hence requiring a major change in social and economic organization’ (Rosen and Rivera-Collazo 2012). Based on isotopic analysis of gazelle teeth from several Natufian sites, Hartman et al. (2016) hypothesized ‘that human groups responded by shifting settlement strategies—increasing population mobility and perhaps moving to the warmer Jordan Valley where wild cereals were more productive and stable’. The mobility of these groups can be investigated through the seasonal procurement of ungulates.

Materials and methods

Materials

The dental remains of the ungulate species (*Bos primigenius*, *Capreolus capreolus*, *Cervus elaphus*, *Dama mesopotamica*, *Gazella gazella* and *Sus scrofa*) analysed in the present study

were sampled from the entire excavated surface of the Final Natufian Layer (Ib) excavated from 1996 to 2005: ca. 125 m². In this area, layer Ib is approximately 50 cm thick. It includes several structures built of stone representing two main phases of occupation, which represent a time span estimated from 10,850–10,250 to 10,140–9750 in ¹⁴C calibrated years BC (Valladas and Kaltnecker in Valla et al. 2007). The studied material was collected both inside and outside the structures and without discrimination in the entire stratigraphy. Jaw and maxilla bones, like the other animal skeletal elements from layer Ib, are heavily fragmented and the dental remains analysed reflect this characteristic (Online Resource 1 Table 1). Identification and ageing of the dental remains were conducted at the National Natural History Collections of the Hebrew University of Jerusalem, following the standard zooarchaeological procedures (cf. “Age and season-at-death based on tooth eruption and wear patterns” section). A total of 81 dental remains (jaw fragments and isolated teeth) were moulded (cf. “Tooth microwear analysis” section). Of these, 47 were suitable for mesowear analysis and 44 for microwear. We also sampled extant wild ungulates from the National Natural History Collections of the Hebrew University of Jerusalem. Persian fallow deer (*Dama mesopotamica*; *N*=5) come from the western and eastern Galilee (Northern Israel), mountain gazelle (*Gazella gazella*; *N*=16) from various areas in Northern Israel and wild boar (*Sus scrofa*; *N*=31) from the Golan Heights (Fig. 1). The full list of materials used for mesowear and microwear analyses, for tooth eruption and wear, and the raw data are available in Online Resource 1 (Tables 1, 2, 3 and 4).

Methods

Tooth mesowear analysis

Mesowear analysis is a method of categorizing 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). Mesowear is scored macroscopically from

Table 1 Summary of the mesowear data for ungulates from the Late Natufian layer Ib of Eynan/Ain Mallaha and for extant ungulates from Israel. *N* number of adult individuals, *MWS* mesowear score

Eynan layer Ib	<i>N</i>	<i>MWS</i>	Extant species	<i>N</i>	<i>MWS</i>
<i>B. primigenius</i>	1	2			
<i>C. capreolus</i>	14	0.9			
<i>C. elaphus</i>	10	1.4			
<i>D. mesopotamica</i>	4	1.8	<i>D. mesopotamica</i>	5	1.6
<i>G. gazella</i>	17	0.6	<i>G. gazella</i>	18	1.2

the buccal side of molars. A diet with low levels of abrasion (high attrition) preserves sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, result in more rounded and blunted buccal cusp apices (Fortelius and Solounias 2000). Unworn (and marginally worn) teeth, extremely worn teeth and those with broken or damaged cusp apices are 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 is suitable for dietary reconstruction. In this study, the standardized method (mesowear ‘ruler’) introduced by Mithlacher et al. (2011) is employed. This 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). Using the mesowear ruler as a reference, cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a value of 0. Cusps that were morphologically intermediate between reference cusp 0 and reference cusp 1, or equal to reference cusp 1, were assigned a value of 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or MWS (Mithlacher et al. 2011). To reduce inter-observer error (as reported by Loffredo and DeSantis 2014), dental mesowear analysis was conducted by a single experienced researcher (FR). All species were analysed except the wild boar, because its bunodont teeth are not suitable for the traditional mesowear analysis. The raw mesowear data are available in the Online Resource 1 Table 1.

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). To avoid problems related to repeatability and inter-observer error (DeSantis et al. 2013; Mithlacher et al. 2012), in the present study, 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 badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features created during the collection process or during storage) were removed from the analysis, following King et al. (1999) and El-Zaatari (2010).

Casts were observed under incident light with a Zeiss Stemi 2000C stereomicroscope at $\times 35$ 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 in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004) which basically distinguishes 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 are not merely longer than they are wide, but have straight, parallel sides. These categories are subdivided as follows:

- Pits are classified as small pits, large pits, or puncture pits. Large pits are deeper, less refractive (always dark), at least twice the diameter of small pits, and often have more irregular outlines than small pits. Puncture pits are large and very deep pits with crater-like features with regular margins, and they appear dark due to low refractivity.
- Scratches are divided into fine scratches (i.e. narrow scratches that appear relatively shallow and have low refractivity), coarse (i.e. wide scratches that are also relatively deep but have high refractivity) and hypercoarse (i.e. very deep and trench-like features which are wider than the other types of scratches).

The presence of some other features is recorded qualitatively. Cross scratches are oriented approximately perpendicularly to the majority of scratches observed on the enamel (Solounias and Semprebon 2002). Gouges are features that have ragged, irregular edges and are much larger (approximately 2–3 times as large) and deeper than large pits. They are relatively dark features with low refractivity. The presence or absence of these features in a microscope field was recorded. In addition, scratch textures were assessed using the scratch width score (SWS) which is obtained by giving a score of ‘0’ to a tooth with predominantly fine scratches, ‘1’ to one with a mixture of fine and coarse types of textures and ‘2’ to one with predominantly coarse scratches. Individual scores for a sample of teeth were then averaged to get the SWS. Scratches and pits were counted in two areas on the paracone of the upper molars and the protoconid of the lower molars. The raw microwear data are available in the Online Resource 1 Table 1. The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon 2002; Rivals et al. 2010) and modern ungulate populations from Northern Israel (Galilee) sampled in the National Natural History Collections at the Hebrew University of Jerusalem (HUJI) (see Online Resource 1 Table 2). All statistics were performed using R (R Core

Table 2 Summary of the microwear data for ungulates from the Late Natufian layer Ib of Eynan/Ain Mallaha and from extant ungulates from Israel. *N* number of adult and subadult individuals, *NP* average number of pits, *NS* average number of scratches, *SD* standard deviation, *CV*coefficient of variation, *%LP* percentage of individuals with large pits, *SWS* scratch width score, *%XS* percentage of individuals with cross scratches, *%G* percentage of individuals with gouges, *%HC* percentage of individuals with hypercoarse scratches

Species	N	NP	SD	NS	SD	CV	%LP	%G	SWS	%XS	%HC
Eynan layer Ib											
<i>B. primigenius</i>	1	14	—	16	—	—	—	—	—	—	—
<i>C. capreolus</i>	9	13.28	3.52	10.28	1.00	0.10	55.6	11.1	0.56	0	0
<i>C. elaphus</i>	8	18.63	3.24	18.63	3.65	0.20	75.0	87.5	1.38	0	37.5
<i>D. mesopotamica</i>	3	15.67	1.76	12.50	1.21	0.10	33.3	66.7	1.00	0	33.3
<i>G. gazella</i>	15	25.90	3.43	16.87	2.37	0.14	100	46.7	1.00	0	0
<i>S. scrofa</i>	8	26.75	3.14	24.38	2.42	0.10	100	100	1.38	100	50.0
Extant species											
<i>D. mesopotamica</i>	5	45.30	5.86	9.60	1.39	—	100	100	1.20	0	20.0
<i>G. gazella</i>	16	30.53	9.93	21.06	2.58	—	93.8	43.8	1.00	0	6.3
<i>S. scrofa</i>	31	19.56	2.59	20.76	1.91	—	58.1	16.1	1.06	1.00	6.5

Team 2019). The bivariate plots were generated using the R package MicrowearBivaR (Rivals 2019; available at <https://zenodo.org/record/2587575#.XJtwI1VKiUk>).

Finally, following Rivals et al. (2015), two measures of the variability of scratch density, namely the standard deviation (SD) and the coefficient of variation (CV), were used to estimate the duration of accumulation of faunal assemblages at the sites. As seasonal changes in diet are recorded by microwear, the variability of the micro-scratches allowed us to detect if accumulation is seasonal or not. It is not possible to directly estimate the exact season but only to evaluate its relative duration. The combination of the two measurements of variability allows assemblages to be classified into one of the following categories: (a) seasonal events or shorter time windows, (b) events longer than one 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, a joint bootstrapped function of CV and SD ($n = 500$, with replacement) using the R code from Domínguez-Rodrigo et al. (2019) was applied. This method was applied on the ungulate assemblages from Eynan as well as on the modern sample of mountain gazelles with known dates of death. For the latter, the sample was divided according to the date of death of the individuals: the full sample of gazelles, representing death throughout the year (G1; $N = 10$), and two sub-samples representing death from the end of the summer to autumn (G2; $N = 6$) and from winter to early spring (G3; $N = 4$).

Age and season-at-death based on tooth eruption and wear patterns

Age-at-death data are used in zooarchaeology to construct mortality profiles and make inferences about herd exploitation strategies (e.g. Stiner 1990). Based on a macroscopic analysis of the cheek teeth, the ages were estimated using published standardized recording systems, reference tables and the osteological collection of the National Natural History Collections at the Hebrew University of Jerusalem (HUJI). We employed the age estimation methods of Munro et al. (2009) for mountain gazelle; Bowen et al. (2016) for fallow deer; Tomé and Vigne (2003) for roe deer; Azorit Casas (2011) and Habermehl (1961, 1985) for red deer; and Ducos (1968, pp. 10–13) for aurochs. The eruption stage and/or wear pattern for each isolated tooth or jaw fragment was recorded and assigned to age ranges, with larger age ranges for isolated worn permanent teeth. In order to estimate the minimum number of individuals, we attempted to refit mandible or maxilla fragments and isolated upper and lower teeth, and match left and right lower and upper elements of the same age ranges, based on idiosyncratic patterns of wear.

Season at death data is essential to determine in which months of the year the various resources were exploited and to infer when a site was occupied. Such data can only be reliably established from young/subadult individuals, i.e. a subset of the total number of individuals whose age could be determined. As the dental remains of *Bos primigenius* are from a single adult, they will not be considered in the seasonal data set. In the present study, seasons could be estimated with a precision of 1 to 5 months, according to the type of remain (isolated tooth or portion of mandible). Information on the

timing of births in modern ungulate populations is critical for inferring season of death of archaeological specimens. Birth peaks occur in spring (April–June) in most ungulate species from Mediterranean regions, coinciding with the period of vegetation growth and availability of nutritionally high-quality forage. In lush Mediterranean habitats or near agricultural areas where water is available most of the year, mountain gazelle populations breed throughout the year, with a single peak in spring (southern Golan Heights, Mendelssohn et al. 1995; Upper Galilee, Baharav 1983a, b) or two, in April and November (Lower Galilee, Baharav 1983a, b) (Online Resource 1 Table 3). On the basis of these studies, and following Davis (1983), we defined spring as the time of gazelle births between mid-April and mid-June. For Persian fallow deer, we referred to a population reintroduced in the upper west Galilee region, with May as the birth time (Bar-David et al. 2005). As red deer were extirpated from the eastern Mediterranean, we referred to extant populations from southern Spain where births occur between mid-May and mid-June (Azorit pers. com.). Similarly, roe deer populations from Mediterranean areas give birth in May (San José et al. 1995, 1997).

Combination of the tooth eruption and micro/mesowear methods

Estimations of seasonality relying on dental age-at-death can be inferred from the young and subadult individuals, while microwear and mesowear observations can be examined on adult individuals with worn permanent teeth. Each method was performed separately on the teeth by two independent researchers (AB for tooth eruption and first wear stages and FR for tooth meso- and microwear). The results of the two analyses were then compared taking into consideration the archaeological setting. Moreover, we examined in detail those cases where the two methods were applied, checking whether they had in fact resulted in a consistent seasonality pattern. Finally, more general interpretations were formulated for the

inherent limitations of the methods and their relevance to the Final Natufian occupation at Eynan.

Results

Tooth mesowear

The mesowear scores for the ungulates from Eynan (i.e. *C. capreolus*, MNI = 14; *C. elaphus*, MNI = 10; *D. mesopotamica*, MNI = 4; *G. gazelle*, MNI = 17) are lower (or equal) than the cut-off value that separate extant grazers (MWS > 2) from browsers (MWS < 2) (Table 1; Fig. 2a). The values fit within the range of values of the extant leaf browsers, but also overlap with the extant mixed feeders. All the ungulates from Eynan layer Ib are either browsers or browse-dominated mixed feeders. In comparison to extant species from the same area, the samples of fallow deer (*D. mesopotamica*) from Eynan exhibit very similar values (Fig. 2a). Conversely, for the gazelle (*G. gazelle*), the modern sample has a MWS double that was found in the fossil sample. Regardless, the two samples fit within the range of browse-dominated feeding.

Tooth microwear

Preservation of the microwear patterns on the enamel surfaces shows strong post-depositional alterations. Only half of the samples were suitable for tooth microwear analysis. We were able to analyse 58.8% of the teeth of *C. capreolus*, 47.1% of *C. elaphus*, 50% of *D. mesopotamica*, 55.6% of *G. gazelle* and 61.5% of *S. scrofa* in detail. Only a single specimen of *B. primigenius* was suitable for microwear analysis. The other teeth were discarded due to taphonomic alteration. Most of the faunal remains are covered with breccia-like sediments that affected the enamel surface and erased the microwear features.

The single specimen of an adult aurochs (*B. primigenius*, MNI = 1) has an intermediate number of scratches (Table 2) and falls between the extant leaf browsers and the extant grazers (Fig. 2b). Due to the small sample size, the data must be considered with caution and cannot be used in future interpretations.

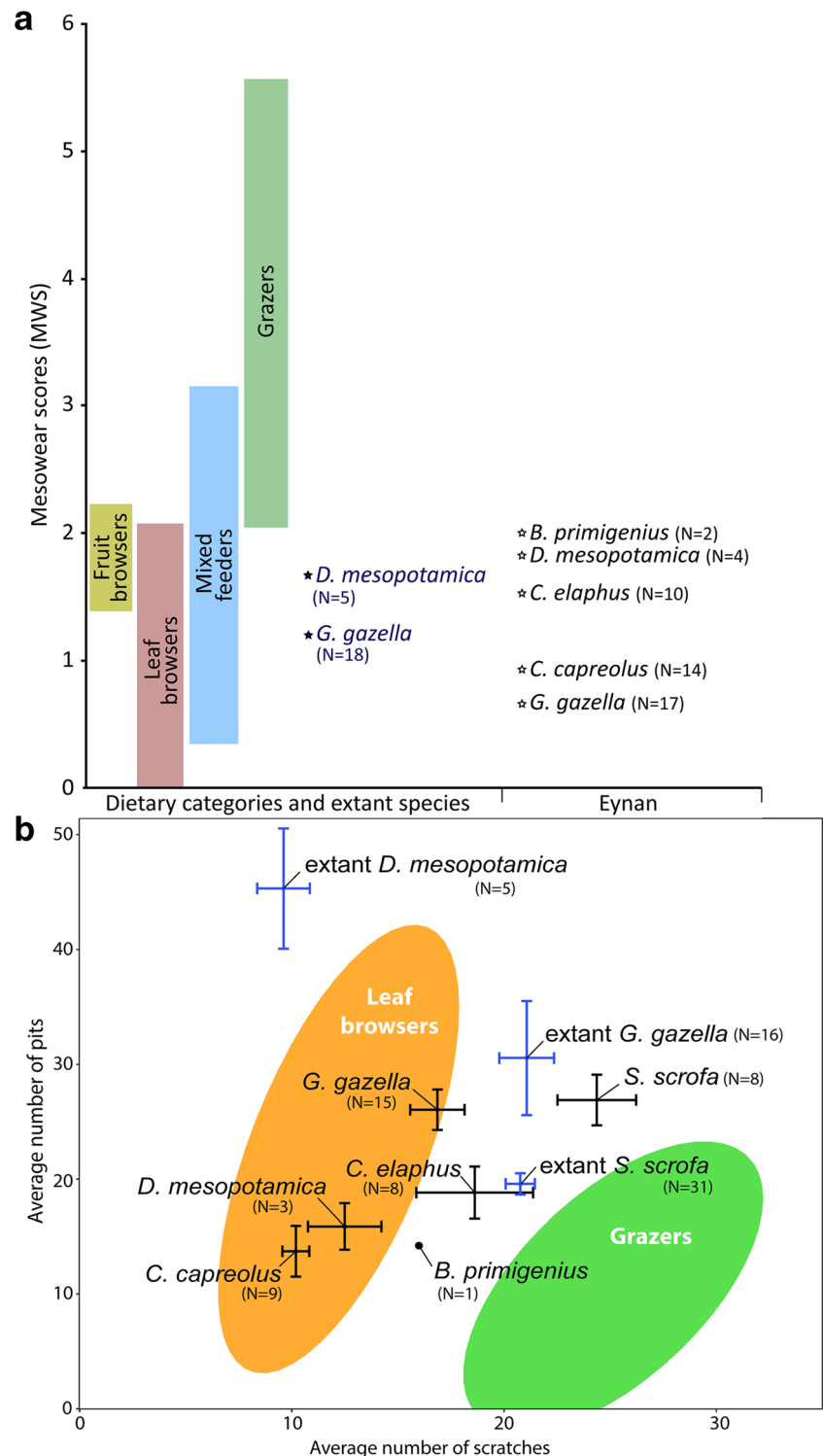
Roe deer (*C. capreolus*, MNI = 9) show the lowest numbers of pits and scratches of all the fossil samples (Table 2). This reflects a low abrasive diet and the sample falls among the extant leaf browsers (Fig. 2b). The low SWS, absence of hypercoarse scratches and low percentages of individuals with gouges (Table 2) suggest that roe deer fed exclusively on leaves of monocot plants (excluding twigs and small branches).

The red deer (*C. elaphus*, MNI = 8) has a moderate number of pits and intermediate number of scratches (Table 2). The sample falls between the extant browsers and grazers (Fig.

Table 3 Minimum number of individuals (MNI) based on the young individuals (according to dental age) that are included in the present seasonality study

Species	MNI
<i>G. gazelle</i>	13
<i>C. capreolus</i>	7
<i>C. elaphus</i>	9
<i>D. mesopotamica</i>	3
<i>B. primigenius</i>	No young individuals
<i>S. scrofa</i>	Ageing not yet performed

Fig. 2 **a** Plot of the mesowear scores for the ungulates from the Late Natufian layer Ib of Eynan/Ain Mallaha in comparison to the dietary categories from Fortelius and Solounias (2000) and the extant species from Israel (in blue). **b** Bivariate plot of the average numbers of pits and scratches for the ungulates from the Late Natufian layer Ib of Eynan/Ain Mallaha. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. The samples in black correspond to the fossil samples, and those in blue to extant species. Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant leaf browsers and grazers based on the reference database from Solounias and Semprebon (2002)



2b). It can be defined as a mixed feeder, which probably shifted its diet on a seasonal basis from browse-dominated to grass-dominated mixed feeding. The presence of gouges and hypercoarse scratches (and the high SWS) indicate that red deer fed not only on leaves but also on twigs from tree or bushes.

The fallow deer (*D. mesopotamica*, MNI=3) has a low number of pits and scratches (Table 2). It falls among the extant leaf browsers, next to the red deer, but these two species do not overlap (Fig. 2b). The sample from Eynan had a diet significantly different than that of the extant Persian fallow deer from the western and eastern Galilee (Northern Israel). The latter falls

above the confidence ellipse of the extant leaf browser due to a very high number of pits (Fig. 2b). It would correspond to the ‘dirty browser’ dietary category (Semperebon and Rivals 2007), in which a high number of pits is related to the presence of high loads of grit and dust on the vegetation.

The mountain gazelle (*G. gazella*, MNI = 15) has an intermediate number of pits and scratches (Table 2). It falls near the edge of the ellipse of the extant leaf browsers, and the variability of the values (standard error of the mean, on Fig. 2b) overlaps with the mixed feeders. The sample from Eynan could be defined as browse-dominated mixed feeder. The extant mountain gazelles sampled from various areas in Northern Israel (see Online Resource 1 Table 2 for more details) falls between the ecospace of the grazers and browsers (Fig. 2b) and is a typical mixed feeder.

The wild boar (*S. scrofa*, MNI = 8) has a high number of scratches that overlap with the range of the extant grazers, but differs in having high numbers of pits (Table 2; Fig. 2b). Moreover, the high proportion of individuals with large pits, gouges, cross scratches and to a lesser extent hypercoarse scratches would indicate an omnivorous diet similar to that of the extant wild boar from the Golan Heights (Table 2; Fig. 2b).

For the species where both mesowear and microwear data are available (*C. capreolus*, *C. elaphus*, *D. mesopotamica*, *G. gazella*), the interpretations from the two proxies are consistent and indicate that browsing or browse-dominated mixed feeding diets prevailed.

Assessing the cumulative nature of the hunting events from the microwear data

In order to distinguish the seasonal variability of the extant gazelle’s diet with known dates of death, we examined their microwear patterns comparing plotted variability values (SD and CV) using the model of Rivals et al.

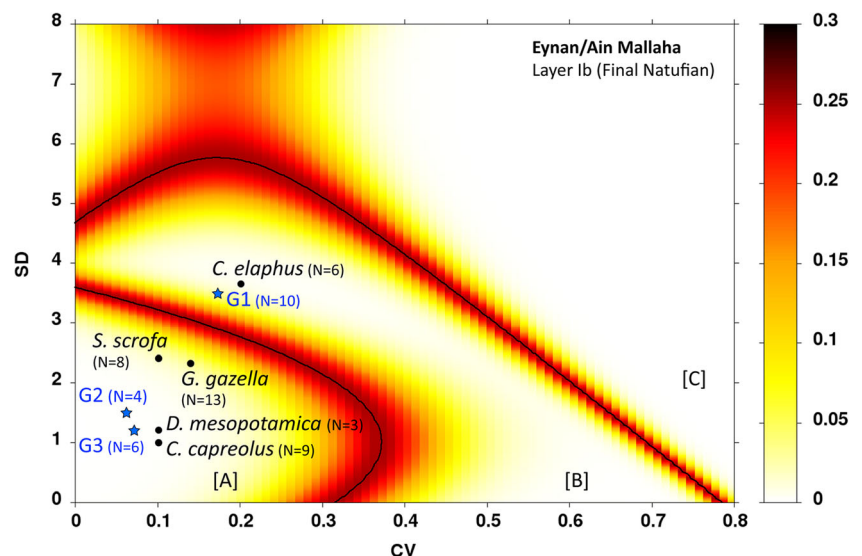
(2015). The three samples fall in two different areas of the bivariate plot (Fig. 3). The sample G1 ($N=10$) falls in area B corresponding to animals that died over a period longer than one season (Fig. 3). The samples G2 ($N=6$) and G3 ($N=4$) fall in area A corresponding to animals that died over one season or less (Fig. 3). The results fit the expected position of each sample. This test supports the accuracy of the model and its application to the gazelles from the site area.

The model was applied to the five species from Eynan. The microwear patterns visible on the red deer indicate high variability of the microwear signal, reflected in both the SD and the CV values. This variability in microwear is due to seasonal shifts in the red deer diet and suggests that the 8 individuals were killed over a period that lasted more than a single season (Fig. 3). Conversely, for the other species—mountain gazelle, roe deer and fallow deer—the low variability of the microwear signal for each species, reflected in both the SD and the CV, indicates that the 27 individuals of these three species were killed during one season or less (Fig. 3). It is not possible, however, to identify in which season each individual was hunted, nor is it possible to establish if the accumulation results from a single occupation of one season or from repeated occupations at the same season over several years. The microwear patterns observed on the wild boar also indicate a low variability, but the results should consider that the model (Rivals et al. 2015) was established on herbivorous species, and did not include omnivores. Therefore, the results from the wild boar should be excluded.

Season at death according to tooth eruption and wear stages

For gazelle, the seasons at death were estimated based on 13 individuals with a dental age between 1–2 and 18–20 months

Fig. 3 Boundary lines with the error probability (heat map) based on standard deviations and coefficient of variation values of microwear data used for the classification of samples into short events (region A), long-term events (region B) or two separate short events (region C). The blue stars correspond to the extant samples of gazelles representing death throughout the year (G1), death from the end of the summer to autumn (G2) and from winter to early spring (G3). The black dots correspond to the samples of ungulates from Eynan level Ib



[illegible]

For fallow deer (MNI = 3), two individuals were culled in April (one newborn and one 12 to 13 months old); the older one (20 months old) indicates a death in January (Table 3, Fig. 4).

Estimates of seasonality based on tooth eruption and wear were established from young and subadults, while

Species	Ne	Nm	Nc	NT
<i>G. gazella</i>	13	15	3	25
<i>C. elaphus</i>	7	8	2	13
<i>C. capreolus</i>	7	9	3	13
<i>D. mesopotamica</i>	3	3	0	6

If the two sets of data are compared globally for each species, we observe the following:

- Gazelle—one main season: the highest peak is between mid-November and mid-December (12 out of 13 individuals) if a minimum range is considered (Fig. 4). If a wider range is considered, then the hunting season extends from

Table 5 Season at death, microwear and diet for individuals where results were obtained from the two methods, tooth eruption and tooth microwear

Indiv. no.	Age (in months)	Season-at-death (dental age)	N micro-scratches	Estimated duration (microwear)	Seasonal diet
<i>Gazella gazella</i>				1 season or shorter	
Ga5	18–20	Mid-October to mid-February	15.5		Mixed feeder
Ga7	7	Mid-November to mid-January	16.5		Mixed feeder
Ga11	3–6	Mid-July to mid-December	17.5		Mixed feeder
<i>Cervus elaphus</i>				Longer than 1 season	
Ce4	10–15	Mid-March to mid-September	12		Browser
Ce7	10–15	Mid-March to mid-September	13.5		Browser
<i>Capreolus capreolus</i>				1 season or shorter	
Ca3	6–7	November to December	9.5		Browser
Ca4	8–11	January to April	9.5		Browser
Ca7	17–20	October to January	11		Browser

summer to early winter. The 15 individuals yielded a microwear signal, corresponding to one season or less. Therefore, the most parsimonious hypothesis is that the adults were hunted during the same seasons as the younger individuals, i.e. in late autumn.

- Red deer—the culling period estimated from dental eruption and wear ranges from mid-March to mid-September (Fig. 4). The high variability of the microwear signal, indicating a duration longer than one season, supports this result. The red deer were hunted from spring to summer.
- Roe deer—the estimated seasons of death for the seven young individuals encompass the entire year, with no evidence of a peak at any specific season, but instead three periods (spring, summer and late autumn) are represented. The low microwear variability, on 10 subadults and adults, suggests a seasonal (3 months or less) procurement of the roe deer. There is a discrepancy between the results obtained from the two methods, unless one considers that the interval of overlapping seasons for the 3 individuals that could be compared (Ca3, Ca4, Ca7) is over two contiguous seasons, i.e. autumn and winter.
- Fallow deer—the season at death and the duration were estimated from 2 young, 1 sub/young-adult and 3 adult individuals, respectively. The newborn and the yearling were killed in spring while the 20-month-old was killed in early winter. The microwear indicates the adults were killed during a single season, which is consistent with the seasonality data. Indeed, this would indicate a number of seasonal hunting episodes.

Discussion

Diet variation in ungulates has been associated with environmental factors such as habitat and season (Gebert and Verheyden-Tixier 2001). As vegetation changes according to the phenology of the plants and the seasons, the feeding traits of ungulates can change, shifting from pure grazing through intermediate feeding to pure browsing (Hofmann 1989; Putman and Flueck 2011). However, in areas where different species coexist, they always differ in their behaviour and ecological requirements by at least some minimal amount to avoid competitive exclusion, as is often observed among cervids (Azorit et al. 2012; Torres et al. 2012). Moreover, intra-specific differences are also evidenced during the spatial separation of sexes and species and also to some extent during the rut season (Azorit et al. 2012). As a consequence, differences in dietary traits and their variability could be related to the composition of the herd, and would depend on the proportion of females and males that were hunted and brought back to the site. Consequently, dietary traits are shaped not only by seasonal changes in resource availability, but also by the presence or absence of species that compete for resources in the same habitat, and by the composition of the herd. In the case of Eynan, three deer species coexisted (red deer, fallow deer and roe deer) and each one may have influenced the dietary behaviour of the others as in present day populations from the Mediterranean area (Azorit et al. 2012; Torres et al. 2012). Mesowear is not affected by these seasonal changes because it records a long-term signal, averaging the diet over periods of

time longer than 6 months (Ackermans et al. 2018, 2020). Microwear, however, expresses a short-term ecological signal which reflects the diet of the last days or weeks of each individual (Grine 1986; Mainland 1998; Teaford and Oyen 1989). Microwear is strongly affected by all the seasonal changes associated with the dietary behaviour of each species. Unlike mesowear, it will reflect the dietary traits of the individuals at the time of death.

Extant gazelles are known to be mixed feeders, whose diets shift seasonally between browsing and grazing (Baharav 1983a; Mendelssohn and Yom-Tov 1999; Martin 2000). From their behavioural ecology, modern mountain gazelles from the Hula Valley in the Upper Galilee are known to be primarily grazers but shift their diet to browsing in the summer and autumn (from July to November; Fig. 4 in Baharav 1983a). The microwear reference sample of modern mountain gazelles, which falls in the middle of the mixed feeding range, probably includes animals that died at different seasons throughout the year, portraying an average of the dietary signal. During the Younger Dryas, gazelles in Northern Israel probably had a similar seasonality pattern in diets, which is supported by carbon and oxygen isotopes values that reflect the typical modern Mediterranean climate pattern (Hartman et al. 2016). The analysed gazelle individuals from Eynan, most likely died at a time of the year when they mainly browsed (browse-dominated mixed feeder). This result supports the estimate based on tooth eruption that suggested these gazelles were probably killed at the end of autumn (12 individuals out of 13) (Table 6).

The red deer is known to be highly flexible in its feeding behaviour (Verheyden-Tixier et al. 2008). In Mediterranean ecosystems, extant red deer use a high proportion of grass during the winter and spring, and the proportion of leaves and fruits from shrub and forest areas increases in summer and autumn (Rodriguez-Berrocal 1978; Carranza et al. 1991). The red deer from Eynan had a mixed feeder diet that probably reflects dietary shifts from browsing to grazing according to resource availability in the different seasons. The mixed feeding signal results from averaging diet over various

seasons (at least two seasons). The seasonality estimated from tooth eruption indicates that red deer died from mid-March to mid-September, i.e. a maximum duration of 6 months. Due to the large value interval for the season of death and the overlap of the individual results, the duration could be much shorter. However, the variability of the microwear signal suggests that death occurred over a period longer than 3 months, supporting the longer duration evidenced by tooth eruption (Table 6). Consequently, the combination of tooth microwear and tooth eruption supports the hypothesis of procurement of red deer during an extended part of the year, between 4 and 6 months, in the spring and summer.

For the fallow deer, tooth microwear only identified a single season of death for the three adult individuals. Even if this result is strongly limited by sample size, we can assume, in view of the low number of scratches, that they died in a season when their diet was leaf browsing (Table 6). The three young individuals provided reliable information about two death events in different seasons (spring for the new-born and the yearling and early winter for the 20-month-old). The extant fallow deer specimens examined in this paper come from Northern Israel (Supplementary Online Material Table 2) and were reintroduced in an area where a few creeks cut through the hills from east to west, in the Nahak Kziv Nature Reserve, where except for the Kziv stream, most of the creeks are ephemeral, flowing only in the winter. Artificial water resources (e.g. pipe leaks, cattle troughs, agricultural watering) are scattered throughout the region. The Mediterranean vegetation in the area is open scrubland of Kermes oak (*Quercus calliprinos*) and spiny broom (*Calicotome villosa*) shrubs; dense forest of Kermes oak, bay laurel (*Laurus nobilis*), buckthorn (*Rhamnus punctata*), mock privet (*Phillyrea latifolia*) and sarsaparilla (*Smilax aspera*); and riparian zones along streams dominated by Oriental plane trees (*Platanus orientalis*). Most of the settlements in the area are agricultural villages and about 20% of the land is used for agricultural orchards (mostly apple and peach trees), fields, hen houses and cattle sheds (Bar-David 2002; Perelberg et al. 2003). The five modern fallow deer

Table 6 Synthesis of the overall results of the different proxies and methods used in this study. Abbreviations: B = browser; B-MF = Browse-dominated mixed feeder; MF = Mixed feeder

Species	Dietary traits		Season at death	
	Mesowear	Microwear	Microwear	Dental eruption and wear
<i>G. gazella</i>	B or B-MF	B-MF	1 season or less	All year except mid-February to mid-April
<i>C. elaphus</i>	B or B-MF	B	1 season or less	All year
<i>C. capreolus</i>	B or B-MF	MF	Longer than 1 season	Mid-March to mid-September
<i>D. mesopotamica</i>	B or B-MF	B	1 season or less	April–May and January

individuals have a microwear pattern significantly different from that of the fallow deer from Eynan. Both are leaf browsers, but the sample of extant individuals has a significantly higher number of pits (Fig. 1), and high proportion of large pits (on 100% of the individuals). The high number of pits corresponds to what Semprebon (2002) coined ‘dirty browsers’, i.e. animals that feed on plants covered by grit or dust or animals that feed on plants or plant parts close to the ground and ingest soil together with the plants. Dirty browsers are very common in arid or semi-arid habitats, e.g. camels, llamas, Mongolian gazelles and Tibetan antelopes (Semprebon and Rivals 2010; Rivals et al. 2011). In the fallow deer sample from Northern Israel, the number of pits is not as high as in dirty browsers from arid habitats, but it reflects dry conditions, or at least animals feeding on plant parts covered by some amount of dust, or parts close to the ground (and ingesting some soil together with the leaves). It may reflect particular conditions of the reintroduced species, possibly due to anthropized habitats. In the population of Persian fallow deer from the Nahak Kziv Nature Reserve, western Galilee, grazing constitutes over 60% of their diet and occurs year-round, but in the summer and autumn, the deer are forced to feed on other sources such as fruits and tree leaves (Dolev et al. 2002). Taking into account this information, it is more likely that the three archaeological adult individuals died in summer or autumn. Even with the absence of individuals studied with the combined techniques of tooth eruption and microwear, it was still possible to propose a hypothesis to place the death events of both young and adult individuals. The death of the three young fallow deer occurred at the beginning of the red deer hunting period and at the end of the mountain gazelle hunting period. The adults were probably killed between these two periods but the results depend on the accuracy of our understanding of the diet at the time of death.

For roe deer, the data regarding the season of death suggest procurement of the young individuals throughout the year, without any evidence for a dominant season. The variability of the microwear signal in the adults shows values consistent with a duration of 3 months or less. Considering the age groups analysed in each case, it is possible to hypothesize that the procurement of the young individuals occurred throughout the year, but for the three individuals analysed by the two methods, results may be interpreted as hunting episodes of about 3 months during late autumn–early winter (Table 6).

Hunting of the main ungulate species (mountain gazelle, red deer, fallow deer and roe deer) during the Final Natufian occupation at Eynan occurred throughout the year. In addition to these four species, human groups focused on other ungulate species such as the wild boar (for which we do not have reliable data), other animals (e.g. fish, birds) and vegetal resources.

Admittedly, this result should be taken with caution regarding its bearing on the manner the site was occupied by

Natufian people, as the studied material originates from a relatively thick layer accumulated over a long period of time, rather than from a deposit representing a single event. On the other hand, the coherency of the data obtained for each species is challenging in that it may suggest long-term hunting habits unmodified throughout the entire Final Natufian occupation at Eynan. Additional analyses of samples with refined stratigraphic definition will be necessary to explore these issues.

At the present stage of research, the significance of the study is mostly methodological. In most cases, the combination of tooth eruption and microwear allowed us to increase the sample size (Table 4), and to achieve a more accurate estimation of the seasonality of game procurement during the Final Natufian occupations at Eynan. The two techniques are complementary and rely on independent sources of evidence, the patterns of tooth eruption and wear and the seasonal changes in diet. Tooth eruption and first wear stages allow the maximum range for the season of death to be established and the variability of the tooth microwear signal can be used to confirm this maximum range or to narrow it down. Seasonal changes in the ungulates’ diet recorded in the microwear patterns allow confirmation of the season at death inferred from dental age in some cases.

Conclusion

The present study is the first attempt to directly combine analysis of tooth eruption and wear and tooth microwear and mesowear. It allowed us to increase the sample size for estimating the season of death by considering the entire population, i.e. young and adult individuals. It also allowed us to increase the accuracy of the estimate of the seasonality of game procurement by narrowing down the timeframe of the season-at-death. Besides the traditional reconstruction of paleodiets and habitats, tooth microwear is of additional interest for its applications in zooarchaeology. This combination of techniques opens new perspectives for investigating seasonal patterns of ungulate procurement in archaeological sites using non-destructive sampling.

The archaeological approach developed on the Final Natufian layer at Eynan attempts to unravel and restore the complexity of the occupation dynamics. What is defined as a layer of occupation is largely an operational shortcut. Actually, it covers a range of events and activities materialized in the space of the site by different interrelated structures which have often been rearranged and reused for different purposes. Understanding the temporalities of occupations requires high-resolution studies. We do not claim to have reached this level of archaeological precision through this study, one limitation being that our sample of dental remains comes from various structures (and from the stony matrix) so

that the strict contemporaneity of the deposits cannot be demonstrated. On the other hand, from a methodological point of view, we believe that the study of the hunting seasons attempted here is part of a high-resolution analytical approach that enables us to contribute to the discussion and to better define what is meant by multi-seasonal occupations.

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Code availability MicrowearBivara: A Code to Create Tooth Microwear Bivariate Plots in R. Zenodo, Version 1. <https://doi.org/10.5281/zenodo.2587575>.

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Data availability All the raw data are available in Online Resource 1.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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