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RESEARCH

Assessing seasonality and mobility from a fragmented faunal assemblage: the case of Amud Cave (Israel)

Anaëlle Jallon[1,2] · Florent Rivals[3,4,5] · Erella Hovers[1,6] · Rivka Rabinovich[1,2]

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Abstract
In this paper we investigate the seasonality of site occupation at Amud Cave (Israel). This site presents a long sedimentary sequence featuring two main late Middle Paleolithic occupation phases (70 – 55 Ka BP) rich in anthropogenic remains, and displaying very high densities of lithic artifacts, faunal remains and evidence of combustion. The abundance of these features appears high relative to the thickness of the sequence, thus raising the question of the duration and frequency of site occupation(s). We aim here to unravel this issue implementing a multiproxy approach to the dental fraction of the faunal assemblage. Combining teeth replacement and wear patterns coupled with micro- and mesowear analyses, we provide insights into the seasonality of occupation and hunting strategies at the site. We found that hunting activities at Amud Cave were conducted mainly in the course of the winter months with possible expansion into the late fall and early spring. This result is consistent with regional and local climate reconstructions and resources procurement locations evidenced in previous works. Assuming a fast depositional rate, we suggest that the sequence results from frequent seasonal returns to the site, forming a palimpsest of short-term occupations. This scenario is compatible with settlements and mobility patterns inferred for the late Middle Paleolithic in the Southern Levant.

Keywords Faunal analysis · Dental wear · Microwear · Age profile · Neanderthals · Southern Levant

Introduction

Context and research questions

Mobility is a key issue in the study of past hunter-gatherer societies. It is an essential aspect of the overall understanding of any particular site. Moreover, considering mobility strategies allows raising and testing hypotheses about a wider settlement system. The topic of mobility goes together with many related issues among which are population density, inter-group relationships, intra-group organization, occupation duration and seasonality of site use. The attributes of lithic artefacts and assemblages are most commonly used to address such issues (e.g. Torrence 1989; Kuhn 1995; Bamforth and Becker 2000; Brantingham 2006; Wallace and Shea 2006; Moncel 2011; Hovers and Belfer-Cohen 2013; Turq et al. 2013; Morales et al. 2015). Over the past forty years, models have been developed on the base of modern ethnographic and archaeological data to determine which features of a site's assemblage best predict the mobility of the human groups that settled in a given site (Binford 1980; Parry and Kelly 1987; Riel-Salvatore and Barton 2007;

✉ Anaëlle Jallon
anaelle.jallon@mail.huji.ac.il

1 Institute of Archaeology, The Hebrew University of Jerusalem, Mt Scopus, 9190501 Jerusalem, Israel

2 National Natural History Collections, The Hebrew University of Jerusalem, Edmond J. Safra Campus, 9190401 Jerusalem, Israel

3 ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

4 Institut Català de Paleoecologia Humana I Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

5 Departament d, Universitat Rovira I Virgili, Història I Història de L'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain

6 Research affiliate, Institute of Human Origins, Arizona State University, Tempe, AZ 85287 - 8404, USA

Parry 2008; or in the specific context of the Levantine Middle Paleolithic, Wallace and Shea 2006). The expectations of such models can be addressed through multiple proxies from diverse lines of evidence such as lithic and faunal assemblage densities and characteristics, evidence of combustion events or geomorphological patterns. Multi-proxy approaches have proved successful in disentangling these questions (e.g., Malinsky-Buller et al. 2021; Mitki et al. 2021). Because seasonality of hunting activities directly reflects on the seasonal occupation of a site, zooarchaeological studies in particular may provide information on this aspect of site use through proxies such as age and sex structures, cementum increments, and meso- and/or microwear data (Fernández-Laso et al. 2010; Rivals et al. 2015; Sánchez-Hernández et al. 2014; Prendergast et al. 2018 and references therein; Rendu and Speth 2019; Livraghi et al. 2022; Uzunidis et al. 2024).

Here we investigate the seasonality of site occupation at Amud Cave (Israel). This site presents a long sedimentary sequence that is extremely rich in anthropogenic remains, amenable to broad stratigraphic distinctions (Chinzei 1970; Hovers et al. 1991; Hovers 2004). Dissecting this series of palimpsests to a more nuanced occupational history proved difficult and could be attempted only in specific contexts, such as the identification of short-term activities at the site through the spatial patterning of specific lithic artefacts types and the study of paleomagnetism of hearths and sediments (e.g., Hovers et al. 2011; Zeigen et al. 2019). The faunal assemblage of Amud Cave consists of nearly exclusively hunted ungulates (see the site description below; Rabinovich and Hovers 2004; Jallon et al. in prep.; cf. Marder et al. 2011; Orbach and Yeshurun 2021; Orbach et al. 2024 on the structure of non-anthropogenic faunal assemblages). Hence, inferring seasonality from the hunted faunal remains offers a means to clarify some of the behavioral ambiguity in dense palimpsests, by addressing questions about the timing and duration of site occupation. In order to obtain insights into the temporality and mobility decisions of the past inhabitants of Amud Cave, we examine age and mortality patterns as well as dental meso- and microwear of animals found at the site (e.g., Sánchez-Hernández et al. 2019; Rivals et al. 2020; Orbach et al. 2024). This in return allows us to draw broader implications regarding the nature of mobility strategies and possibly land use patterns of the site's occupants, and offer new insights on human mobility patterns in the Southern Levant at the end of the Middle Paleolithic period.

The site

Amud Cave is a Middle Paleolithic site, located within the narrow valley of Nahal Amud, ca. 5 km northwest of the Sea of Galilee in the Dead Sea Rift (Fig. 1). At an elevation of 110 m below current sea level the cave is situated ca. 30 m above the present valley floor. Located in the Eastern Upper Galilee (northern Israel), Amud Cave is set in the Eastern Mediterranean ecological zone, characterized by a mosaic landscape with vegetation that varies significantly according to altitude and water availability (Ne'eman and Goubitz 2000). This region experiences consistently hot and dry summers (May to September), leading to a dry landscape and a decline in grass coverage (Kushnir et al. 2017). Today, monthly average maximum temperatures exceed 36 °C between June and September, while minimum temperatures during these same months barely drop below 24 °C (Ziv et al. 2014). Winters are cooler, with most of the annual precipitation falling within the wet-season (October to April; Kushnir et al. 2017). The end of the wet season sees an increase in plant productivity. This generally goes hand in hand with a greater attractiveness for animal resources as well (Mendelssohn and Yom-Tov 1999:20–22). In this part of the Levant, landscapes range from open forests and grasslands typical of the Mediterranean area to a more continental, semi-arid to arid irano-turanian vegetation (Danin

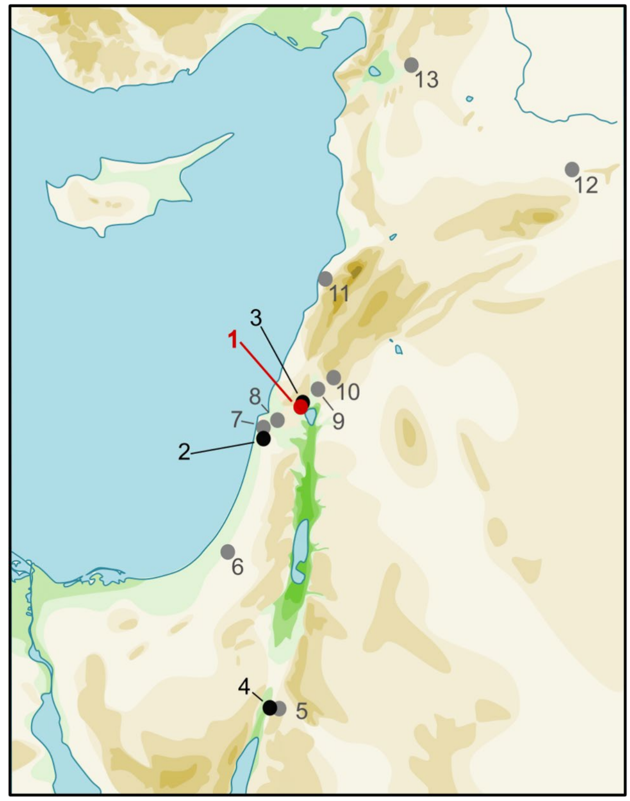


Fig. 1 Location map of Amud Cave (1) and other major sites of the late Middle Paleolithic in the Southern Levant – Kebara cave (2); Shovakh cave (3); Tor Faraj rockshelter (4); Tor Sabiha (5); Farah II and other sites of the lower Besor basin: B37 and B27 (6); Tabun (7); Ein Qashis (8); Nahal Mahanayem Outlet (NMO, 9); Quneitra (10); Nar Ibrahim (11); Um el Tlel (12) and Dederiyeh (13). Sites mentioned in the discussion are shown in black

1988; Madella et al. 2002; Hovers et al. 2017; Kushnir et al. 2017). In areas of sharp relief (such as the slopes of the Rift Valley where Amud Cave is located), the topography allows plant successions that vary over relatively short distances. In this context, where a wide variety of environments can be exploited from a given location, a provisioning strategy based on the moves of consumers to resource patches seems a suitable solution (Goring-Morris et al. 2009).

The first excavations at Amud Cave were conducted between 1961 and 1964 by a Tokyo University expedition (Suzuki and Takai 1970). Two main stratigraphic units were identified: the uppermost unit (Unit A) consisting mostly of mixed Holocene sediments, and an underlying unit (Unit B) containing the Middle Paleolithic (MP) deposits, which were divided into three archaeological sub-units: B1, B2 and B4 (from top to bottom). Sub-unit B3 is a sterile deposit of angular gravels, resulting from the collapse of the cave's roof (Fig. 2), which separates sub-unit B4 from the younger archaeological sub-units (B1 and B2). This framework was followed during renewed excavations by a joint Israeli-American team between 1990 and 1994, with some more nuanced internal division of the sub-units (Hovers et al. 1991). Thermoluminescence (Valladas et al. 1999) and ESR-U series (Rink et al. 2001) ages place the MP occupation of the site at the end of Marine Isotope Stage (MIS) 4 and MIS3 (Table 1). The mean TL dates obtained for layers B1 and B2 are statistically indistinguishable, which is consistent with the sedimentological similarities between these two layers and suggests a continuous deposition. All three archaeological sub-units are rich in lithic artifacts and faunal remains (Hovers 1998, 2004, 2007; Rabinovich and Hovers 2004; Alperson-Afil and Hovers 2005; Hovers et al. 2011). The two main occupation phases (corresponding to sub-unit B4 on one hand, and both sub-units B2 and B1 together on the other hand) display a very high density of artifacts and evidence of combustion relatively to the thickness of its sequence (Hovers 2004). Several human remains attributed to *H. neanderthalensis* (Rak et al. 1994; Rak 1998) were found in sub-units B1 and B2 (Hovers et al. 1995). This abundance of material and the lack of evidence of carnivores, together with the nature of the thick ashy sediments suggests that the site was intensively occupied, almost exclusively by humans (Rabinovich and Hovers 2004; Shahack-Gross et al. 2008; Zeigen et al. 2019).

Local and regional paleoclimatic reconstructions suggest that climate and environment during the times of occupation differed slightly from those of the present (Madella et al. 2002; Belmaker and Hovers 2011; Hovers et al. 2017). Changes in vegetation cover around the site could be tracked via several proxies, in particular isotopic data and plant micro-remains (Madella et al. 2002; Hartman et al. 2015). Thus, we expect land use strategies in this area to involve a high degree of mobility, with varying occupation durations (e.g., task-specific sites, ephemeral camps; Sharon and Oron 2014; Malinsky-Buller et al. 2021; Mitki et al. 2021). These occupations may have been repetitive and frequent or long-term occupations, or may have alternated between these two extremes (Meignen et al. 2006; Malinsky-Buller et al. 2021; Mitki et al. 2021). The question of the duration and frequency of site occupation is particularly interesting at Amud Cave as the fairly rapid accumulation of its sequence could be the outcome either of long-term occupation throughout the year or of frequent seasonal returns to the site. This article aims to unravel this issue and offer new insights regarding the length and frequency of occupations at the site. Given all the site characteristics mentioned above, we expect that Amud Cave has been a residential base occupied for few rather long-term or many short-term occupations. To better understand the site occupation dynamics, we consider specific tooth eruption/wear patterns and meso/microwear patterns.

If the site primarily represents repeated single-season occupations, we would expect low variability in the mesowear and microwear patterns, specifically in the evidence for consumption of abrasive vegetation and in the proportions of browsing versus grazing patterns on teeth. In addition, since the feeding habits of animals can switch with seasonal changes in vegetation availability, microwear signatures linked to specific diets of the hunted animal would be more consistent with single-season occupations. On the other hand, long-term occupations extending across multiple seasons would likely exhibit greater variability in microwear signatures, reflecting higher dietary diversity associated with seasonal fluctuations of the resources available to the animals. Extended multi-season occupations should show more overlapping dietary signals among individuals.

This expanded framework helps clarify our approach to interpreting the data in the context of occupational strategies at Amud Cave. These data can be evaluated with regards to reported diachronic changes in hunting territories and raw material procurement patterns (Hartman et al. 2015; Ekshtain et al. 2017), which indicate that exploited territories may have changed over the time of site occupation.

Material and methods

Materials

The faunal assemblage of Amud Cave reflects the diversity of habitats in the surroundings of the site as it comprises taxa from open to semi-open and closed environments. The faunal spectrum was published earlier (Rabinovich and Hovers 2004). It consists mostly of ungulates, represented by three species of bovids: mountain gazelle (*Gazella gazella*), wild goat (*Capra* sp.) and aurochs (*Bos primigenius*); three

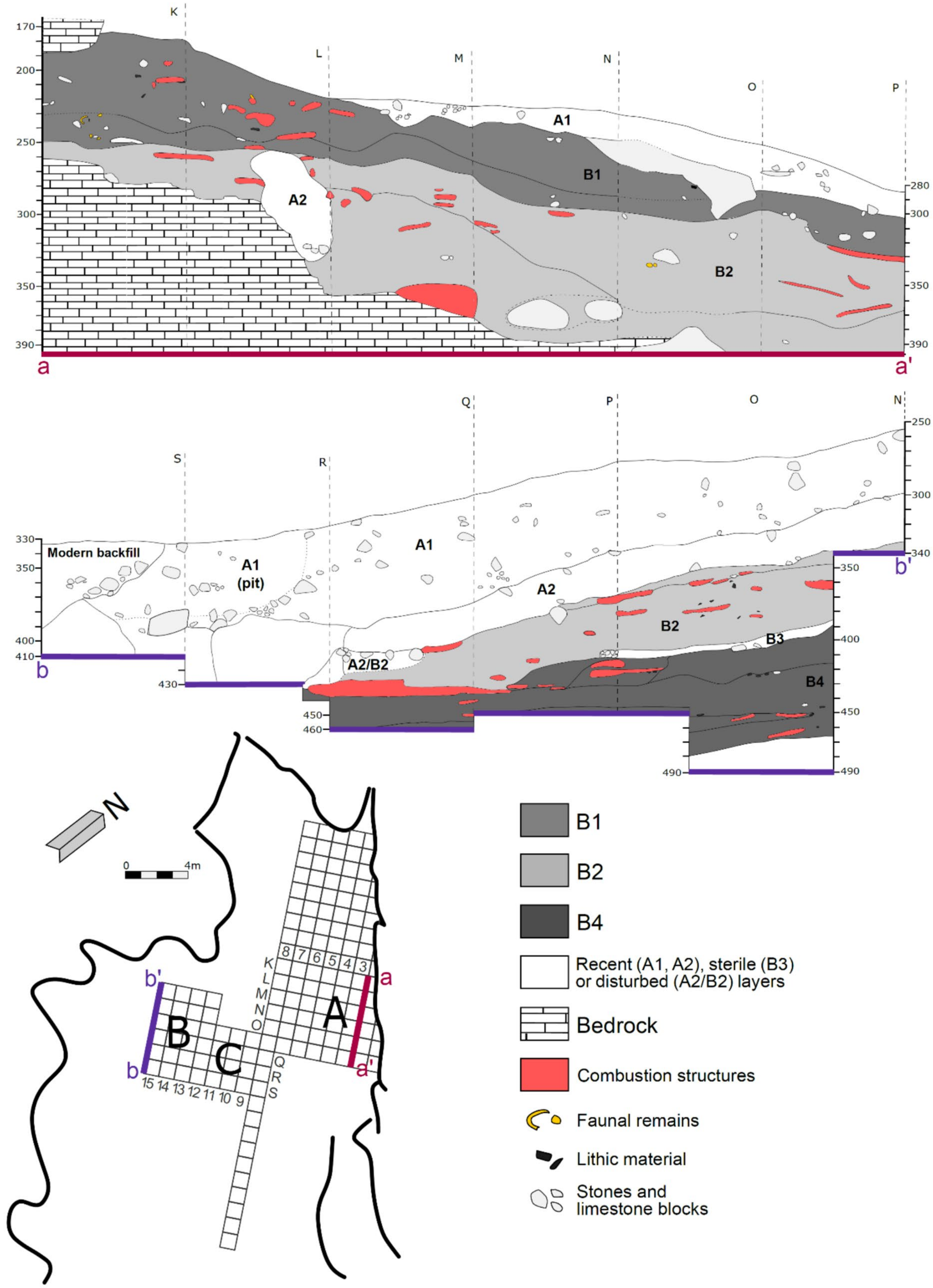


Fig. 2 Northern (a-a') and southern (b-b') sections of Amud Cave in relation to the plan of the site

Table 1 Average of TL dates (*) and ESR dates (**) of the sub-units of Amud Cave (Valladas et al. 1999; Rink et al. 2001)

Sub-unit	Area B	Area C	Area A
A1-A2		Holocene	
B1			57.6 ± 3.7*; 53 ± 7** Ka
B2	56.5 ± 3.5*; 61 ± 9** Ka		
B3	[archaeologically sterile]		
B4	68,5 ± 3,4*; 70- ± 11** Ka		

species of cervids: Persian fallow deer (*Dama mesopotamica*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), as well as the wild boar (*Sus scrofa*). They have also noted the presence of bear (*Ursus* sp.) and larger ungulates such as the rhinoceros (*Stephanorhinus* sp.) on the basis of isolated teeth, while carnivores are almost absent from the site and are represented only by the rare presence of the common fox (*Vulpes vulpes*). Due to the high fragmentation of the assemblage, a large portion of remains do not display sufficient diagnostic features to be identified taxonomically and were rather classified into body-size categories (Rabinovich and Hovers 2004). Nonetheless the distribution of taxa they observed suggests that the faunal spectrum in the MP deposits of Amud Cave is similar to that known from anthropogenic assemblages of contemporaneous Levantine cave sites such as Kebara Cave, and of earlier Middle Paleolithic sites like Hayonim Cave and Misliya Cave, all with a predominance of medium-sized ungulate, and mountain gazelle being the most abundant identified taxa in the assemblage followed by fallow deer (Davis et al. 1988; Kaufman 2002; Rabinovich and Hovers 2004; Stiner 2005; Speth and Tchernov 2007; Yeshurun et al. 2007; Yeshurun 2013). This distribution is also observed when considering only teeth (Fig. 3) with the mountain gazelle representing over 36.8% of the total number of identified dental remains.

The bones and teeth in this assemblage are highly fragmented. In all sub-units, most of the fragments are pieces of shafts of long bone diaphysis (see Rabinovich and Hovers 2004, Fig. 5b). Intact bones are mainly sesamoid, carpal and tarsal bones as well as phalanges. In consequence, it is often impossible to estimate the state of epiphyseal fusion of the post cranial fragments in this assemblage (Rabinovich and Hovers 2004). In contrast, dental elements are better preserved with about a third of the identified dental remains being complete or nearly complete (Table 2). There is also less taxon or anatomy related bias, compared to the bones, such that different teeth are preserved in similar proportions among the ungulate taxa. Therefore, teeth are the most reliable—and possibly the only—proxy to estimate individual ages at death from this assemblage.

Studied specimens were either collected with reference to their 3D provenience (n = 18, 8.8% of the assemblage) in the site's grid and datum system (Hovers et al. 1991), or derive from the sieving and sorting (n = 187, 91.2% of the assemblage) of sediments from the three Middle Paleolithic anthropogenic units (B1, B2 and B4). In the latter case,

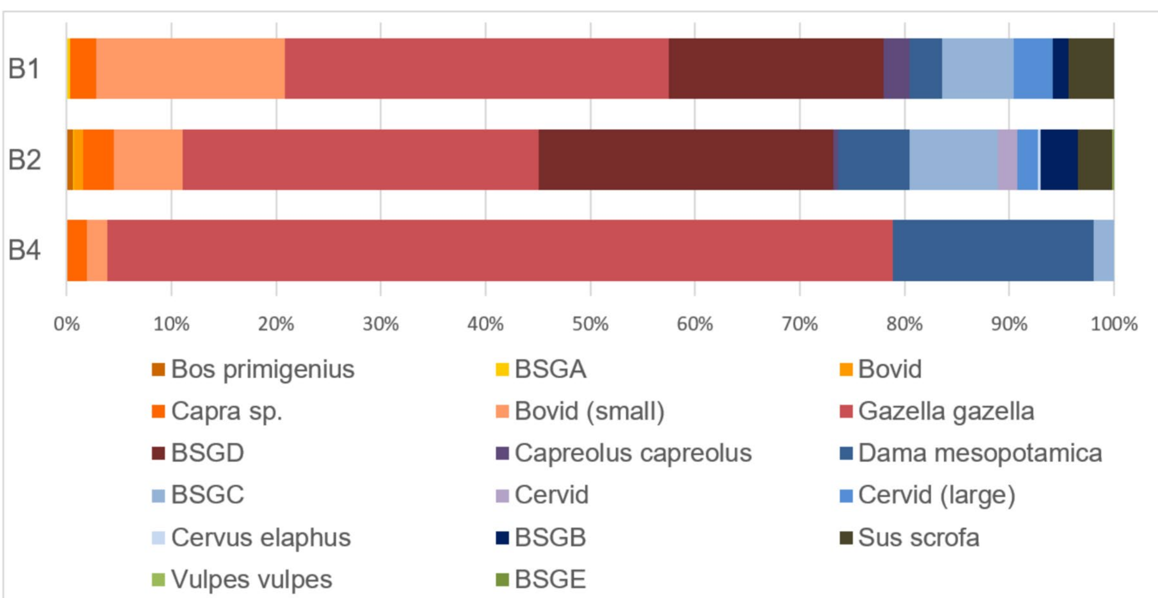


Fig. 3 Taxonomic composition of sub-units B1 (N= 160), B2 (N= 698) and B4 (N= 55) of Amud cave. Body-size groups abbreviations (following Rabinovich and Hovers 2004): BSGA, aurochs or rhinoceros; BSGB, red deer, fallow deer or wild goat; BSGC, fallow deer or wild goat; BSGD, gazelle or roe deer. Taxonomic groups abbreviations: Bovid (small), gazelle or wild goat; Cervid (large), red deer or fallow deer

Table 2 Number of identified dental remains by degree of preservation and by archaeological sub-unit, (a) in the whole dental assemblage, and (b) in the sample used for this study

a	Preservation				Total
	100%	> 50%	50%	< 50%	
B1	55	16	32	60	160
B2	121	66	92	419	698
B4	25	10	15	5	55
Total	201 (22%)	92 (10%)	139 (15%)	484 (53%)	913 (100%)

b	Preservation					Total
	100%	> 50%	50%	< 50%	NA	
B1	27	5	3	0	10	45
B2	41	27	19	3	16	106
B4	29	12	11	2	0	54
Total	97 (47%)	44 (21%)	33 (16%)	5 (2%)	26 (13%)	205 (100%)

provenience was defined down to the sub-square (50 × 50 cm) and vertical spit (typically 5 cm).

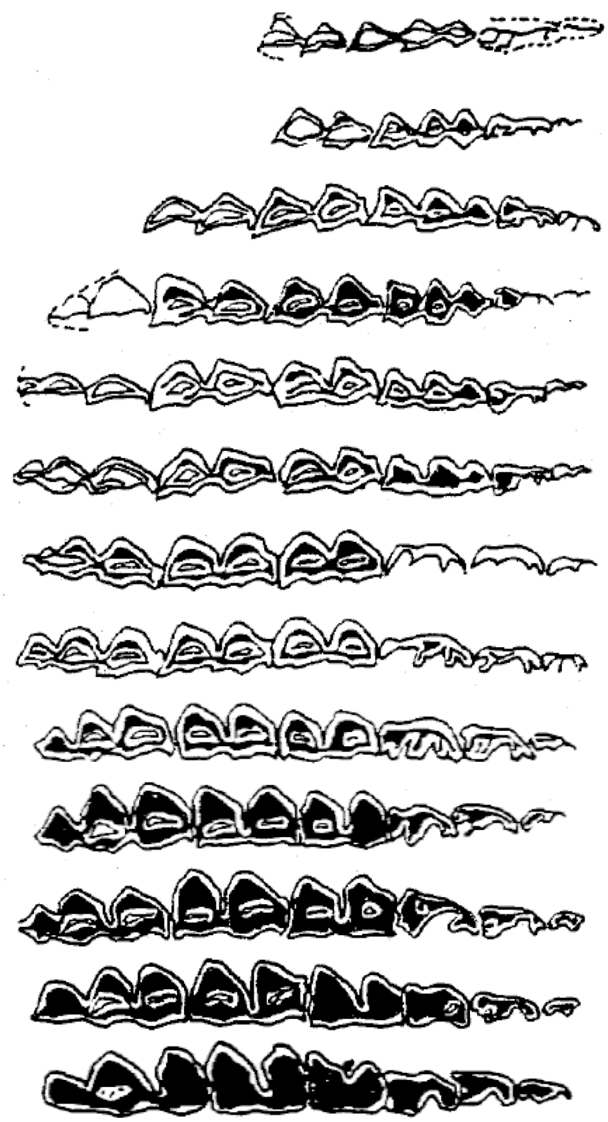
For the two predominant taxa of the assemblage—the mountain gazelle and the fallow deer—individual ages were estimated from all the mandible fragments and isolated lower teeth considered suitable (i.e., sided elements with a clean and unbroken occlusal surface), Mesowear and microwear analyses were conducted on samples of teeth including these two taxa as well as wild goat, red deer, wild boar, and aurochs. The number of elements studied with either one or all of these three methods, and their stratigraphic provenance is listed in Table 3.

Estimating individual age on the base of patterns of tooth eruption, replacement and wear

Identifications were conducted using the comparative osteological and zooarchaeological collections housed at the National Natural History Collections of the Hebrew University of Jerusalem (NNHC, Israel). The eruption stage and wear patterns were determined for each tooth individually and scores were assigned to them using the method of Munro et al. (2009) for mountain gazelles and of Bowen et al. (2016) for fallow deer. The scores were then used to attribute each dental element to an age range, following the correspondence established in each of these publications. In few suitable cases (mandibles bearing several teeth, lower P4 and lower M3 in early wear stages), we refined the age ranges provided by the method of Munro et al. (2009) using the stages of eruption replacement and wear (thereafter 'wear stages') described and drawn by Rabinovich (1998) for mountain gazelle. The wear stages established by Rabinovich (1998) do not use a scoring protocol and are therefore less reliable, especially for the adults and mature individuals (i.e. after the replacement of decidual teeth with the permanent ones). However they are based on the observation of a vast amount of well documented material, and provide narrower age ranges. The age ranges set by Munro et al. (2009) and Rabinovich (1998) correlate well up to 18 months, and overlap for older individuals (Fig. 4). For this reason, Munro et al. (2009) was used to establish the age ranges for all suitable

Table 3 Number of remains used for the analysis depending on the taxa, stratigraphic context, and method used

	Eruption and wear only			Mesowear only			Microwear only			Both meso-and microwear			All three methods			Total		
Taxa	B1	B2	B4	B1	B2	B4	B1	B2	B4	B1	B2	B4	B1	B2	B4	B1	B2	B4
Mountain gazelle	20	37	32	10	20	3	2	1	2	1	5	5	3	13	-	36	76	42
Fallow deer	2	3	9	-	2	-	1	4	1	-	1	-	1	6	-	4	16	10
Wild goat	-	-	-	4	4	1	1	1	-	-	4	1	-	-	-	5	9	2
Red deer	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	3	-
Aurochs	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-
Wild boar	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-
Total	22	40	41	14	26	4	4	8	3	1	13	6	4	19	0	45	106	54



Rabinovich (1998)		Munro et al. (2009)	
1 - 2	0 to 3 months old	I	0 to 3 months old
3	3 to 7 months old	II	3 to 7 months old
4	7 to 14 months old	III	7 to 18 months old
5 - 6	14 to 18 months old		
7	18 to 20 months old	IV	18 to 36 months old
8	20 to 30 months old		
9	30 to 40 months old		
10	40 to 44 months old	V	36 to 54 months old
11 - 12	44 to 76 months old		
		VI	54 to 76 months old
13	80 months old or more	VII	76 months old or more

Fig. 4 Mountain gazelle wear stages showing the correlation between age ranges defined in Rabinovich (1998) and Munro et al. (2009)

teeth, and Rabinovich (1998) was used to narrow down the age ranges of young gazelles when the wear stages 4, 5—6 or 7 from Rabinovich (1998) could be identified unambiguously from the diagnostic dental elements mentioned above.

These age ranges can be used to estimate the overall number of juveniles and adults in the assemblage. Mountain gazelle reach full maturity around 20 months old although females were observed to be fertile from an age as young as six months old (Wronski and Sandouka 2010) while fallow deer reach their sexual maturity between 16 to 24 months of age (Dolev et al 2002; Bar-David et al. 2005; Rendu and Speth 2019).

We used Minimal Number of Individuals (MNI) per age class to discuss age-at-death distributions in the assemblage as well as season of death. These MNI were estimated for each of the stratigraphic units based on the count of the most abundant sided dental element (teeth embedded in a same mandible fragment being counted separately). In order to avoid representation biases when drawing mortality profiles, MNI per age class were weighted by the time span that each age class represents (in months), and were then turned into relative frequencies as recommended by Gerbault et al. (2016).

Dental mesowear and microwear

Dental mesowear is a proxy that averages the abrasiveness of food over a long temporal frame, spanning from months to years (Fortelius and Solounias 2000; Ackermans et al. 2020). Mesowear scores, which combine cusp shape and relief, were categorized on a scale from 0 to 6 and scored on the lower and upper molars following the method proposed by Mihlbachler et al. (2011). The scale reflects a gradient of abrasiveness, from a diet of browsers with low abrasion to a diet of grazers with high abrasion. Since mesowear scores are dependent on the ontogenetic age of the individuals (Fortelius and Solounias 2000; Rivals et al. 2007), only the teeth from adults were analyzed.

Dental microwear analyzes the microscopic features produced by food items on the occlusal surfaces of the teeth. It reflects the diet on a short temporal scale of days to weeks (Grine 1986). Different types of food produce micro-features in varying proportions depending on their abrasiveness and hardness (e.g., grazing produces higher proportions of striations in comparison to pits than browsing). Thus, different diets result in distinctive microwear signals, making it possible to determine the main components of an animal's diet. In an ecological context where plant resources distributions change significantly with the seasons, such as that of Amud Cave, this distinction provides clues about season of death of the animal. Dental microwear analysis was performed following the protocol established by Solounias and Semprebon (2002). The occlusal surfaces of the teeth were cleaned with acetone and 96% ethanol to remove any consolidant or dust from the enamel. Occlusal surfaces were molded using high-resolution dental silicone (Heraeus Provil novo regular set) and casts were produced using transparent epoxy resin. Casts were examined under a Zeiss Stemi 2000 C stereomicroscope with transmitted light at 35 × magnification. Teeth presenting taphonomic damages that erased the original microwear pattern were discarded (King et al. 1999; Uzunidis et al. 2021; Micó et al. 2024a, b). Microwear features, such as pits and scratches, were identified using the categories of Solounias and Semprebon (2002) and Semprebon et al. (2004). Data were compared with a reference dataset (Solounias and Semprebon 2002) on bivariate plots of pits and scratches using the R code MicrowearBivaR (Rivals 2019).

Estimating season at death and comparison of the results of teeth eruption and wear, mesowear and microwear

Season at death could be estimated only for a subset of the aged individuals (n = 16 out of 105). This subset consists of the specimens for which the age estimate does not exceed 20 months (to maintain accuracy) and for which the estimated age range covers no more than 8 months (as broader ranges would render the results uninformative). The period during which death was most likely to have occurred was obtained for these suitable individuals by representing their age estimates on a time scale while considering the most probable period of birth. Because the age ranges tend to get broader after 20 months old, the plotted specimens are exclusively young individuals, most of them younger than 1 year old. In many cases, the ranges of age estimates and period of birth added up to a time interval exceeding one year. In these cases, individuals were considered uninformative, since their death could have occurred at any month of the year.

We estimated that birth would have most likely occurred from June to mid-July based on reproductive strategies in female mountain gazelles described by Baharav (1983) and by Martin (2000). They noted two reproduction patterns usually observed for the modern populations of mountain gazelles, depending on the conditions in their habitat: in lush environments with water available year round, reproduction takes place year-round with birth peaks in April and November, while in drier conditions, when the animals' level of nutrition is constrained by seasonal rainfall and plant growth, reproduction is seasonal and birth happens from June throughout to mid-July. This latter pattern is nowadays witnessed in the Upper Galilee. The reproductive behavior of wild mountain gazelle populations might vary from one year to another as a form of rapid adaptation to environmental fluctuations (Martin 2000). The paleoenvironmental reconstruction of the surroundings of Amud Cave (Belmaker and Hovers 2011; Hovers et al. 2017) suggests a pattern involving one unique birth season happening in the early summer would be the more likely to have occur at the time of occupation of the cave. The biology and ecological behavior of Persian fallow deer are known with less details than the ones of mountain gazelles, due to their only recent reintroduction to the region after local extinction. Nevertheless it was observed that the fawning season happens between the months of April and July.

The ecological niches of gazelle and fallow deer differ widely. Mountain gazelles tend to occupy the open grassland areas and feed primarily on grasses. Depending on the availability of the latter, their diet may however switch, thus gazelles tend to browse on shrub leaves when grasses are too rare, especially during the summer months. Persian fallow deer live primarily in more densely forested areas, and they are mainly leaf browsers.

Dietary shifts from grazing to browsing driven by seasonal changes are reflected in the variability of microwear scratch values. This variability has been linked to the duration of accumulation of remains at archaeological and paleontological sites and can thus be used to estimate the duration faunal assemblage formation (Rivals et al. 2009, 2015). A Bayesian model incorporating microwear data from modern ungulates with known dates of death correlates two variability measurements –standard variation (SD) and coefficient of variation (CV)– with the duration of mortality events in modern samples (Rivals et al. 2015). Both SD and CV values increase as the duration of the events increases. Represented on a heat-map, this Bayesian model allows to distinguish between three types of occupation durations: single-season accumulations, multi-seasons accumulations, or separate accumulations occurring in non-consecutive seasons (e.g., summer–winter or spring–autumn; Rivals et al. 2015).

Since some of the samples used here are too small to accurately reflect the true CV and SD values of the larger population they represent, a joint bootstrapped function of CV and SD (n = 500, with replacement) was applied using the R code provided by Domínguez-Rodrigo et al. (2019). This approach has been successfully tested on modern and archaeological samples from the Levant (Rivals et al. 2020, 2021), demonstrating its reliability for analyzing ungulates from Amud Cave. In the Levant, all species analyzed in this study exhibit seasonal dietary shifts from grass to browse (Baharav 1983; Carranza et al. 1991; Mendelssohn and Yom-Tov 1999; Martin 2000; Dolev et al. 2002; Verheyden-Tixier et al. 2008), making them well-suited for analyzing seasonal variability.

The results obtained from teeth eruption and wear, and microwear and mesowear could then be compared. This comparison is limited in the sense that both methods give results whose degree of precision and accuracy are not identical. Moreover, as explained above, seasonality results can be obtained from the tooth eruption and wear patterns from young individuals, whereas the study of microwear necessitates teeth in wear, and thus includes only adult individuals. Nevertheless, we expect the results obtained from both methods to correlate.

Results

The range for age-at-death could be estimated for 105 mountain gazelle and 20 fallow deer specimens, representing a total MNI of 33 mountain gazelles and 8 fallow deer. MNI per age class in each stratigraphic sub-unit is presented in Table 4. Since the estimated ages of numerous individuals spanned several age classes, some MNI also had to be calculated for ranges of several of age classes. For this reason, the values shown in these tables are not all integer numbers.

Nearly all age classes are represented in the assemblage for both taxa, with the exception of mountain gazelles younger than 3 months, which are absent from all sub-units.

Given that MNI data provide a more accurate reflection of the assemblage, it was preferred over NISP whenever possible. The small MNI obtained for the fallow deer does not allow us to create a mortality profile. Moreover, the age ranges obtained for most fallow deer dental remains were too wide to allow for discussion of the relative frequencies of each age class. For the mountain gazelles, the resulting MNIs are large enough to enable discussion. Mortality profiles are presented in Fig. 5. The age class frequencies for B1 and B2 seem to be similarly distributed. Sub-unit B4 shows higher proportions of juveniles, and fewer adults in comparison. However, this last observation could not be validated statistically.

Juveniles and prime adults seem to be the main exploited age classes in all sub-units, while older and senile individuals are less abundant. None of the samples shows a typical U-shaped attritional mortality pattern expected in a natural population. Thus, all reflect a human selection of prey, regardless of the observed differences.

Season of death could be estimated for 16 gazelle specimens. The results are presented in Table 5 and Fig. 6. All the plotted intervals fall between September and mid-March, and intervals per sub-unit overlap each other. The large range of these intervals is due in particular to the age estimates

Table 4 Minimum Number of Individuals of (**a**) gazelle and (**b**) fallow deer, estimated per age class

a – mountain gazelle

Age class	0–3 months	3–7 months	7–18 months	18–36 months	36–54 months	54–76 months	76 + months	Total
B1	0	1	1	4.5	2.5	0.5	0.5	**10**
B2	0	2	1	4	2.66	1.66	1.66	**13**
B4	0	1	3	2	2	1	1	**10**

b – fallow deer

Age class	Just born	0–2 months	4–5 months	5–12 months	13–20 months	20–33 months	33–54 months	44–147 months	61–183 months	118–189 months	Total
B1	0	0	0	0	0	0	1	0.33	0.33	0.33	**2**
B2	0.2	0.2	0.2	0.2	1.2	0	0.33	0.33	0.33	0	**3**
B4	0	0	0	0.5	0.75	0.25	0.25	0.25	0.5	0.5	**3**

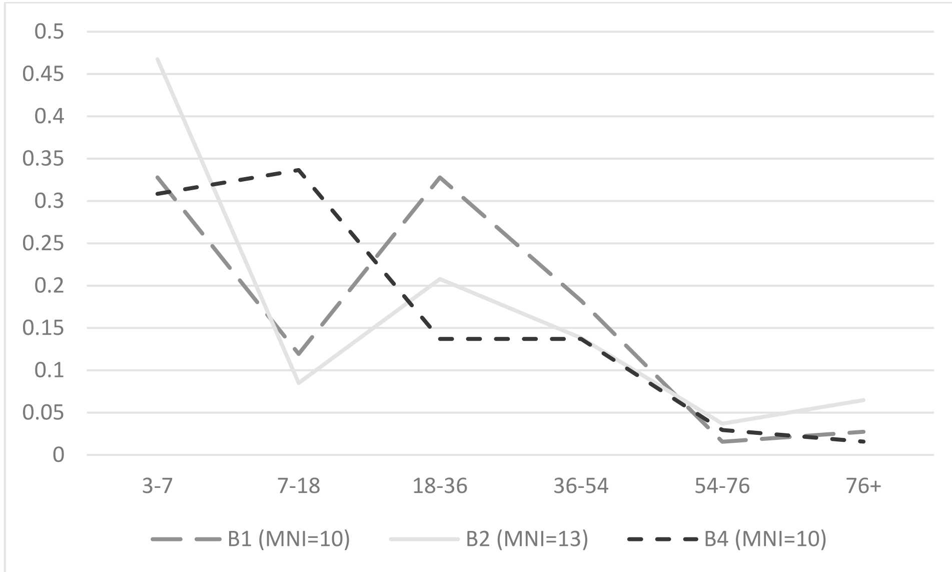


Fig. 5 Age-class relative frequencies of mountain gazelles for the three stratigraphic units of Amud Cave

Table 5 Age estimates, and the corresponding season at death of the studied specimens

Age estimate	Most probable period of death	NISP		
		B1	B2	B4
0–3	Jun-Oct	0	0	0
3–7	Sept-Feb	1	3	1
15–18	Sept-Jan	0	0	3
15–20	Sept-Mar	0	1	0
18–20	Dec-Mar	2	4	1
All other ages	All year round	20	42	27

ranges being quite wide, to which is added the birth period range.

The low mesowear values indicate a diet based on browsing for the mountain gazelles and wild goats from sub-unit B1 (Table 6; Fig. 7). The microwear data support this interpretation for the wild goat, with low numbers of scratches (Table 6; Fig. 8). However, there is a discrepancy regarding the results obtained for the mountain gazelles. The high number of scratches suggests a more abrasive diet (based on grazing) at the time of death than the rest of the year. In sub-unit B2, the mesowear data suggest an annual mixed feeding diet for most taxa. The microwear data indicate a shift towards a more browse-based diet at the time of death for all species excepting the mountain gazelle which is consistently present as a mixed feeder (Table 6; Figs. 7 and 8).

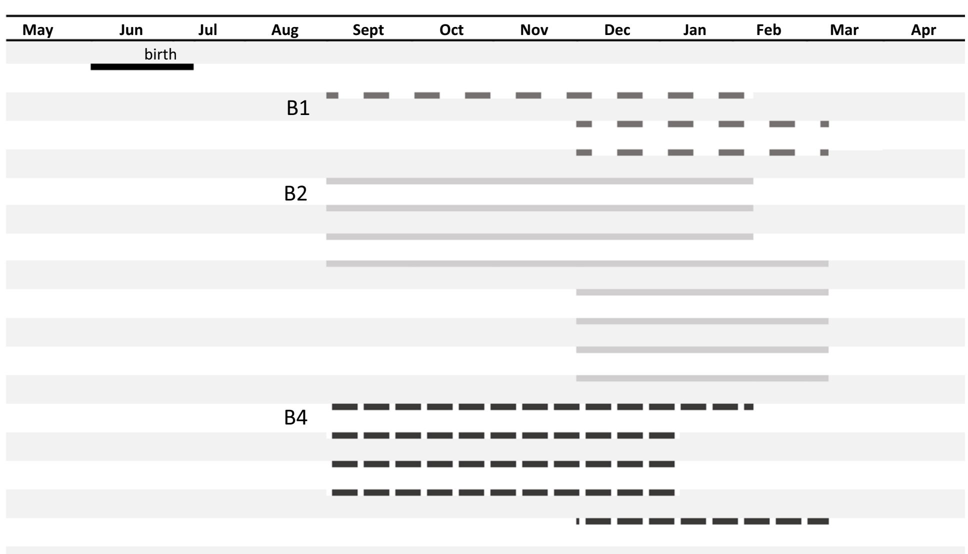


Fig. 6 Estimates of the season of death of mountain gazelles for each of the three stratigraphic units of Amud Cave. Each line in shades of grey represents one specimen. Different line patterns correspond to stratigraphic sub-units (as in Fig. 5)

Table 6 Summary of the microwear data for the ungulates from Amud Cave

		Mesowear		Microwear								
Level	Species	N	MWS	N	Npit	Nscr	%LP	%G	SWS	%XS	%HC
B1	Fallow deer	1	2	2	14.5	10.75	-	-	-	-	-
	Wild goat	4	1.5	1	22	18	-	-	-	-	-
	Mountain gazelle	12	1.5	4	13.75	22.6	100	0	1.3	0	0
B2	Red deer	2	1	3	16.3	15.5	-	-	-	-	-
	Fallow deer	9	2	11	21.9	13.8	90.9	72.7	1.1	0	0
	Aurochs	1	2	1	16.5	19.5	-	-	-	-	-
	Wild goat	8	3	5	25.3	14.5	100	100	1.2	0	40
	Mountain gazelle	39	2	20	18.55	19.2	100	35	1.2	0	0
B4	Fallow deer	-	-	1	15.5	10.5	-	-	-	-	-
	Wild goat	2	2.5	1	39.5	14.5	-	-	-	-	-
	Mountain gazelle	8	1.5	7	18.3	22	100	28.6	1.1	0	14.3

N number of specimens, *MWS* Mesowear score (median value), *Npit* average number of pits, *Nscr* average number of scratches, *%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 hyper-coarse scratches

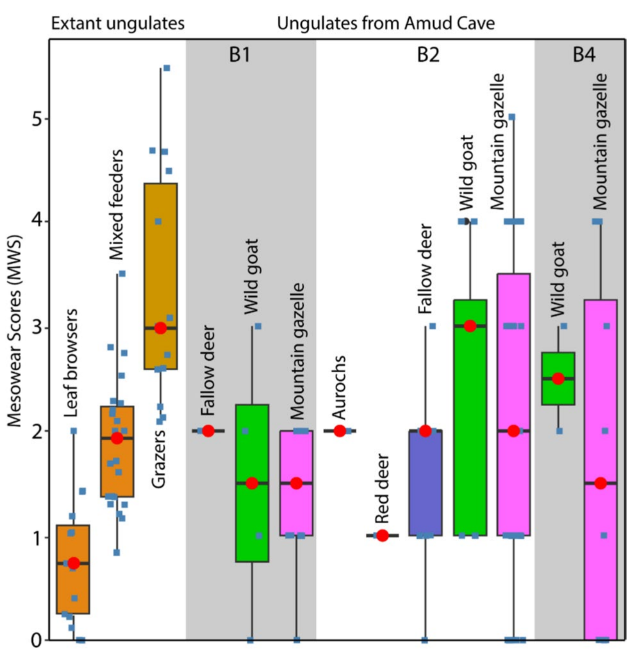


Fig. 7 Mesowear scores (MWS; median values) for the ungulates from Amud Cave compared with the dietary categories in extant ungulates (i.e., leaf browsers, mixed feeders, and grazers). Error bars correspond to the standard error (± 1 SE) for each sample

In sub-unit B4, we observed the same pattern as in sub-unit B1, with fallow deer tending towards browsing and gazelles towards grazing at the time of death (Table 6; Figs. 7 and 8).

We observe a diversity of diets across all sub-units, with dietary abrasiveness ranging from leaf browsing to grazing. This diversity indicates niche partitioning among ungulates, as different species exploited distinct dietary resources to reduce competition. For example, some ungulates primarily consumed abrasive grasses in open habitats, while others specialized in softer, leafy vegetation in closed environments. This dietary differentiation suggests that hunting activities occurred in both open grasslands and wooded areas, reflecting the exploitation of diverse ecological niches by the hunters.

In comparison to extant gazelles from Israel with a known season of death (Rivals et al. 2020), the low number of pits recorded on the gazelles teeth from Amud suggests variations in the season of death during different periods of site occupation. The inference of winter occupations for sub-units B1 and B4 is based on the similarity of their microwear signatures to those of modern gazelles that died during winter months, when diets typically consist of more abrasive vegetation. For sub-unit B2, the microwear pattern indicates a slightly broader dietary range, suggesting a prolonged season of death spanning late fall to early spring. This interpretation relies on the established relationship between microwear variability and dietary shifts linked to seasonal changes in vegetation availability, as demonstrated by modern reference datasets. The intra-population variations of the microwear scratches (Fig. 9) reveal that mountain gazelles from sub-units B1 and B4, as well as fallow deer and red deer from sub-units B1 and B2, were hunted over a single season. The discrepancy observed between the results of mesowear and microwear data for Amud gazelle is consistent with this interpretation. Indeed, Sánchez-Hernández et al. (2016) suggested that strong discrepancies between mesowear and microwear results most likely correspond to short hunting periods. In contrast, wild goats and mountain gazelles from the sub-unit B2 were most likely hunted over a longer period or during occupations that took place at different times of the year.

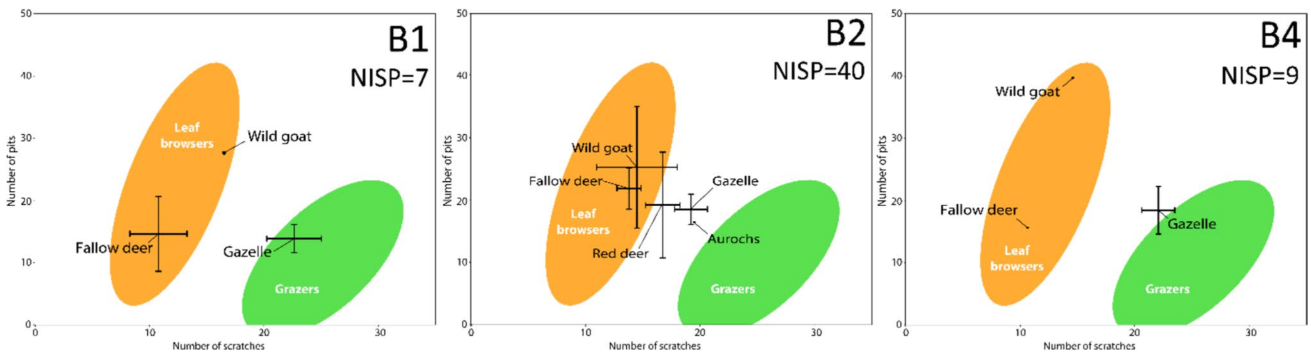
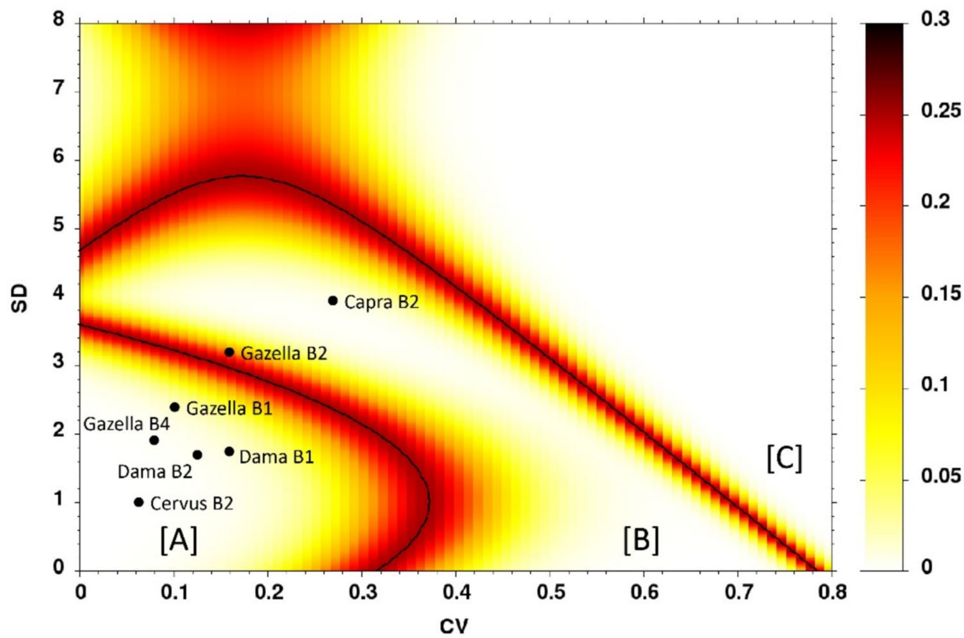


Fig. 8 Bivariate plots of the average numbers of pits and scratches for the ungulates from each stratigraphic unit of Amud Cave. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. Plain ellipses correspond to the Gaussian confidence ellipses ($p=$ 0.95) on the centroid for the extant leaf browsers (LB) and grazers (G) based on the reference database from Solounias and Semprebon (2002)

Fig. 9 Amud Cave ungulate samples plotted on a heat map (boundary lines with error probability) based on standard deviations and coefficient of variation values of microwear data. The areas of the map correspond to short events (region A), long-term events (region B) or two separate short events (region C)



Discussion

Interpreting season of death in a palimpsest context

The estimation of the season of death for the mountain gazelle is subject to uncertainty, due to two main factors—the imprecision associated with the individual age estimate method, which limits the number of specimens that can be included in this analysis, and uncertainties as to the reproductive behavior of gazelles that may vary from one year to another depending on the water availability. The deposits in Amud Cave, as in most of the other long-sequenced prehistoric sites in general, are palimpsests formed by sequential and spatial accumulations of numerous events, which are not necessarily strictly continuous in time (Hovers 2001; Bailey 2007; Malinsky-Buller et al. 2011). The temporal resolution with which the context of these sites is approached, their dating, and the climatic events with which they can be correlated, rather ranges on a millennial time scale (Banks 2015) and cannot be used to address annual fluctuations in gazelle population size (or indeed other events on a similar temporal scale). Some high resolution studies can help partially in bridging this gap. For Amud Cave, Zeigen et al. (2019) used paleomagnetic data to constrain the maximal deposition interval of individual hearths in relatively undisturbed sediments to a millennium at most. Their study provides the highest temporal resolution obtained so far for this site. Therefore, within the time span of each of the two occupation phases in late Middle Paleolithic Amud Cave, it is likely that both reproductive strategies of mountain gazelles, responding to secular environmental changes that are not depicted in high level, coarse-grained models, are represented in our sample.

Analyses of tooth material for stable isotopes, and dental wear in particular, provide results that relate to short temporalities, and thus can help identify and characterize specific events in the record (Romagnoli et al. 2018). Hallin et al. (2012) suggested, based on isotope analyses of goat and gazelle tooth enamel, that wetter climatic conditions prevailed in Amud cave at the time of occupation, with multiple gazelle birth seasons over the year. Hartman et al. (2015) later contested these interpretations. According to these authors, the isotopic data from gazelle tooth enamel suggests improved climatic conditions (i.e., increase of temperature and precipitations) during the deposition of sub-unit B1 when compared to B4, consistent with their respective dating to MIS3 and MIS4. Overall, their data point towards an environment much dryer than suggested by Hallin et al. (2012), with no indications of summer rains.

Bearing in mind the necessary time-averaging as discussed above, we maintain that, given the past climatic conditions reconstructed for Amud Cave and its surroundings (Madella et al. 2002; Belmaker and Hovers 2011; Hartman et al. 2015, see also Keinan et al. 2019), the parsimonious model of gazelle age at death for Amud Cave involves a single reproduction season that peaks in June through mid-July. Macroscopic wear patterns and their implications for seasonality are interpreted within this simplified framework.

Seasonality during the various phases of occupation

The mortality profiles of mountain gazelles suggest that hunting strategies may have differed for the various phases of occupation. This observation could not be substantiated statistically, and because the sample used in this study constitutes the entire set of identified ungulate teeth for which age estimates were possible, we are currently unable to add material to clarify and confirm this result. Still, we note that sub-unit B4 displays higher proportions of young individuals whereas sub-units B1 and B2 show overall similar proportions of each age class, with a focus on prime adults and younger individuals. Assuming that this trend reflects a shift in human settlement and subsistence strategies between the oldest Middle Paleolithic occupation and the two more recent ones, we would expect to see differences between the assemblages related to duration of occupation and changing attitudes towards resources. For example, one might expect shifts in the faunal species representation, selection of body parts transported into the site, age structure of the hunted fauna or in the processing of animal resources (Speth 2013; Rendu and Speth 2019; Jallon et al. in preparation). Indeed, Rabinovich and Hovers (2004) noted taphonomic differences between the sub-units, whereby higher proportions of exfoliation and lower frequencies of burning have been observed on the remains from sub-unit B4 compared to sub-units B1 and B2. Tentatively, those differences may correspond to less intensive use of the site and longer periods of abandonment when bones were exposed to the elements during B4 times. Ongoing work on the faunal assemblages addresses such issues in tandem with the inferences from faunal and lithic richness and densities. Currently, however, such patterns do not seem to correlate with seasonality of site use.

The tooth microwear data suggest that occupations at Amud occurred primarily during the winter season, as it reflects a diet dominated by more abrasive plants typically available during winter months. Winter in the region is characterized by higher precipitation, leading to greater surface water availability, which would have made the area more attractive to both ungulates and to the human groups relying on these resources. These results are also in line with our estimates of the season of death as obtained from patterns of tooth eruption, replacement and wear. Notwithstanding, the broad uncertainties of these estimates, the hypothesis of a winter occupation would be rejected if we observed individuals that likely died during the dry season. Such individuals (i.e., young specimen falling in the 0—3 months old or 7—14 months old age groups) were not observed in our sample.

It has been shown that the inhabitants of Amud Cave relied on plant resources for fuel and as a food supply (Madella et al. 2002). The presence of phytoliths derived from mature grass panicles suggests that part of the occupation period extended into spring, or even early summer (Madella et al. 2002). This is compatible with our interpretations for sub-unit B2, but less so for sub-units B1 and B4.

Availability and distribution of plant resources was suggested to be the main determining drivers of human subsistence-related mobility in the Southern Levant (Hovers 1997, 2006, 2009:201–207; Madella et al. 2002; Lev et al. 2005; Goring-Morris et al. 2009). As mentioned above, local and regional paleoclimatic reconstructions suggest that environmental parameters during the times of occupation were roughly similar to the present (Belmaker and Hovers 2011; see also Madella et al. 2002; Hovers et al. 2017). With that in mind, limiting seasonal occupations exclusively or broadly to the winter season also seems a reasonable settlement decision when considering the location of Amud Cave on the margins of the Dead Sea Rift Valley, where temperatures tend to rise to extremely high levels in the summer. The reconstruction of winter occupations at Amud Cave is also consistent with the higher diversity and productivity of plant and faunal resources of the Mediterranean ecosystem during the wet season, i.e. winter and early spring (Ne'eman and Goubitz 2000). The reason for a winter-focused occupation may also arguably be linked to more favorable conditions for hunting fallow deer and gazelles in this season, as both these species tend to group in larger herds, show less aggressive behaviors and reach their maximum weight in winter and early spring before the breeding season in late spring – early summer (e.g., Geffen et al 1999; Rendu and Speth 2019:249–250). However, since Amud Cave is located in an open forest habitat typical of the eastern margins of the Mediterranean ecological zone, the suitable time for occupation might have been more narrowly restricted to the winter months compared to other sites located in the heart of the Mediterranean zone.

Our results bear on the general interpretation of the differences between the successive phases of occupation at Amud Cave. Hartman et al. (2015) suggest that mountain gazelles were present (and thus hunted) in different territories throughout the time of deposition of Amud's sequence, switching from higher elevations during the early occupation phase (end of MIS4) to lower elevations in the latter periods (early MIS3). They link this shift in gazelle hunting territories to changes in environmental conditions that impacted the productivity of gazelle hunting areas. Indeed, the humidity peak of 56—54 Ka (Bar-Matthews et al. 2003; Langgut et al. 2011) may have led to higher vegetation cover on slopes around the site, as reflected in the composition of the high paleo-terrace of Nahal Amud (Inbar and Hovers 1999), dated to this time range (N. Porat, pers. comm. 2018).

The trend discussed above, with sub-unit B4 displaying higher proportions of juveniles at the expense of prime adults in comparison to the later occupation periods, should also be considered in light of these interpretations. This observation could be in line with more distant and restricted hunting territories during the occupation of B4, adding constraints on prey selection in the hunting process and transport decisions (cf. Speth and Clark 2006 about Kebara Cave). This diachronic change is parallel to the decrease in the frequencies of non-local raw material from B4 to B1 times, unrelated to notable differences in flint quality (Ekshtain et al. 2017).

Impact of such environmental changes is not reflected in the spectrum of hunted fauna and in the natural accumulation of microfaunal elements (Rabinovich and Hovers 2004; Belmaker and Hovers 2011). Our dental microwear data also failed to capture such changes. Thus, the same resources remained exploited in the surroundings of the site throughout the whole time of its occupation. Our study shows that the modalities of occupation of the site are similar in the two phases, and thus strengthens the hypothesis that Neanderthals at Amud Cave adapted to changes in the distribution of resources in the surroundings of the site by adjusting their task-related mobility decisions rather than modifying their group mobility strategies (cf. Malinsky-Buller et al. 2021).

Broader implications for the Late Middle Paleolithic record of the Southern Levant

Late Middle Paleolithic cave sites, well documented in the Levant, are characterized by higher densities of finds and high inter-assemblage variability compared to the early Middle Paleolithic (Hovers and Belfer-Cohen 2013). This co-occurs with increasing evidence for spatial differentiation of activities, 'house cleaning', depletion of faunal resources in cave sites and open-air sites that are either task-specific or displaying generalized activities (Hovers et al. 1995, 2000; Hovers 2001; Alperson-Afil and Hovers 2005; Meignen et al. 2006, Meignen and Bar-Yosef 2019; Speth 2006, 2019; Speth and Clark 2006; Speth et al. 2012; Ekshtain et al. 2014, 2017, 2019; Sharon and Oron 2014; Malinsky-Buller et al. 2021; MartÍn-Viveros et al. 2023; Yaroshevich et al. 2023). The cumulative evidence has led to suggestions that a progressive shift in population mobility occurred towards the end of the Middle Paleolithic, with shorter residential moves within relatively constrained territories (Hovers 1997, 2001, 2006; Meignen et al. 2006; Hovers and Belfer-Cohen 2013). More frequent/more intensive occupations would be reflected in the fauna proxies by an increase in the proportions of burnt bones, accompanied with changes in game exploitation strategies. The record seems to show an evolution towards a higher reliance on middle size game, as well as increasing proportions of young individuals in the assemblages towards the end of the Middle Paleolithic which were suggested to reflect evidences of overhunting at Kebara cave (Speth and Clark 2006; Speth 2013).

The late Middle Paleolithic depositional sequence of Amud Cave displays high artifact densities, several burials and abundant evidence of burning including high frequencies of burnt bones (Rabinovich and Hovers 2004; Alperson-Afil and Hovers 2005; Shahack-Gross et al. 2008; Zeigen et al. 2019), suggesting that it was used as a residential site all throughout its occupational history (Hovers 2004; Hovers et al. 2017). The tooth microwear results suggest that all taxa sampled from sub-units B1 and B4, and the cervids from sub-unit B2 were hunted over one season at most (i.e., a few months). These results are consistent with the interpretation of the mortality patterns indicating winter hunting. The combination of the two lines of data supports an interpretation of the sequence as a palimpsest of a series of many short-term seasonal occupations. Each sub-unit of the site would correspond to one continuous or several repetitive settlements during a relatively short period, with sub-unit B2 likely covering a slightly longer part of the year (the temporal resolution does not allow us to test whether this extended occupation might be related to the height of the humid 56—54 Ka peak; see above).

The abundance of material remains combined with the near-absence of carnivore bones and their minimal impact on the faunal remains, suggest that humans were the primary (if not only) authors of the assemblage. This makes the site highly informative for understanding the choices made by human groups about settlement and mobility. It is of interest to compare the modalities of occupation evidenced at Amud Cave with settlement patterns deduced for other Levantine Late Middle Paleolithic sites, although the number of faunal assemblages where such studies were conducted is rather small.

Shovakh Cave, some 600 m upstream from Amud Cave, is assigned to the late Middle Paleolithic. The sequence is comparable to Amud Cave in both dates and the presence of two occupation period separated by a hiatus in deposition (Friesem et al. 2019) while the Paleolithic remains are likely a negligible remnant of the original occupations (Malinsky-Buller et al. 2021). The faunal assemblage consists of the usual spectrum of anthropogenic accumulations, with some differences (e.g., the absence of fallow deer) attributed to the small sample size. Seasonal data are not available from this site. Given its location and chronology, one may expect winter occupations similar to Amud cave. Unlike any of the occupation phases at Amud Cave, carnivores are present in the rear part of Shovakh Cave. Additionally, the lithic assemblages show spatial differences between the entrance and rear areas of the site with evidence of fire use and the presence of only the later stages of core reduction at the entrance of the cave. In contrast, the debitage sequence at the rear of the cave is comparatively more complete. Altogether, the faunal and lithic evidence and their depositional context were interpreted as indicating ephemeral settlements during each of the three periods of occupation (Malinsky-Buller et al. 2021). Regardless, these were likely of a short duration/lesser intensity compared to Amud Cave, as suggested by the incompleteness of the debitage sequence in both areas (Malinsky-Buller et al. 2021).

A comparable pattern of occupation is observed in the southern part of the Rift Valley, along the slopes of the Ma'an plateau and high piedmont (Jordan), where sites situated at low- to mid-elevation are more likely occupied during the winter and spring seasons (Henry 2011). The best documented example is Tor Faraj rockshelter (60—50 Ka BP; Henry 2003, 2012), where phytolith studies have shown that this site was likely occupied between the months of February and June (Rosen 2003). On the other hand, in the same region, sites of high-elevation seem to be better suited for occupations during the dry warm season when surface water is available there from springs flowing onto the slopes of the plateau (Henry 2011).

Kebara Cave, with much of its depositional sequence contemporaneous with that of Amud Cave, is particularly interesting as a comparative case study. Both sites display thick sequences and high density of finds, resulting from similar human activities (residential contexts, differential use of space separating the knapping, butchery activities and dumping areas, presence of human burials; Hovers et al 1991, 1995, 2011; Hovers 1998; Rabinovich and Hovers 2004; Alperson-Afil and Hovers 2005; Speth et al. 2012; Meignen and Bar-Yosef 2019). The seasonality of occupation at Kebara Cave was assessed from sex ratio data and analyses of dental cementum annuli (Speth and Tchernov 2001; Speth and Clark 2006; Rendu and Speth 2019). These studies indicate that the sequence of Kebara Cave results from repetitive occupations, of varying length, during the winter and/or spring season, i.e. same season as at Amud cave.

As in Amud Cave, the hunting season identified at Kebara corresponds to the time of year when males and females of both gazelle (Lieberman 1993) and fallow deer (Rendu and Speth 2019) were in physical prime condition, when plant productivity is the highest and resources are easily available, leading to aggregation of herds. Rendu and Speth (2019) also note that the hides of fallow deer of both sexes would be in excellent condition and this may have induced an additional incentive to exploit them at this season. Thus, at both sites it seems that Neanderthals have adapted their patterns of mobility to overcome seasonal constraints associated with lower quality of resources available in these environments during the summer. At Amud, adjustments to longer-term shifts in climate may have been optimized by shifting both the distance and elevations hunting territories, but not seasonality.

Notably, in the Upper Paleolithic sequence at Manot Cave (in the Mediterranean ecozone in the Western Galilee), sex and age structures of the exploited gazelle and fallow deer suggest summer and/or autumn occupations (Yeshurun et al 2021). If that is the case, it would potentially suggest a change in settlement decisions between the Middle and Upper Paleolithic. More research is needed to confirm that this is a widespread pattern. If true, future research might focus on the question whether such a change was related to external factors (i.e., changes in ecological or environmental conditions in the heart of the Mediterranean ecozone) or it was a behavioral change due to shifts in extractive technologies, to hominin taxonomic differences, or to social reorganization.

Conclusion

This study represents the first use of faunal assemblage proxies to discuss seasonal patterns in the occupation and mobility at Amud Cave. We provide new lines of evidence to narrow down the range of plausible interpretations of the history and timing of deposition of this site's sequence. Combining analysis of tooth eruption and wear and dental meso- and microwear allowed us to increase considerably the sample size used to estimate the seasonality of game procurement at Amud Cave. We found that hunting activities at the site were conducted mainly in the course of the months of winter and early spring. During the time of deposition of sub-unit B2, occupation season(s) may have been longer. This result is consistent with regional and local climate proxies indicating a wet peak at this time against a long-term trend of drying climate (Bar-Matthews et al. 2003; Langgut et al. 2011). The single-season occupations throughout the whole sequence are consistent with the reconstruction of palimpsests of relatively short-term occupations. In combination with independent lines of evidence about regional climatic trends and resource procurement locations, our results also suggest that Amud Cave's occupants adapted to the changes through time in the spatial availability of resources by changing their local mobility but overall retained decisions about season of occupation and selection criteria of their prey. Comparison to a limited number of cases where seasonal data were discussed suggests that while this may reflect flexible responses to the ecological affordances in the Mediterranean habitat, it also shows behavioral long-term retention of this settlement preferences and prey choices.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by A. Jallon and F. Rivals. The first draft of the manuscript was written by A. Jallon and all authors commented on previous versions of the manuscript.

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Data availability The list of analyzed specimens, as well as the raw data from tooth mesowear and microwear analyses are available at https://doi.org/10.5281/zenodo.14710073 (Rivals et al. 2025).

Declarations

Competing interests The authors declare no competing interests.

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