Cooperative hunting and meat sharing 400–200 kya at Qesem Cave, Israel

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Zooarchaeological research at Qesem Cave, Israel demonstrates that large-game hunting was a regular practice by the late Lower Paleolithic period. The 400- to 200,000-year-old fallow deer assemblages from this cave provide early examples of prime-age-focused ungulate hunting, a human predator–prey relationship that has persisted into recent times. The meat diet at Qesem centered on large game and was supplemented with tortoises. These hominins hunted cooperatively, and consumption of the highest quality parts of large prey was delayed until the food could be moved to the cave and processed with the aid of blade cutting tools and fire. Delayed consumption of high-quality body parts implies that the meat was shared with other members of the group. The types of cut marks on upper limb bones indicate simple flesh removal activities only. The Qesem cut marks are both more abundant and more randomly oriented than those observed in Middle and Upper Paleolithic cases in the Levant, suggesting that more (skilled and unskilled) individuals were directly involved in cutting meat from the bones at Qesem Cave. Among recent humans, butchering of large animals normally involves a chain of focused tasks performed by one or just a few persons, and butchering guides many of the formalities of meat distribution and sharing that follow. The results from Qesem Cave raise new hypotheses about possible differences in the mechanics of meat sharing between the late Lower Paleolithic and Middle Paleolithic.

Acheulo-Yabrudian | Levant | zooarchaeology | cut marks | Lower Paleolithic

Carnivory and meat sharing are central features of the social lives of recent hunter-gatherers (1–6), such that these behaviors must embody important evolutionary developments in human economics and social relationships (e.g., ref. 2). Meat is one of the highest quality foods that humans may eat, and it is among the most difficult resources to harvest from the environment. The roots of carnivory are known to stretch deep into the past (7–8). The development of meat provisioning and sharing systems is less well-understood. Because of their strong links to social relations and energetics, changes in meat-sharing behaviors during the Lower Paleolithic may have paralleled the last burst in hominin brain expansion between roughly 500 and 250,000 years ago (9).

In the Levant, the culture complex dating to this period is known as the Acheulo-Yabrudian or "Mugharan Tradition" (10–11), based on stratigraphy and distinctive stone tool industries. Information on the subsistence practices and social adaptations that accompanied the physiological changes has been limited up to now by the small samples available for study, poor faunal preservation, or severe cementation of site sediments (11–15). Qesem Cave (Fig. 1) stands apart in that it contains large, well-preserved faunal assemblages alongside lithic artifacts (16–18) in soft or lightly concreted deposits. Located at the interface of the Samaria Hills and the Mediterranean coastal plain, the cave and its sediments were shaped by karst dissolution (19). The sediments are generally in situ. ^{230}Th/^{234}U dates on speleothems (20) indicate that hominins visited the cave repeatedly between circa 400,000 to 200,000 years ago.

The 7.5-m sediment column in Qesem Cave is divided into Lower and Upper Sequences (21). Lithic artifacts and bones damaged by tools or fire co-occur consistently in the deposits and are abundant in every layer. The Lower Sequence averages 3 m thick and is dominated by clastic sediments. Here, wood ash remnants generally occur in small amounts, but they are abundant near the top of this deposit. The Upper Sequence is rich in wood ash, most of which was completely combusted and reworked locally. Thus far, intact hearth features have been found in the contact zone between the Lower and Upper Sequences, and possibly also within the Upper Sequence. Burned bones are common throughout the site (Table 1), but concentrations of burned bones generally follow the northeastwardly retreat of the cave entrance (21).

A faunal sample of 4,740 identified specimens (NISP; 2,808 of these are species-specific identifications) (Tables 2 and 3) and 38,976 nondiagnostic fragments from the 2001–2003 excavations at Qesem Cave provides robust findings on hominin prey choice and butchering, cooking, and meat-sharing practices during the late Lower Paleolithic. The faunal samples were divided for analytical purposes into vertical units I and II within the Upper Sequence and units III–V within the Lower Sequence. Data on Middle and Upper Paleolithic faunal records from Hayonim (22), Misliya (23), and Kebara Caves (24, 25) and the open site of Gesher Benot Ya'akov (26) in the southern Levant (Fig. 1) and Üçağızlı Caves I and II in the northern Levant (27) provide points of comparison.

Results

Fallow deer (*Dama cf. mesopotamica*) was the main prey animal throughout the late Lower Paleolithic occupations of Qesem Cave (73–76% of specimens that could be identified to species). Other prey were aurochs (*Bos*), horse (*Equus*, caballine form), wild pig (*Sus scrofa*), tortoise (*Testudo cf. graeca*), wild goat (*Capra aegagrus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild ass (*Equus cf. hydruntinus*), and rarely, rhinoceros (*Dicerorhinus hemitoechus*). There is little variation in the prey spectrum through time (Table 2).

The macromammal assemblages contain only palearctic species, in contrast to earlier and later faunal records of the southern Levant. Palearctic mammals had begun to swamp all other biotic influences (Turanian, Afro-Arabian) by the late Acheulean period. The effect intensified during the subsequent Acheulo-Yabrudian (12, 28, 29). Speleothem records from Soreq and Peqiin Caves (30) do not cover the entire temporal span of the Qesem sedimentary series, but available data indicate that cooler, wetter conditions prevailed 250–185,000 years ago in the southern Levant and in the eastern Mediterranean as a whole. Markedly drier conditions followed with the beginning of the Middle Paleolithic period.

Cut marks occur on 9–12% of ungulate bone fragments (Table 1), except for the very small sample from Unit I. Cone fractures caused by stone hammers, typical of marrow extraction (7, 8, 31), occur on 19–31% of the ungulate bone fragments and are somewhat more frequent in the older layers. Cut marks and cone fractures are at least twice as abundant on the Qesem ungulate remains as they are in a wide range of Mediterranean Middle and

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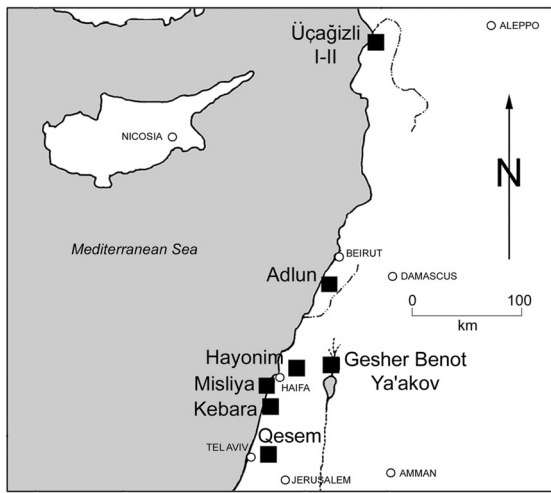
Fig. 1. Locations of selected Paleolithic cave sites in the Mediterranean hills of the Levant.

Upper Paleolithic faunas studied by the same methods (1-4% cut marked; 5-18% cone fractured; refs. 22 and 32).

Gnawing damage from carnivores and hyena coprolites are present in some of the Qesem assemblages, but these traces are extremely rare (Table 1). No gnawing damage from rodents was found, although a few porcupine bones are present. Burning damage is common only on ungulate and tortoise bones (12–19%), demonstrating the economic importance of these animals to the hominins. The bones of large birds (probably owls) and hyenas were never burned, probably because these animals were occasional visitors to the cave rather than prey carried in by the hominins.

The frequency of burning damage on the bones of fallow deer and other medium-sized ungulates—the most abundant prey category—varies according to body part (Fig. 2). Bones of the skull, axial column (spine, ribs, pelvis), scapula, and ulna are less-often burned than the limb bones that possess large medullary cavities (χ^2 = 54.6, df 16, $P < 0.0001$), the latter being seasonally rich sources of consolidated bone marrow. Slow roasting is the simplest way to prepare heads for consumption, yet burning damage is uncommon on these parts. The equivalent frequencies of crania and mandibles may mean that the skulls were roasted whole, with soft tissue effectively shielding the fresh bones and teeth from the flames and coals. The presence of fetal bones and the lack of deer antlers in the assemblages suggest that some of the hunting activities took place in late winter through early summer, when dietary fat would have been at a premium and myelin-covered nerve tissues of the head especially valuable food (33).

A similar burning bias for ungulate limb bones is found at the late Middle Paleolithic site of Kebara Cave (60–50 kya). Here, the bias is attributed to techniques of marrow extraction (33) because gentle localized heating of complete bones aids in preparing the marrow for consumption (31). At Qesem, however, the ends and shafts of the major limb bones are burned at similarly high rates, pointing to

the randomizing overprint of postdepositional burning (34). The burning damage is comparatively intense, and calcination (complete combustion) of bones is commonplace. The limb bones do not appear to have been used as supplemental fuel (*cf.* ref. 35), because grease-rich limb ends were burned no more often than limb shaft fragments. The generally higher rate of burning for the major limb bones nonetheless suggests that processing and discard of these body parts occurred in close proximity to hearths.

The mortality patterns of the Qesem fallow deer (Table 4) speak to the hunting capabilities of early hominins and the development of prime-age-focused harvesting, a uniquely human predator–prey relationship (36). Prey mortality patterns are mediated principally by a predator's approach to its quarry. A fundamental division exists between the death patterns produced by long chase hunters (wolves, wild dogs, cheetahs, spotted hyenas), which tend to kill young, old, or weak individuals and produce attritional or U-shaped mortality patterns, and stalk-and-ambush hunters (lions, tigers, leopards) that are generally less selective and whose large-prey kill patterns usually resemble the structure of the living prey populations. The contrasting ways that chasers and stalkers interact with

Table 2. Prey frequencies based on the number of identified skeletal specimens (NISP) by vertical unit in Qesem Cave

Taxon/body-size class	Unit I, NISP	Unit II, NISP	Unit III, NISP	Unit IV, NISP	Unit V, NISP
Lacertidae	—	4	—	—	—
Testudo cf. *graeca*	1	15	15	29	28
Medium bird	—	—	1	1	4
Large bird (e.g. Strigidae)	—	1	1	—	1
Hystrix indica	—	7	2	8	6
Small ungulate	2	—	4	3	4
Capreolus sp.	—	1	1	—	—
Capra aegagrus	—	—	2	1	—
Dama cf. *mesopotamica*	33	524	579	731	236
Sus scrofa	—	9	22	20	4
Equus cf. *hydruntinus*	—	1	4	7	—
Medium ungulate	8	320	438	718	199
Cervidae	1	36	23	43	25
Cervus elaphus	—	12	13	1	2
Equus caballus	—	26	53	39	1
Bos primigenius	9	46	56	76	13
Large ungulate	—	25	61	55	12
Dicerorhinus hemitoechus	—	6	16	14	1
Megafauna	—	4	2	2	—
Medium mammal	4	1	29	14	4
Hyaenidae	—	2	12*	1*	—
Total	58	1,040	1,334	1,768	540

Counts by taxon-specific and body-size classes combined. —, not present.
*Five specimens from Unit III and one from Unit IV are hyena coprolites.

Table 1. Frequency of damage types on all ungulate bones (% of NISP) by vertical unit

Damage type	Unit I	Unit II	Unit III	Unit IV	Unit V
Burning, %	4	19	13	12	12
Cone (percussion) fractures, %	0	20	19	31	25
Cut marks, %	2	9	11	12	10
Gnawing, %	0	<	<	<	0
Atmospheric weathering, %	0	1	1	1	1
Total NISP sampled	53	907	1,057	1,198	328

Teeth are excluded. <, present at less than 1% of NISP.

Table 3. Prey frequencies based on taxon-specific percentages for mammals and tortoises in Qesem Cave

Taxon	Unit I	Unit II	Unit III	Unit IV	Unit V
Testudo cf. *graeca*, %	2	2	2	3	9
Histrix indica, %	0	1	<	1	2
Capreolus sp., %	0	<	<	0	0
Capra aegagrus, %	0	0	<	<	0
Dama cf. *mesopotamica*, %	75	76	73	75	75
Sus scrofa, %	0	1	3	2	1
Equus cf. *hydruntinus*, %	0	<	<	1	0
Cervidae, %	2	5	3	4	8
Cervus elaphus, %	0	2	2	<	1
Equus caballus, %	0	4	7	4	<
Bos primigenius, %	20	7	7	8	4
Dicerorhinus hemitoechus, %	0	1	2	1	<
Hyaenidae, %	0	<	1	0	0
Total taxon-specific NISP	44	685	793	970	316

<, present at much less than 1% of NISP.
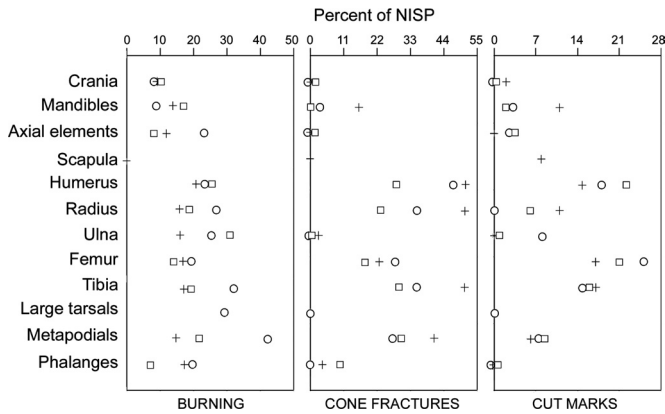
Fig. 2 Frequencies of medium ungulate bone fragments with burning damage, cone fractures, and cut marks by element or element group and stratigraphic unit in Qesem Cave. Data are based on subsamples of the faunal assemblages examined intensively for all types of surface damage: circle, units I–II NISP = 404; square, unit III NISP = 414; +, units IV–V NISP = 710.

Fig. 3. Modeled (*A*) and observed (*B*) artiodactyl ungulate mortality patterns generated by large predators. (*B*) Means for recent spotted hyena (square 1), wolf (square 2), Cape hunting dog (square 3), tiger (square 4), African lion (square 5), Holocene and recent human hunters (square 6), Mediterranean Epipaleolithic and Upper Paleolithic hunters (square 7), and Mediterranean Middle Paleolithic hunters (square 8). *, Average for the Acheulo-Yabrudian fallow deer assemblages from Qesem Cave, Israel.

a prey population in the same environment reduces interference competition and reflects a long legacy of niche differentiation (37, 38). Humans are ambush predators, but they are somewhat more selective than other predators in this strategy group, producing mortality patterns in artiodactyl ungulates that range from nonselective to strongly biased to prime-adult animals. In terms of averages, a mild bias to prime animals has been noted in a variety of recent and prehistoric contexts, and the human species is ecologically unique in this respect (32).
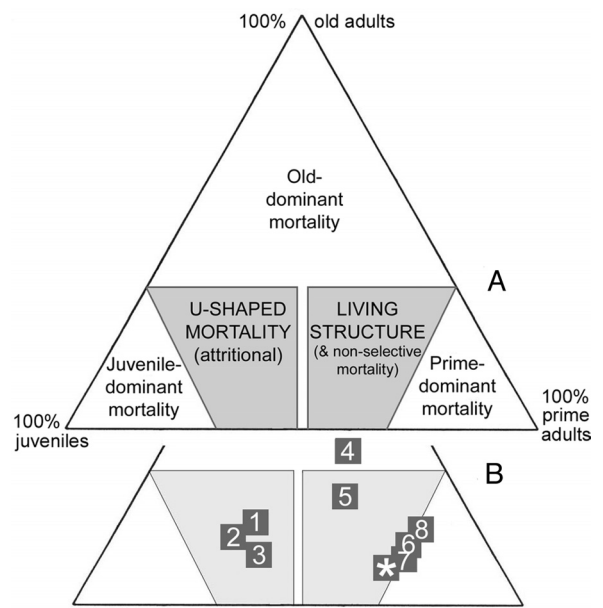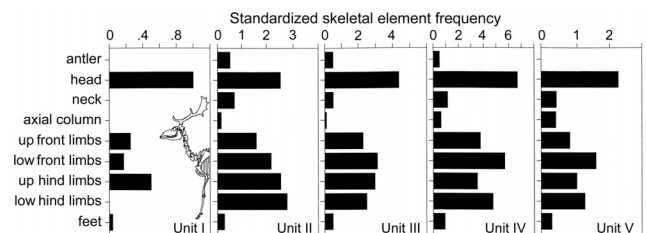
How ancient is this "human" pattern of prey-age selection? Expectations for nonselective and selective hunting patterns are modeled in tripolar format based on the relative proportions of juveniles, prime adults, and old adults that are killed (ref. 36; Fig. 3*A*). Broad prey age selection patterns are generalized in Fig. 3*B* as averages of many cases to compare niche-level differences between nonhuman and human predators, including recent humans and Middle, Upper, and Epi-Paleolithic foragers represented by archaeological cave sites in Israel, Italy, Turkey, and Lebanon (22–24, 32, 39). The mean values generated by humans are consistent across periods and technologies, and all of the human means are distinct from those of the nonhuman predators. The averaged mortality pattern for fallow deer from Qesem Cave is consistent with those for Middle Paleolithic through recent human cases. This finding indicates that the prime-adult hunting niche had already developed in hominins by 400,000 years ago, if not earlier.

Deer and other ungulates in the Qesem faunal assemblages are represented mainly by limb bones and head parts, whereas vertebrae, ribs, pelves, and toe bones (phalanges) are underrepresented to a great extent. This discrepancy in body-part representation is readily apparent from Fig. 4, wherein the numbers of skeletal elements (MNE) are grouped into 9 anatomical regions and standardized to a complete skeleton model (32). All values in the bar charts would be equal if every part of each prey animal were carried to the cave. As a partial correction for the greater durability

of teeth in fossil records, only bony features of the skull were used to estimate the number of crania and mandibles.

Correlation results for the relative representation of spongy and dense limb bone features against independent standards for bone tissue bulk density (40, 41) indicate that in situ destruction potentially explains 6–30% of the variation seen in body-part representation. Preservation biases, therefore, could partly account for the low frequencies of fragile vertebrae and ribs in Qesem Cave, but not for the low frequencies of denser portions of the pelvis or toe bones. To avoid any anatomical biases that may have been introduced by density-mediated bone destruction, the counts of parts across the prey skeleton were based only on those bony diagnostic portions of element that have similar densities (ref. 42). The high proportions of head and limb parts and the low proportions of axial and toe bones in Fig. 4 therefore reflect the transport decisions of the hominins from kill site to cave.

Caves generally are places to which food must be brought. Ethnographically, foragers' decisions about which prey body-parts to transport depend on food value, weight, and travel times between kill sites and safe havens. Greater travel distances are expected to discourage the transport of low utility (31) or very heavy parts (43). The body part profiles of the Qesem faunas are similar to those of all of the later Paleolithic cave faunas considered in this study. The

Table 4. Mortality patterns for fallow deer

Unit	Juveniles	Prime adults	Old adults	*N*
I and II	0.42	0.53	0.05	38
III	0.42	0.52	0.06	31
IV	0.27	0.65	0.08	40
V	0.24	0.67	0.09	21

Sample (*N*) is based on the dP4-M3 dental series and combines right and left sides.

Fig. 4. Standardized skeletal element frequencies (observed/expected) by anatomical region for fallow deer by stratigraphic unit in Qesem Cave.

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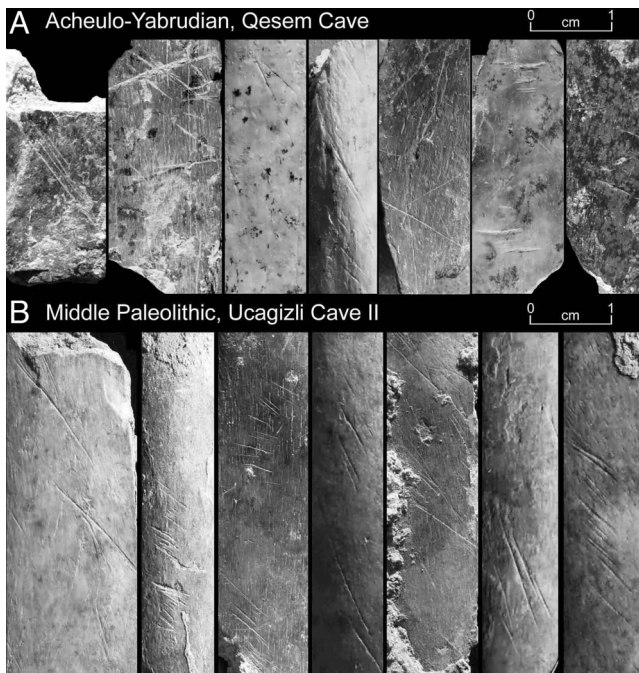
Fig. 5. Clustered cut marks on ungulate limb shaft fragments from (*A*) late Lower Paleolithic Qesem Cave and (*B*) Middle Paleolithic layers of Üçağızlı Cave II.

Fig. 6. Cut-mark angle differences (MDAA, means and sd) for limb shaft samples from the Acheulo-Yabrudian (late Lower Paleolithic; LP) of Qesem Cave in comparison to a Middle Paleolithic (MP) sample from Üçağızlı Cave II and an early Upper Paleolithic (UP) sample from Üçağızlı Cave I. Each point represents 1 bone specimen with multiple cut marks on its surface; specimen means are arranged in order of increasing value. Horizontal line represents the mean value for all specimens from all periods.
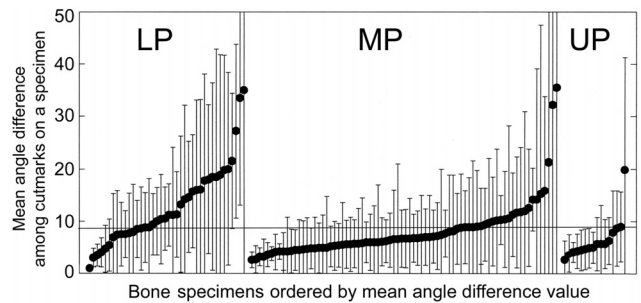
dominance of high utility parts in the Pleistocene Mediterranean cave sites is also consistent with the range of body parts that modern high-latitude foragers typically carry to residential sites (31). The assemblages created by recent arid-tropical foragers at residential camps can be quite different (44, 45), possibly because much meat eating, stripping, and drying is undertaken at kill sites (44) and these people use metal containers for boiling the meat on complex axial bones and grease extraction (32, 45).

The bias against low utility body-parts at Qesem Cave implies that the hominins often carried meat over long distances to supply the site with food. The consistency of the body-part biases over a long time-span also suggests that the hunters were very mobile as a rule and the number of persons available to help move meat to the cave was invariably small.

Cut marks are simple types with V-shaped cross-sections, made by slicing motions (46), and indicate a narrow range of flesh cutting and removal activities. Hack marks are present but rare, and no axial scraping marks were found. Lithic technology (16, 17, 47) and use-wear (48) analyses indicate that the most common cutting tools were unmodified blades, and there seems to have been little concern for renewing tool edges.

Many of the fragments from upper limb bones display loose aggregations of cut marks (3–44 strokes) (Fig. 5*A*). The comparatively high incidence of crossed marks and the diverse angles of the cut marks on the Qesem bones is striking in comparison to Middle and Upper Paleolithic faunas (Fig. 5*B*) from Mediterranean cave sites (22, 32). Because cut marks on the Qesem bones are concentrated on meaty skeletal elements, especially the humerus and femur (Fig. 2), the relatively chaotic arrangements of the cut marks cannot be explained as geological scratches (*cf.* ref. 29). Scratching from small-scale sediment movements (49) should be much less biased with respect to body part. Nor are the marks from excavators' tools—many of the marks were discovered beneath light concretions, and the channels invariably share the coloration of the bone surfaces (50).

A quantitative comparison of variation in cut-mark angles tests the possibility of greater disorder in the Qesem assemblages relative to Middle and early Upper Paleolithic cases from Üçağızlı Caves II and I, respectively. These comparison samples from southern Turkey formed in similar climatic and geologic environments, contain the same or similar prey (27) and body parts, and bone surface preservation and visibility is equivalent to that of the Qesem sample. All 3 sites contain multiple stratigraphic layers and faunal assemblages, and the samples represent time-averaged behavioral patterns. The cut-marked specimens in this comparison are compact bone fragments from limb shafts exclusively, many but not all of which could be attributed to skeletal element.

The differences in angles between adjacent cut marks were calculated (always between 0–90°). The mean of these measurements was then calculated for each bone specimen: This "mean difference of adjacent angles", or MDAA, is the main parameter used to estimate the amount of variation in cut-mark angles per period. Given that fragment surface areas could affect the number and orientation of cut marks (51, 52), we estimated fragment sizes (cm²) by multiplying the length by the width.

Fig. 6 shows that the MDAA per specimen is more variable in the LP sample (Table 5). We also observed that fragment sizes (surface areas in cm²) are greater on average in the later samples, whereas the group mean angle difference for cut marks clearly decreases with time. However, Table 6 shows that, although MDAA is higher in the Lower Paleolithic sample than in the Upper or Middle Paleolithic samples, there are also significant differences in sample size. Thus, we must ask whether there is a causal (mechanical) relationship between fragment size and MDAA, or whether changes in the 2 variables represent independent temporal trends. A mechanical link between MDAA and fragment size would undermine a behavioral explanation for the trends.

The correlation between fragment size and MDAA approaches statistical significance for the aggregate sample containing all periods (Table 7). However, the coefficient of determination is very

Table 5. Summary of mean difference of adjacent cut-mark angles (MDAA) for Qesem Cave (late Lower Paleolithic), Üçağızlı Cave II (Middle Paleolithic), and Üçağızlı Cave I (early Upper Paleolithic)

Site	Period	N specimens	Group mean angle difference	Mean specimen surface area, cm²
Qesem	LP	38	13.4 ± 7.5	6.0 ± 3.7
Üçağızlı II	MP	78	8.1 ± 5.4	12.3 ± 6.5
Üçağızlı I	UP	16	6.4 ± 4.0	14.5 ± 8.3

Group mean is a mean of means for the site and period. LP, Lower Paleolithic; MP, Middle Paleolithic; UP, Upper Paleolithic.

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Table 6. Pair-wise statistical analyses for MDAA and specimen surface areas between periods

Sub-sample pair	t-test, separate	df	P value	Mann-Whitney U	n	P value
MDAA						
LP, MP	3.925	56.4	<0.001	2,264	38,78	0.0001
LP, UP	4.444	48.7	<0.001	507.5	38,16	0.0001
UP, MP	1.421	27.4	0.167	809.5	78,16	0.062
Surface area, cm²						
LP, MP	−6.593	110.7	<0.001	524.5	38,78	0.0001
LP, UP	−3.915	17.7	0.001	81	38,16	0.0001
UP, MP	−0.969	19	0.345	529.5	78,16	0.342

low (0.027) and indicates that variation in fragment size has the potential to explain only a small part of the variation (3–8%) in MDAA on the bone specimens. Importantly, the correlation is negative, meaning that smaller fragments have more variable cut-mark angles. This tendency is the opposite of what one would expect if lesser surface area had reduced the chance of detecting multiple (multioriented) strokes on a given bone specimen. Moreover, when we remove the temporal element, and examine the correlations between the 2 variables within individual periods (Table 7), the correlations between fragment size and MDAA disappear. The whole-sample correlation between fragment size and cut-mark angle variation does not seem to stem from a mechanical relationship but rather is a result of parallel trends through time.

Table 8 presents further evidence that the trend toward more organized (aligned) cut marks is not a mechanical consequence of differing fragment sizes. Here, analysis is confined to bone fragments in the size interval between 5–15 cm², excluding the largest and the smallest specimens. There is absolutely no correlation between cut-mark angle variation and area for fragments in this size range (r = −0.025, P = 0.827), yet the contrasts in MDAA between periods remain. In other words, trends in cut-mark angle variation among time periods are apparent even when controlling for fragment size.

Cut-mark orientations in the Qesem faunas are indeed more chaotic than in later periods. The diverse cut-mark orientations at Qesem suggest that butchering postures, or the ways of holding a body part while cutting away the meat, may have been more varied as well. The cut-mark patterns of the Middle and Upper Paleolithic samples exhibit greater regularity, with more consistent orientations of cut marks over small areas of bone. Although wider comparisons to other sites are needed to fully evaluate this phenomenon in the late Lower Paleolithic, the observed differences among the study samples are highly significant.

Discussion

Important axes of behavioral change in Pleistocene hominins include hunting tactics, technology, food transport and processing behaviors, and social feeding habits. A small but growing number of late Middle Pleistocene sites in Eurasia provide clear evidence of large-game hunting and of prime-biased prey selection in particular (e.g., refs. 22, 23, and 53). Qesem Cave extends the history of this distinctly human niche characteristic back to at least 400,000 years ago, and earlier cases are anticipated. Comparisons to older Lower Paleolithic cases in East Africa are

Table 7. Correlation coefficients for MDAA and specimen surface area (fragment size)

Sample set	r	n	P value
All periods combined	−0.164	132	0.06
LP only	−0.283	38	0.085
MP only	0.102	78	0.375
UP only	0.271	16	0.310

desirable but prevented by the low incidence of head parts (8, 54), which in itself could testify to further differences in meat acquisition before 1 Mya.

Late Lower Paleolithic hominins probably hunted large-game animals with hand-held wooden spears. Although well-crafted in some cases (55), the rather basic nature of these weapons underscores the necessity of close cooperation among hunters, because the body weights of some prey (e.g., *Bos*) greatly exceeded that of the individual hunters. Also important is the observation that the hunters delayed consumption of high quality meaty parts until they could be moved to the cave, a central place where sharing would have been inevitable.

Although not the earliest record of fire as technology in the Levant (56, 57), Qesem Cave preserves contextual information about cooking and marrow extraction during the late Lower Paleolithic. Hearths clearly were magnets for butchering and feeding activities on site. The damage to bones at Qesem was heavy-handed, with many more cut marks and cone fractures than normally occur in later Paleolithic cave faunas. The stone implements of the Acheulo-Yabrudian are generally not much more massive than those of the Levantine Middle Paleolithic. This situation is particularly true at Qesem Cave, where handaxes are extremely rare (or absent from some units) and cutting tools are mainly blades. It is possible that such heavy marking of the bones instead reflects a situation in which processing was not hurried or particularly efficient once the food arrived on site and perhaps also a distinct mode of social feeding (see below).

Butchery practices evidenced at the much older Lower Paleolithic site of Gesher Benot Ya'akov indicate that hominins were sensitive to variations in the anatomical and nutritional structures of prey anatomy (26). The same can be said for the late Lower Paleolithic hominins at Qesem Cave. The consumption patterns in evidence at Qesem are somewhat at odds, however, with what we are accustomed to finding in later periods. Among recent humans, the butchering of large animals nearly always involves a chain of focused tasks performed by one or just a few persons, and butchering tends to result in fairly well-aligned, orderly marks on bone surfaces. These tendencies have social significance in that butchering procedures guide many of the formalities of food distribution and sharing that follow. Whereas few hard and fast rules about field butchering and body part transport exist among recent foragers (40, 58, 59), the social valuation of meat sharing is universally high and the chains of transfer are often complex (1–6).

It is reasonable to expect that hominins of all Paleolithic periods lived in social groups, but the patterns of cooperation could have differed greatly with time, including the manner in which meat was distributed and consumed within the group. The behavioral implications of the cut-mark results for Qesem Cave will remain difficult to evaluate until more Paleolithic and recent cases are examined for cut-mark "disorder" under well-controlled conditions, but some speculation is in order. Hypothetically speaking, a simpler or less evolutionarily derived model of meat consumption could be appropriate for the late Lower Paleolithic at Qesem Cave. Perhaps the meat distribution systems were less staged or canalized than those typical of Middle Paleolithic, Upper Paleolithic, and later humans. The evidence for procedural interruptions and diverse positions while cutting flesh at Qesem Cave may reflect, for example, more hands (including less experienced hands) removing meat from any given limb bone, rather than receiving shares through the butchering work of one skilled person. Several individuals may have cut pieces of meat from a bone for themselves, or the same individual may have returned to the food item many times. Either way, the feeding pattern from shared resources may have been highly individualized, with little or no formal apportioning of meat. If the cut-mark patterns observed at Qesem Cave prove to be widespread for the Lower Paleolithic (possibly at Gesher Benot Ya'akov; see specimens in ref. 26, figures 9–11), then the data may expose subtle but important differences in the practical and social mechanics of

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Table 8. Pair-wise tests of difference in central tendency (separate variance t-test and Mann-Whitney U) for MDAA between culture periods, for specimens with surface areas ranging between 5 and 15 cm²

Sub-sample pair	Means	t value	df	P	Medians	Mann-Whitney U	n	P
LP, MP	11.4, 7.4	2.594	24.4	0.016	9.7, 6.3	734	18, 54	0.001
LP, UP	11.4, 5.3	3.889	23.4	0.001	9.7, 4.5	140	18, 9	0.002

meat-sharing between the late Lower Paleolithic and the Middle Paleolithic periods.

Materials and Methods

Burning damage on bones was identified by using a combination of microscopic (60) and macroscopic criteria on identifiable and unidentifiable specimens (34). A large fraction of each faunal assemblage from Qesem Cave was subjected to an intensive analysis of surface damage traces (NISP = 3,680, or 78% of all identified specimens). For the cut-mark study, specimens with multiple cut marks (3- 44 strokes) were extracted from each assemblage in the order in which they were encountered during general zooarchaeological analysis, so the sample is representative. Low-level microscopy was used to identify tool marks on the Qesem bones, and the surface of every specimen was examined. Measurements of cut-mark angles were made on high-resolution digital images, with the natural long axis of the bone oriented vertically. Angle measurements on each bone specimen began at the lower left area of the image and advanced arbitrarily to the next closest mark until the angle of every stroke was recorded.

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