The Natufian economy at el-Wad Terrace with special reference to gazelle exploitation patterns

Guy Bar-Oz[a,b,*], Tamar Dayan[b], Daniel Kaufman[a], Mina Weinstein-Evron[a]

[a]*Zinman Institute of Archaeology, University of Haifa, Haifa 31905, Israel*
[b]*Department of Zoology, Tel-Aviv University, Tel-Aviv 69978, Israel*

Abstract

We carried out a detailed taphonomic and zooarchaeological analysis of the faunal remains from the new excavation of the Late Natufian layers of el-Wad Terrace. We focused on gazelle exploitation patterns and examined them within the context of the established Epipalaeolithic sequence from the coastal plain of Israel. Mountain gazelle (*Gazella gazella*) is the most heavily exploited species. The taphonomic history of the assemblage suggests minor loss of bones caused by post-depositional processes and indicates that bone destruction occurred during occupation. Cut marks from all stages of activities, absence of selective transport, and body part representation suggest that gazelle were butchered at the site. Analysis of gazelle sex composition shows male overrepresentation during the Natufian. Size trends show an increase of gazelle body-size during the Natufian in comparison to previous periods. The patterns of body-size increase show the same tendency in proximal and distal limb-bones. The trends in gazelle body-size from the Epipalaeolithic of the coastal plain do not demonstrate any sign of morphological dwarfism, increased variation, or allometric changes in the morphology of Natufian gazelles and thus do not support the previously suggested hypothesis of "proto-domestication".
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1. Introduction

The process of animal domestication, one of the most significant developments in the culture and economy of ancient civilizations, has shaped human societies and their environment to this day (e.g., [23,24,29–31,39,75]). It is therefore not surprising that a large volume of literature has focused on understanding the evolution of cultural control of natural resources (examples of major publications are [23,29,31,39,114]). Of special interest have been the earliest stages of animal domestication, which may hold the key to understanding the roots of this process. They may help us to understand the choice of species domesticated and possible hunting practices and incipient cultural control that may have been the

forerunners of true domestication (sensu [31]), as well as to gain insight into aborted attempts that may tell us the equally interesting story of the roads not taken [82]. Studying animal exploitation just prior to domestication can help us understand a few important issues: first, what species were chosen for domestication and why; second, whether incipient cultural control or specialized hunting practices that led to true domestication were practiced in the Natufian; and third, whether there were aborted attempts at domestication which may tell an equally interesting story about the road not taken [82]. The roots of this cultural and economic change may be found in the Natufian culture of the southern Levant, when sedentary communities, or at least less residentially mobile societies were first established (e.g., [11,13,14,17,62,101]), dogs were domesticated [42,44,97,100], and incipient cereal agriculture may have been practiced [1,98,99]. We studied the faunal remains of el-Wad Terrace (EWT) in order to gain further insight

* Corresponding author. Tel.: +972-4-824-00-70; fax: +972-4-824-98-76

E-mail address: guybar@research.haifa.ac.il (G. Bar-Oz).

into the economy of this critical stage. In particular, we focused on the exploitation pattern of Natufian gazelles and on the way they were hunted. Some investigators have suggested that we may find the beginning of cultural control of gazelles during this period [32,70,95,96].

Many prehistorians suggest that the Epipalaeolithic cultures—the Kebaran (20/18–15/14.5 kya BP; uncalibrated dates), Geometric Kebaran (15/14.5–13/12.8 kya BP), and Natufian (13/12.8–10 kya BP) in the eastern Mediterranean region, developed during the Late Glacial from mobile and aggregation/dispersal foragers (Kebaran and Geometric Kebaran) into more complex societies of non-egalitarian hunter–gatherers using long-term occupation sites (Natufian) (e.g., [12–14,62,66]). Following earlier studies of the faunal remains from three Epipalaeolithic pre-Natufian sites in the northern coastal plain of Israel (i.e., Neve-David—6; Nahal Hadera V—8, 11; Hefzibah—9), we carried out a detailed analysis of the faunal remains from the new excavation at the Late Natufian layers of el-wad Terrace (11–10.5 kya BP, uncalibrated).

Mountain gazelle (*Gazella gazella*), and to a lesser extent Persian fallow deer (*Dama mesopotamica*), were the major hunted animals in the diet of human populations throughout the Late Pleistocene of the Mediterranean region of the southern Levant (e.g., [15,55]). Towards the end of this period fallow deer exploitation decreased dramatically, a trend that may reflect paleoclimatic change and its affect on the Mediterranean environment ([15,36]; but see also [60] for a cultural explanation). The heavy exploitation of gazelles during the entire period, and particularly during the Natufian, has generated research on gazelle hunting patterns and theories about their implications (e.g., [27,32,36,37,41,64,70,85]). The focus has been the possibility that the Natufians practiced some kind of 'herd management', as evidenced by an increase in the percentage of gazelle exploited (e.g., [61,62,70,94–96]), an increase in the proportion of young gazelles hunted [37,41], and a high proportion of male gazelles hunted [32,94–96].

Cope [32] suggested that the intensive sex culling practiced by the Natufians represents "an intermediate area between management of wild animals and true domestication" and proposed the term 'proto-domestication' for this stage of cultural control. She also suggested that the Natufian interference of gazelle mating systems was pronounced dwarfing and measurable phenotypic aberrations in a high percentage of individuals. Cope [32] argued that although all limb bones showed some degree of diminution, proximal limb-bones were less affected than others.

Later studies, however, have questioned many of her findings. Dayan and Simberloff [45] analyzed Cope's published data (all sample statistics) and found no statistically significant evidence for dwarfing or increased variation in Natufian gazelles, and thus no support for the hypothesis of 'proto-domestication'. Ducos and Horwitz [51] recently studied morphological change in Late Pleistocene–Early Holocene gazelles, using size indices (for each measurable bone, the ratio of its measurement calculated relative to the measurement taken on the same bone from a reference individual or population) as a measure of morphological change. They interpreted their results as showing the largest sized population during the Kebaran, followed by a marked size reduction during the Geometric–Kebaran and Early Natufian, and then a slight increase in size during the Late Natufian. They published size indices alone, compared to a 'Grand Mean' of the species-specific size index, and refrained from statistical analysis of their data, arguing that "The intervals $x - 2SD$ and $X + 2SD$, whose meaning here differs from that of a so-called 'confidence interval', overlap widely, and it would be nonsensical to demonstrate whether the differences are significant or not on the basis of a statistical analysis" ([51]:241). Dayan and Simberloff [45] pointed out that statistical analysis of raw morphometric data would be a major step towards resolving this intriguing issue.

Ducos and Horwitz [51] point to two potential sources of bias: changes in sex ratios, for which they could not account, that may change the mean sizes in this sexually dimorphic species, and the compilation of sites from different geographic zones. Bar-Oz et al. [6] also raised the latter issue, analyzing patterns of gazelle exploitation in the southern Levant and showing that the evidence so far published is insufficient to demonstrate increased hunting of gazelle in the Natufian. Bar-Oz et al. [6] emphasized the need to study diachronic change in gazelle exploitation patterns within a well-defined geographic region and ecological zone, so that patterns are not confounded by regional differences.

Did the Natufians practice cultural control of gazelle herds? Following three decades of extensive discussion of the significance of gazelle exploitation, only high-resolution studies of patterns of gazelle exploitation and their morphological ramifications can further our understanding of the evolution of cultural control of this wild ungulate during the Natufian period of the southern Levant. Here we present the results of a detailed taphonomic and zooarchaeological analysis conducted on the faunal remains retrieved from the new excavation in the Late Natufian layers of el-Wad Terrace (1995–2000 seasons). Following a description of the faunal assemblage and the taphonomic history of the site, we focus on gazelle hunting patterns and examine them within the context of the Pre-Natufian Epipalaeolithic sequence from the coastal plain. In addition, we explore size variation of Natufian gazelles in comparison to three pre-Natufian Epipalaeolithic assemblages from the same
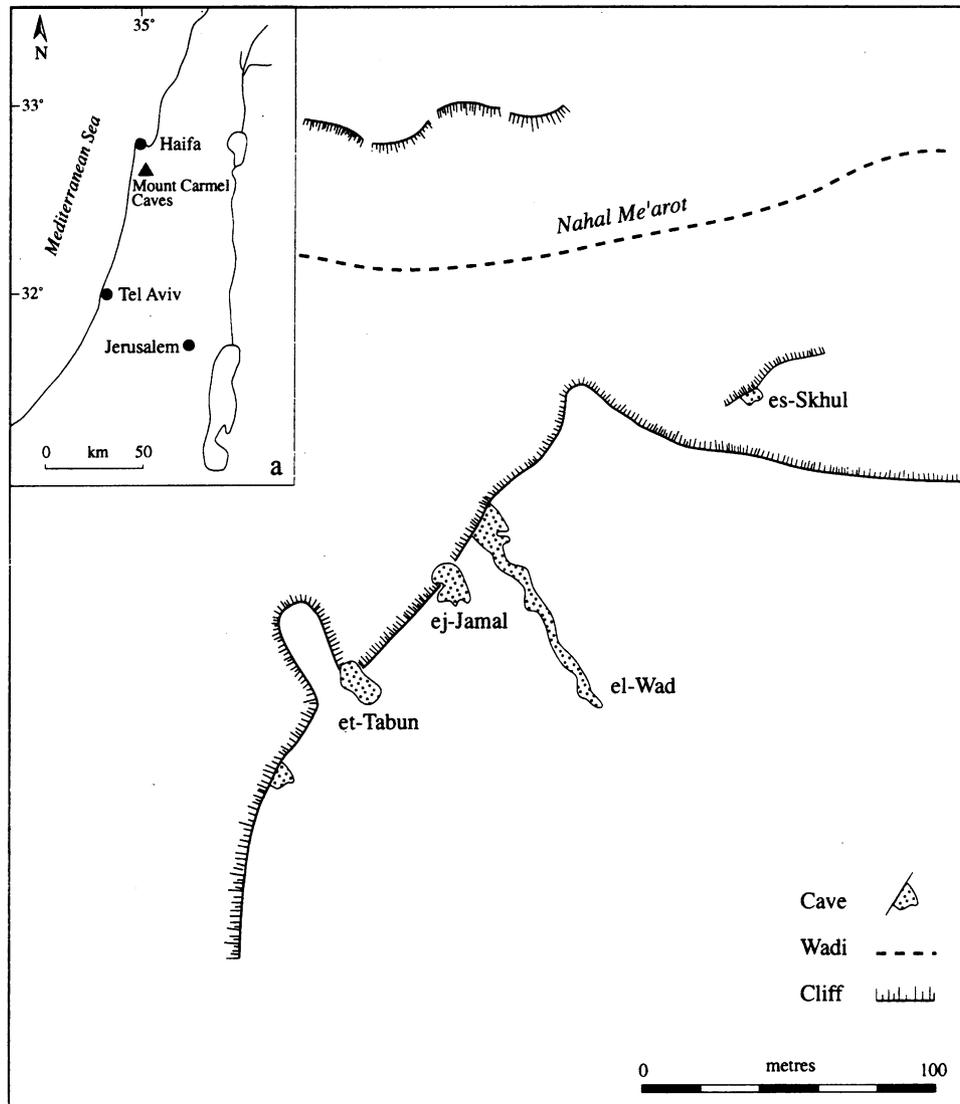
Fig. 1. Location map of the Mount Carmel caves (a), showing el-Wad as the largest of the caves within the cliff.

general region in the coastal plain of Israel (Nahal Hadera V [Early Kebaran; 11], Hefzibah [layers 7–18—Late Kebaran; 12], and Neve-David [Geometric Kebaran; 6]) that were studied previously using the same methods. On the basis of morphometric analyses we ask: (a) Is there a preference for culling male gazelles during the Natufian? (b) What are the body-size trends of gazelles during the Epipalaeolithic? (c) Can we detect a pattern of increased variability in the morphology of Natufian gazelles?

2. The site and its setting

El-Wad Cave and its adjacent terrace, along with three other caves (Tabun, Skhul, and Jamal), are situated at the foot of the western slope of Mount Carmel, on the southern cliff of Nahal Me'arot (Wadi el-Mughara; Fig. 1). The cave faces to the north-west and is situated 44 m above sea level at a point where the wadi opens out to the coastal plain. Nahal Me'arot drains into the Mediterranean Sea some 3.5 km west of the cave.

The cave is large and elongated and consists of an outer and an inner chamber (Chambers I and II) and a 71 m long corridor (Chambers III–VI; [57]). The site was originally excavated by Charles Lambert in 1928, who found two burials, later identified as Natufian, on the terrace, and a decorated sickle haft in the cave [57,107,108]. Dorothy Garrod excavated el-Wad over five seasons from 1929 to 1933. Chambers I and II were excavated to bedrock. Chamber III was partially excavated, and the terrace was dug to bedrock over an area of ca. 270 sq m. The stratigraphic sequence yielded Middle and Upper Paleolithic (layers G-C), Natufian

(layers B2 and B1), and Holocene (layer A) deposits. The Natufian layer is the best represented at the site and stretches across Chambers I and II of the cave and the entire terrace. The Natufian deposits yielded the most notable finds including a few architectural remains, close to 100 burials [18], a rich lithic assemblage, decorative items, bone tools, ground stone implements, and a large faunal assemblage [57]. The latter provided the basis for the first palaeoenvironmental sequence of the Levant [15]. Many of the architectural features, decorated burials, and most bone implements on the terrace were assigned to the lower Early Natufian (layer B2). In contrast, bone implements and art objects were rare in the Late Natufian phase (layer B1) ([57]; see also [56]).

In 1980 and 1981, limited excavations were conducted on the terrace by François Valla and Ofer Bar-Yosef to the north-east of Garrod's terrace excavations. On the basis of techno-typological criteria, the excavation revealed that layer B1 could be further sub-divided into Late and Final Natufian phases [102]. Excavations in Chamber III were renewed by Mina Weinstein-Evron in 1988 and 1989. These later excavations enabled the collection of vital information regarding the Natufian habitation of the site and their mode of environmental exploitation [102,107], such as large and small game exploitation [79,81,90].

Three radiocarbon determinations, based on charcoal from the Early Natufian occupation of Chamber III, yielded dates of 12.95 ± 0.2 kya BP (RT-1368) for the lower part, 12.62 ± 0.11 kya BP (PTA-5435) for the middle part, and an average of 10.71 ± 0.137 kya BP (two counts of the same sample; RT-1367) for the upper part of the layer (all dates are uncalibrated; [105]). According to the available data, it is most likely that the earlier el-Wad dates indicate the oldest occurrence of the Early Natufian in northern Israel [105,107]. While no other absolute dates are available, the presence of Late and Final Natufian phases at the site suggests that it was inhabited throughout the Natufian.

Based on recent excavations within the cave and the re-evaluation of archival materials it has been suggested that the Natufian of el-Wad extended over the entire terrace and that it was considerably more varied and complex than the original excavations indicated [106,107]. On the basis of these observations new excavations were initiated on the terrace by Mina Weinstein-Evron and Daniel Kaufman starting in 1995. The new excavations are located to the north-east of Garrod's trench and over an area of 60 m². This area seems to be less disturbed than that at the front of the cave. To date, only the upper parts of the Natufian layers have been excavated. The rich material culture belongs to the Late Natufian ([109]; based on the appearance of numerous small abruptly retouched lunates) and includes characteristic flint tools, ground-stone implements, bone tools, decorative items (shells

and beads), and art objects. Zooarchaeological remains, including microfauna [111,112], fish (being studied by Irit Zohar) and molluscs (being studied by Daniella Bar-Yosef), are abundant and well preserved. In addition, individual and group burials of some 11 Natufians (being studied by Israel Hershkovitz and Noga Bachrach) were uncovered on the terrace.

The bone sample analyzed in this study includes only faunal remains that originated from undisturbed Late Natufian contexts (excluding fish, microfauna, and molluscs). The excavated sediments were wet-sieved through 3 mm and 1 mm meshes, sorted, and stored at the Zinman Institute of Archaeology, University of Haifa. The complete zooarchaeological and taphonomic coding and analysis procedures used to collect and present the data for this paper and the complete data sets for all studied assemblages are detailed in Bar-Oz [5].

3. The el-Wad Terrace faunal assemblage

The total mass of the faunal assemblage examined from el-Wad Terrace is 45,435 g (retrieved from 405 excavation units [0.25 m² each ca. 5 cm thick]). All excavation units with a total faunal mass of more than 200 g (n=54) were sieved through 10 mm mesh, and the remains of the identifiable and the unidentifiable elements were counted. This sample yielded 5653 complete and fragmentary bones larger than 10 mm in maximum dimension, of which 979 were identified to taxon and part of skeleton.

The abundances of the remains of the 16 taxa represented are detailed in Table 1 (NISPs and MNIs were calculated using the assumptions described in Ref. [68]). The Late Natufian inhabitants of el-Wad Terrace subsisted mainly on mountain gazelle (75.5%). Persian fallow deer contributed only 2% to the assemblage. Small game are represented by the fox (*Vulpes vulpes*), hare (*Lepus capensis*), tortoise (*Testudo graeca*), and partridge (*Alectoris chukar*) and constitute approximately 20% from the entire bone assemblage. In the Early Natufian assemblage of el-Wad Cave fallow deer constitute 10% of the assemblage [81] and small game comprise 40% (over 76% are hare; [90]).

4. The taphonomic history of el-Wad Terrace

4.1. Mode of bone preservation

The relationship of gazelle bone survivorship to bone density served to assess the mode of bone preservation of the el-Wad Terrace assemblage and to measure the amount of bone loss caused by either pre-depositional or post-depositional processes [71,72]. The regression line for gazelle bone survivorship (based on proportional frequency of elements observed [%MNI]) and bone

Table 1
Number of identified specimens (NISP) and minimum number of individuals (MNI) of each taxon represented at el-Wad Terrace

	Gazella gazella	Bos primigenius	Dama masopot.	Capreolus capreolus	Sus. scrofa	Lepus capensis	Canis lupus	Vulpes vulpes	Felis chaus	Meles meles	Erinaceus sp.	Testudo graeca	Ophiosaurus apodus	Agama stellio	Alectoris chukar	Total
Head:																
Horn/Antler	20															
Sk. frag.	66		3			1								2	3	
Man. Cond.+frag.	35		2					12	3	1	1	3		35	5	
Teeth	214	4	3	5	5		2	71	2			6				
Body:																
Ver: Cervical	52		2			18		2					[640]			
Ver: Thoracic	32					1		2								
Ver: Lumbar	93					5		1								
Ver: Caudal	7															
Sternum	4															
Rib frag.	74					3										
Carapace+Plastron/Scale													126	[632]		
Forelimb:																
Scapula-glenoid fos./shold.b.	29/25		1/1			5/2		2/1					14	1	4	
Humerus-pro/dis/sh	12/42/25		1/0/1			2/12/3		2/2/5					34		3	
Radius-pro/dis/sh	35/11/14		2/0/0			3/1/2			1				15			
Ulna dis	16		1			2		2								
Metacarpal-pro/dis/sh	13/3/5		0/1/0													
Carpals	135		2		1											
Hindlimb:																
Acetabulum-isch./il./pub.	28/16/8		3/4/1					2/3/2								
Femur-pro/dis/sh	30/36/20	1	0/1/0			12/1/3		10/8					24		3	
Tibia-pro/dis/sh	1/43/18		0/1/1			0/3/5		0/4/1					16		1	
Patella	33		1			4		5								
Astragalus	64		3		1	12		4								
Calcaneum	35		2			4		1								
Cuboid	24		1													
Metatarsal-pro/dis/sh	28/1/3															
Tarsals	64		2					1								
Toes:																
Phalanx 1	211		3		1	35	1	20	2						3	
Phalanx 2	158		9		2	10		18	3							
Phalanx 3	61		1			12	1	4								
Seasamoid	74		1													
Metapod cond.	177	1	1			24	2	12							28	
NISP	2095	6	56	5	10	185	6	197	11	1	1	9	229	37	9	42	2899
MNI	28	1	2	1	1	6	1	7	1	1	1	1	8	6	3	5	73
%NISP	72.27	0.21	1.93	0.17	0.34	6.38	0.21	6.80	0.38	0.03	0.03	0.31	7.90	1.28	0.31	1.45	100

density (based on domestic sheep bone densities from Ref. [71]) indicates a significant relationship between the two variables (MNI=0.88*[bulk density]−0.16; R^2=0.22, P=0.012; Fig. 2a), which accounts for 22% of the observed variance. The ratios of the proximal humerus and tibia (low density elements) to distal humerus and tibia (high density elements) of gazelle (6:27 and 1:25, respectively) accord with the previous results and point to loss of gazelle bone fragments owing either to pre- or post-depositional taphonomic disturbances.

We found no relationship between gazelle bone survivorship and the food utility index (FUI; [76]). Bone survivorship is based on the minimum number of gazelle units [MAU] and FUI is based on the weight of useable tissue of caribou (*Rangifer tarandus*) body parts. The relationship between the variables measures the relative strength of selective transport. However, bone frequency of gazelle shows no relation to FUI (MAU=−0.003*[food utility index]+40.6; R^2=0.03, P=0.38; Fig. 2b). Lack of a relationship between bone abundance and the food utility index, and the significant relationship with bone density, suggest that bone survivorship at el-Wad Terrace was affected by selective destruction (density) alone and was unaffected by selective transport (food value) (see Ref. [67] for discussion).

4.2. Specific attritional processes

We sought specific attritional processes that may have caused bone loss and fragmentation at el-Wad Terrace. The ratio of cranial bones to teeth (based on MNI) was used to evaluate the relative strength of taphonomic disturbances caused by processing and post-depositional processes [88]. The petrosum, a morphologically distinctive bone located at the posterior region of the skull, is by far the most abundant among all cranial bones of gazelle. The ratio of petrosum to teeth (14/16, based on MNI for both elements) suggests minor loss of identifiable bones caused by decomposition and/or advanced fragmentation processes, which could have occurred during the depositional phases of the site. Similar results were obtained by using Marean's [73] method for measuring the impact of post-depositional destruction. The completeness index of the astragalus (79% of 64 examined bones) and central and fourth tarsal (70% of 24 examined bones) bones of gazelle suggests that the bone assemblage did not suffer significantly from post-depositional decay processes.

Surface modifications were examined on all epiphyses and near-epiphysis shaft fragments; the results further suggest that major loss by decay did not affect the el-Wad Terrace assemblage. The long bone assemblage contained minor signs of surface weathering. Over 97% (of 143 examined bones) were recorded in weathering

Table 2
Relative frequencies of fracture angle, fracture outline, fracture edge, and shaft circumference from el-Wad Terrace

Fracture angle	Oblique (fresh)	78 (52%)
	Right (dry)	57 (38%)
	Intermediate	16 (10%)
Fracture outline	V shaped (fresh)	77 (50%)
	Transverse (dry)	53 (34%)
	Intermediate	25 (16%)
Fracture edge	Jagged (fresh)	85 (59%)
	Smoothed (dry)	45 (31%)
	Intermediate	15 (10%)
Shaft circumference	Less than 1/2	113 (72%)
	More than 1/2	18 (11%)
	Complete	26 (17%)

stages 0–1 of Behrensmeyer's [16] six weathering stages. Of the examined bones, 6 (0.6%) had signs of root marks on their surfaces [72], suggesting that root activity also had little effect in biasing the bone assemblage. None of the bone edges (of 144 examined bones) displayed rounding and/or smoothing of break surfaces (see Ref. [84]), suggesting that abrasion caused by physical erosion was also an insignificant destructive factor. No typical signs of surface modifications (i.e., shallow parallel scratches, as in Ref. [52]) stemming from pre-burial bone trampling were found in the entire assemblage. Adequate representation of elements according to their surface-volume ratio (Voorhies Group I, II, III; [104]; based on their dispersal potentials in flowing water, as defined by Ref. [83]) suggests that loss of bones by fluvial transport is unlikely. In addition, traces of animal activities (see Ref. [53] for description and references) are almost absent from the identifiable elements of the entire assemblage (including shaft fragments). Only four long bone fragments bore signs of carnivore gnawing, and three first phalanx fragments bore signs of carnivore chewing. No digestion signs (e.g., [63]) were observed on any of the bone remains. Signs of rodent activity are also extremely rare and were observed on only four bone fragments. These results suggest that neither carnivores nor rodents played a major role in biasing the el-Wad Terrace assemblage.

Analysis of the breakage patterns examined on all long bone epiphyses fragments (according to fracture angle, fracture outline, and fracture edge; see Ref. [103] for typological description of the fractures) revealed a predominance of fresh bone fractures with low proportions of dry bone fractures (Table 2). The ratio of fresh to dry bone fractures suggests that the breakage patterns found at el-Wad Terrace rarely reflect dry bone trampling or compaction and indicates that fractures were made on fresh bones, probably for marrow extraction.

Table 3
Summary of butchery marks on gazelle bones from el-Wad Terrace and possible activities with which they may be associated (after Ref. [20])

Dismemberment	n	Filleting	n
Scapula	2	Humerus	1
Humerus	2	Femur	1
Tibia	1		
Metapod	3		
Astragalus	2		
Calcaneus	1		

Table 4
Skeletal part representation of gazelle from el-Wad Terrace pooled into five carcass parts (expected values are based on MNI)

	Observed	Expected	Observed/Expected
Head[a]	27	56	0.48
Body[b]	120	532	0.23
Forelimb[c]	144	224	0.64
Hindlimb[d]	63	112	0.56
Toes[e]	204	448	0.46
Total	558	1372	0.41

[a] Petrosum.
[b] Thoracic and lumbar vertebrae.
[c] Humerus, radius, ulna.
[d] Tibia, femur.
[e] Phalanges 1 and 2.

4.3. Human subsistence behavior

Butchery marks were found primarily on gazelle remains (Table 3); fallow deer and fox each bore a single butchery mark on an astragalus and on a first phalanx, respectively. Most of the butchery marks were made during the process of dismembering the carcass (85%; using Ref. [20] cut mark typology). In addition, we found 12 cases of percussion marks [21] close to the fracture edges, which could have been made during marrow processing.

We studied skeletal part representation of gazelle in order to determine which body parts were present at the site. We grouped bones into five parts of the carcass: head, represented by the petrosum bone; trunk, represented by the thoracic and lumbar vertebrae (centrum, pre- and post-zygapophyses); forelimbs, represented by the humerus, radius, and ulna; hindlimbs, represented by the femur and tibia; and toes, represented by phalanges 1 and 2. Only post-cranial bones with similar densities (0.21–0.3 g/cc, based on *Ovis aries* densities from Ref. [72]) were used in this analysis. No published density for cranial elements is available. The high fragmentation and poor survivorship of braincase bones, mandibles, and maxillae suggest that these bones are poor candidates for identifying the presence of cranial elements. The petrosum bone is usually found complete and was found to be easily identifiable to body-size group [7].

Analysis of skeletal part distribution of gazelles reveals a significantly different representation from that expected (Table 4; $\chi^2=60.32$, $P<0.001$), based on MNI. The ratio of the observed to the expected reveals low representation of trunk elements (vertebrae), and a high and similar representation of head, limbs, and toes. A comparison of skeletal parts without the axial parts reveals a homogeneous representation of heads, limbs, and toes ($\chi^2=6.78$, $P=0.08$). Under-representation of vertebrae is common in other studied Epipalaeolithic assemblages [5,79], among numerous other assemblages (e.g., [88]), and may result from various cooking and processing techniques (e.g., [25]), such as processing of vertebrae for rendering bone grease [19,86], or density-mediated attrition. In addition, we found a relatively high proportion of pelves suggesting that certain axial elements were present at the site. Thus, the skeletal part distribution of gazelle from el-Wad Terrace displays anatomical profiles that approximate anatomical completeness, apart from the problematic counts of the vertebral elements.

5. Demographic composition of el-Wad Terrace gazelles

Analysis of gazelle demographic composition enables us to discern whether selection for individuals of particular sex and/or age class took place. We analyzed age structure of the gazelle population based on dental wear in comparison to degree of tooth wear of recent gazelle skulls in the Tel-Aviv University Zoological Museum, whose age at death was recorded. The percentage of young individuals, under the age of approximately 24 months, is 37%. The percentage of young individuals based on gazelle epiphyseal fusion [34] of several skeletal elements (i.e., radii, metapodia, femora, tibiae, calcanea) whose fusion ages range between 10–16 months (method developed by Ref. [37]) is 34.2%. Thus, the gazelle epiphyseal age profile resembles the dental profile quite closely. Comparison of the age structure of the hunted population in el-Wad Terrace to that of recent gazelle herds (35% under 18 months of age; Ref. [2]) suggests a hunting pattern that is not selective for a specific age group ($\chi^2=0.25$, $P=0.62$).

Although gazelles display some sexual dimorphism, there is much overlap in most measurements between the sexes, with the exception of the atlas and axis [64], both of which are rarely represented in our entire assemblage. Similarly, pubis bones that also display sexual dimorphism on the basis of morphological observations (Speth pers. comm.; see illustrations in Ref. [22]) are almost entirely absent from the studied assemblage. Davis [33,38] suggested that distal epiphyses measurements of
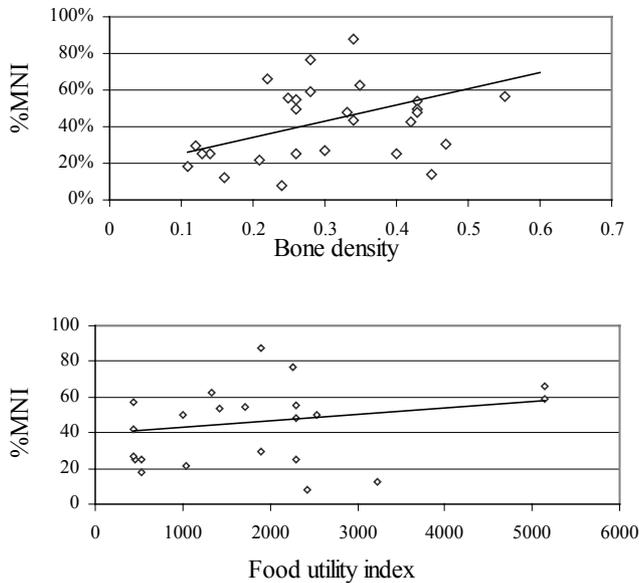
Fig. 2. Relationship between bone density (Ref. [72]) and skeletal part frequency (%MNI) (top) and between food utility (Ref. [76]) and skeletal part frequency (bottom) in gazelle from el-Wad Terrace.

the humerus (breadth of trochlea [50] versus the minimum diameter of trochlea [33]) show some separation of the sexes. Distal humeri are the most common complete representative bones of gazelle in el-Wad the Terrace assemblage. We follow Weinstock's [110] recommendations and present our measurements in bivariate plots, since possible sex differences are best reflected in the proportions of the bones.

Distal humerus measurements of a sample of recent gazelles (12 females and 26 adult males from the Mediterranean region of Israel) show some overlap between the sexes (Fig. 3). However, a discriminant function analysis (using STATISTICA software) places the 12 larger fossil specimen measurements within the cluster of males, and only a single small measurement within the females (at $P<0.01$).

The mean of el-Wad Terrace fossil specimens is significantly higher than that of the recent specimens for both measurements ($t=4.09$, $P<0.001$ for breadth of trochlea and $t=2.02$, $P<0.05$ for minimum diameter of trochlea). Moreover, a comparison between 26 recent males and the 12 fossil males (identified as such by the discriminant function analysis) from el-Wad Terrace reveals that the mean of the latter is significantly higher in breadth of the trochlea ($t=4.20$, $P<0.001$) and marginally significant in minimum diameter of trochlea ($t=1.81$, $P=0.08$). This result indicates that our sexing results may be invalid. It could be that the discriminant function analysis excluded some males that exhibited a lower breadth of trochlea. Two of the el-Wad Terrace gazelle measurements fall in the mid range of recent gazelle males in size. If we consider the overall body-size increase of the population these may actually represent

large females rather than small males. If that is so, the sex ratio still remains strongly biased towards males (but at 10:3 rather than 12:1), and the size difference between male Natufian gazelles and those of the recent becomes more pronounced ($t=5.36$, $P<0.001$ for breadth of trochlea and $t=2.22$, $P=0.03$ for minimum diameter of trochlea).

Horn cores are the only skeletal element that can be used for sexing the gazelles unequivocally. In el-Wad Terrace we found eight horn core bases of male gazelles and three of female gazelles, indicating that more than one female gazelle were indeed brought to the site, and probably many more, given how delicate the female horn core is compared to the male horn core.

Comparison of the hunted population from el-Wad Terrace (at least 1 female, 12 males) with a recent herd of gazelles (100 females over 18 months of age for every 81 males in the lower Galilee [based on monthly drive counts and counts from fixed observation sites]; Ref. [2]) shows a significant difference in sex ratio ($\chi^2=10.99$, $P<0.001$; and $\chi^2=5.04$, $P=0.02$ for ratio of 3 females and 10 males). A similar marginally significant difference was found when we compared the relative abundances of horn cores (3 females, 8 males; $\chi^2=3.26$, $P=0.07$). While the sex ratio (and age structure) of the modern herd is not affected by natural predators as that of the prehistoric herd would have been, it is our closest approximation for comparison. These comparisons suggest selective hunting of male gazelles by the Natufians of el-Wad Terrace.

6. Morphometric patterns of Epipalaeolithic gazelles

Although the degree of sexual size dimorphism in gazelles is not particularly high, the analysis of patterns of size change and of variability can be biased by changes in body-size through time (see Ref. [51]). Because only few bone elements can be used to separate the sexes by shape, sexing of gazelles is often carried out using measurements of the more dimorphic elements (i.e., Ref. [64]), a process that may, in turn, be affected by overall size change of the population. Therefore, careful analysis of body-size patterns must accompany morphometric analyses.

Previous studies of patterns of size change of gazelles were conducted on mixed-sex populations [32,51] and sometimes on elements where the analyst could not tell if the bone came from the fore- or hindlimb (first and second phalanges, metapodials; Ref. [32]). Moreover, gazelles from different geographic areas were compared, although some regional variation may occur. Since the concept of cultural control of gazelles rests on sex ratios and size, careful consideration of the possible biases is crucial for resolving this issue.

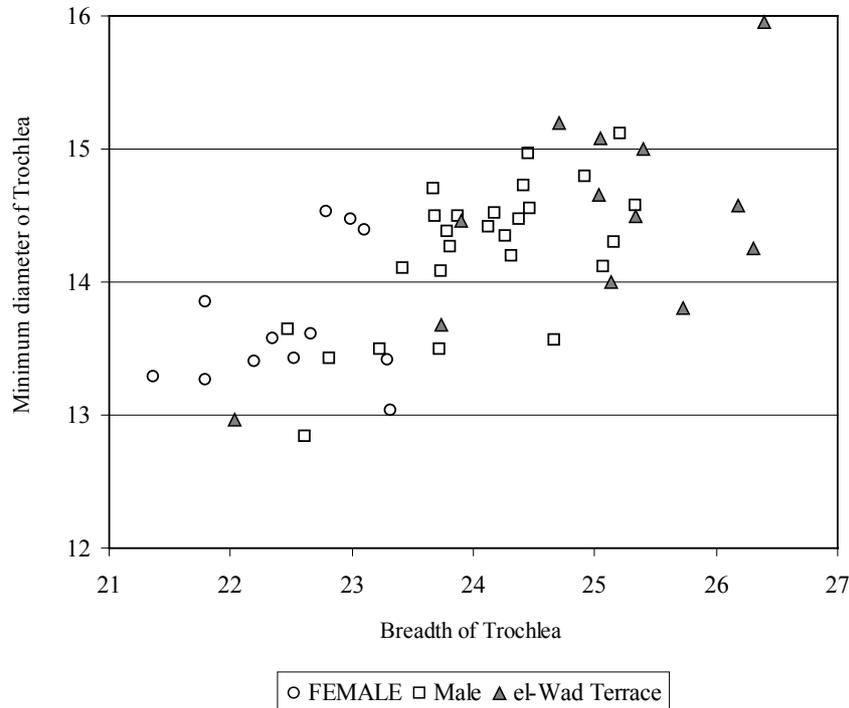The mean size of the el-Wad Terrace gazelle population significantly exceeds the means of Nahal Hadera

Fig. 3. Scatter plot of distal humerus measurements (breadth of trochlea versus minimum diameter of trochlea) of recent sexed gazelles (female=○; male=□) and fossil gazelles from el-Wad Terrace (▲).

V (t=6.72, P<0.001 for breadth of trochlea; t=6.61, P<0.001 for minimum diameter of trochlea; all measurements are given in Ref. [5]), Hefzibah (t=3.98, P<0.001 for breadth of trochlea; t=2.53, P<0.05 for minimum diameter of trochlea), and Neve-David (t=4.83, P<0.001 for breadth of trochlea; t=6.12, P<0.001 for minimum diameter of trochlea). These results are opposite to the pattern of morphological size diminution previously suggested for Natufian gazelles [32,35].

A high-resolution size trends profile of Epipalaeolithic gazelle from the coastal plain in comparison to recent populations (12 randomly pooled males and 12 females) from the Mediterranean region of northern Israel (Fig. 4, Table 5) enables us to compare the size of Natufian gazelles to those of other periods. In order to eliminate age-dependent variation and because of the fragmented state of the majority of bones, we measured epiphyseal width (increase in this dimension following the bone ossification is assumed to be minimal; epiphyses with a porous surface which indicate incomplete ossification were excluded). On the basis of distal humeri, we find that gazelles show a minimum size during the Kebaran (Nahal Hadera V) and Geometric Kebaran (Hefzibah and Neve-David), followed by a significant size increase during the Natufian period (el-Wad Terrace [Late Natufian] and el-Wad Cave [Early Natufian; data from Ref. [81]]) (Table 6). A similar pattern is depicted by the other three measurements taken, representing both proximal (scapula

glenoid-fossa) and distal limb-bones (distal metacarpal, distal metatarsal) (Table 6). Results for the distal metacarpal and metatarsal are marginally significant. Tukey's multiple comparisons tests revealed that, for the distal humerus and metacarpus, the differences were between the Natufian sample and those of other Epipalaeolithic periods. In addition, the means of distal humeri of both the Early and Late Natufian gazelles of Hayonim Cave (Munro, unpub. data) are significantly greater than the means of the pre-Natufian studied sites (i.e., Nahal Hadera V, Hefzibah, Neve-David; t=6.51, P<0.001 for breadth of trochlea and t=2.29, P=0.02 for minimum diameter of trochlea) and not statistically different from the means of the Natufian gazelles from el-Wad (t=1.39, P=0.17 for breadth of trochlea and t=1.46, P=0.15 for minimum diameter of trochlea). Comparison between the Early and Late Natufian phases of Hayonim Cave shows no significant size changes (t=0.15, P=0.88 for breadth of trochlea and t=0.41, P=0.69 for minimum diameter of trochlea). A Late Natufian size increase (distal humerus, metacarpal, and metatarsal) in comparison with the preceding cultures was found also for Hatoula gazelles [43]. In addition, there is clearly no tendency for Natufian coefficients of variation (CV=(sd/Mean)*100) to differ from those of non-Natufian assemblages (Table 5). Two-tailed Z-tests (Ref. [113]: equation 8.42) for differences between Natufian and pre-Natufian coefficients of variation on the basis of distal humerus measurements (the character for which sample sizes

Table 5
Means, standard deviations, and coefficient of variation (CV) of gazelle bone measurements from the Epipalaeolithic sites of Israel and modern gazelles from northern Israel (data from Ref. [5]). Based on the breadth of the distal condyle of the humerus (BT), the greatest breadth of the scapula glenoid-fossa (BG), and the distal width of metacarpus and metatarsus (Bd). Measurements in millimeters taken according to Ref. [50]

	Range of variability	Mean	S.D.	CV	N
Humerus BT					
Nahal Hadera V	19.87–25.31	22.72	1.08	4.75	59
Hefzibah	21.48–26.21	23.43	1.40	5.97	34
Neve-David	20.74–25.00	22.94	1.25	5.45	23
El-Wad Terrace	22.03–26.40	25.01	1.16	4.64	13
Recent females	21.36–23.32	22.51	0.63	2.81	12
Recent males	23.72–24.92	24.25	0.40	1.64	12
Scapula BG					
Nahal Hadera V	18.30–21.40	19.5	1.60	8.20	5
Hefzibah	17.89–21.33	19.24	1.47	7.64	4
Neve-David	16.42–21.66	19.32	1.63	8.44	14
El-Wad Terrace	17.15–23.02	20.52	2.21	10.76	8
Recent females	17.15–20.46	18.68	1.06	5.66	12
Recent males	19.7–22.11	20.81	0.67	3.22	12
Metacarpus Bd					
Nahal Hadera V	17.60–20.26	19.10	1.16	6.07	5
Hefzibah	17.93–21.44	19.70	1.03	5.23	11
Neve-David	17.49–21.11	19.40	1.36	7.01	9
El-Wad Terrace	21.20–21.89	21.54	0.49	22.28	2
Recent females	18.87–20.42	19.44	0.52	2.70	12
Recent males	19.9–21.41	20.78	0.39	1.88	12
Metatarsus Bd					
Nahal Hadera V	19.67–21.06	20.36	0.98	4.81	2
Hefzibah	19.07–21.78	20.52	1.09	5.32	6
Neve-David	20.51–22.37	21.36	0.94	4.40	3
El-Wad Terrace	22.59–23.43	23.01	0.60	2.61	2
Recent females	20.34–22.3	21.14	0.65	3.07	12
Recent males	21.62–23.33	22.55	0.48	2.12	12

Table 6
Results of 1-way ANOVA to determine size patterns of mountain gazelles in the Epipalaeolithic sites of the coastal plain, Israel

	Sum of squares	df	Mean square	F	Sig.
Distal Humerus (BT)					
Between groups	104.47	3	34.82	23.19	0.000
Within groups	201.25	134	1.50		
Total	305.72	137			
Scapula glenoid-fossa (BG)					
Between groups	7.02	3	2.34	0.78	0.515
Within groups	90.26	30	3.01		
Total	90.28	33			
Distal Metacarpus (Bd)					
Between groups	12.11	3	4.04	2.71	0.067
Within groups	37.27	25	1.49		
Total	49.38	28			
Distal Metatarsus (Bd)					
Between groups	8.97	3	2.99	2.89	0.084
Within groups	11.38	11	1.03		
Total	20.35	14			

Table 7
Two tailed Z-tests for differences between Epipalaeolithic coefficients of variation of gazelle distal humerus measurements

	Hefzibah	Neve-David	El-Wad Cave	El-Wad Terrace
Nahal Hadera V	Z=0.187 P>0.50	Z=0.166 P>0.50	Z=0.275 P>0.50	Z=0.020 P>0.50
Hefzibah	–	Z=0.022 P>0.50	Z=0.073 P>0.50	Z=0.153 P>0.50
Neve-David	–	–	Z=0.095 P>0.50	Z=0.181 P>0.50
El-Wad Cave	–	–	–	Z=0.230 P>0.50

sufficed for analysis) show that the intrinsic variability is the same between the studied assemblages (Table 7). These comparisons indicate that the degree of variation of gazelles does not change through the Epipalaeolithic. These results are in accord with Dayan and Simberloff's [45] statistical reanalysis of Cope's [32] data (Fig. 4).

7. Discussion

Mountain gazelles were the most heavily exploited prey species at el-Wad Terrace. A similar abundance of gazelles was recorded at other Natufian sites from Israel [6,36]. The low proportion of fallow deer (2%) differs from the general Epipalaeolithic Pre-Natufian trend that is typified by over 20% fallow deer [5]. The reduction in fallow deer percentages was first interpreted by Bate [15] as reflecting deforestation and increased aridity of the southern Levant during the Natufian. Other large

mammals from the coastal plain are represented in the site in relatively small numbers. Small game are found in high proportions, relative to Pre-Natufian sites from the region (i.e., Nahal Hadera V, Hefzibah and Neve-David; Ref. [5]). The increasing proportions of small, low-ranked game are suggested by Stiner and colleagues [78,79,89–92] to reflect long-term food stress, rising human population densities, and increasing environmental exploitation during the Natufian period of the southern Levant (see also Ref. [40,41] for the first description of this pattern in the Natufian of the Levant).

The taphonomic history of the el-Wad Terrace assemblage suggests minor loss of bones owing to various diagenetic processes and indicates that most bone
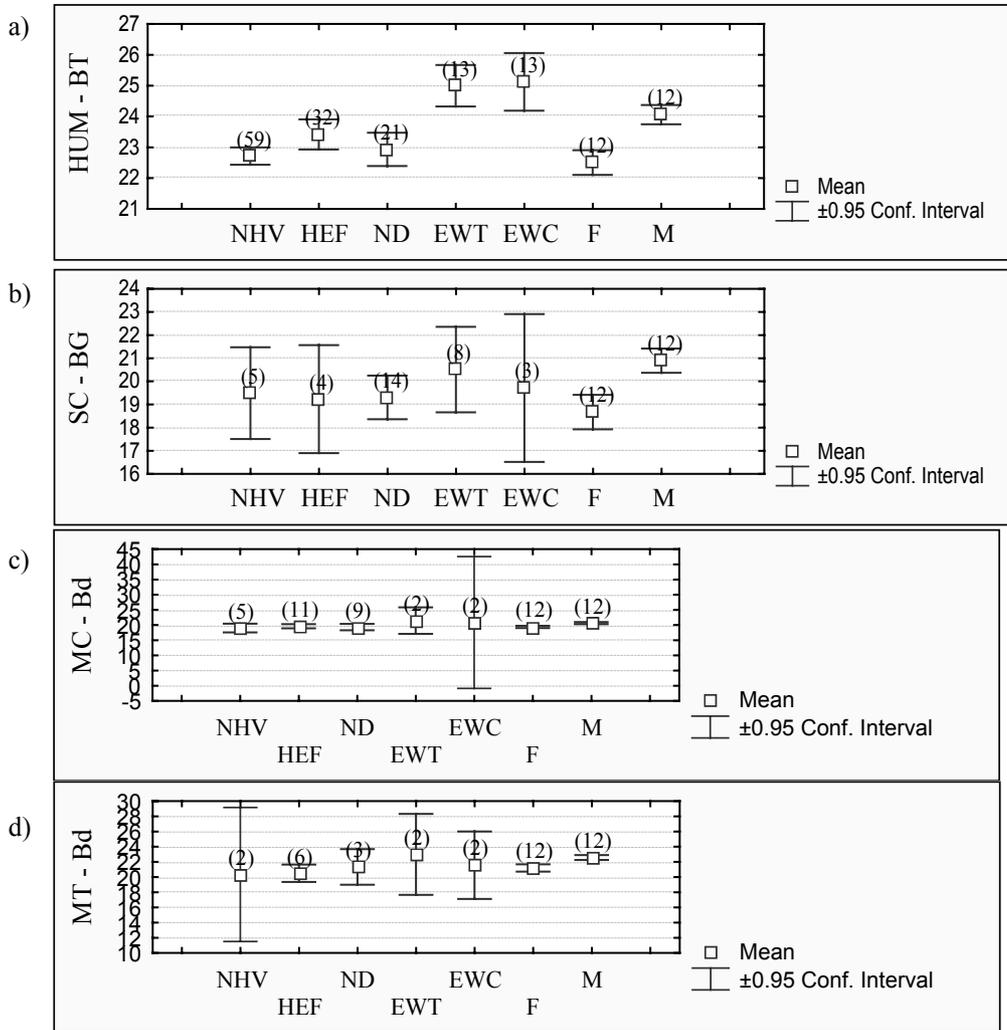
Fig. 4. Size trends of *G. gazella* in the coastal plain of Israel during the Epipalaeolithic cultural sequence in comparison to recent females and males specimens from northern Israel. Data from Table 5. Plots of: (a) breadth of distal condyle of the humerus (HUM-BT), (b) greatest breadth of scapula glenoid-fossa (SC-BG), (c) distal width of metacarpus (MC-Bd), and (d) distal width of metatarsus (MT-Bd). Graphics represent the mean and 95% confidence limits. Key: NHV—Nahal Hadera V (Early Kebaran); HEF—Hefzibah (Geometric Kebaran); ND—Neve-David (Geometric Kebaran); EWT—el-Wad Terrace (Late Natufian); EWC—el-Wad Cave (Early Natufian)—data from Rabinovich, 1998; F—recent females; M—recent males. Sample size for each assemblage is given in parentheses.

destruction occurred during the time of occupation, probably as a result of exploiting bones for marrow, an action that produced large numbers of fragments, most of which exhibited green bone fractures (see detailed discussion in Ref. [5]). Presence of cut marks from all stages of activities, absence of selective transport, and body part representation suggest that most butchering of gazelles was carried out at the site.

Analysis of the gazelle remains shows that the percentage of juveniles matches what one would expect from a living population. The percentages of male and female gazelles in el-Wad Terrace are heavily biased in favor of males, on the bases of both dimorphic distal humeri and horn cores. The Late Natufian gazelles of el-Wad Terrace are significantly larger than those of

recent populations, a pattern that holds when recent male gazelles are compared with hypothesized fossil males.

The high number of male gazelles in the Natufian site of el-Wad Terrace contrasts with the hunted gazelle population from Neve-David (16 females, 3 males; Ref. [6]), Nahal Hadera V (32 females, 27 males; Ref. [10]), and Hefzibah (16 females, 16 males; Ref. [9]). Predominance of male gazelles was reported by Cope [32] for the Early Natufian site of Hayonim Cave (ratio of 4:1) and the Late Natufian sites of Hayonim Terrace (3:1), Eynan (2.6:1), and Hatoula (3:2; but see Ref. [43]). A high percentage of male gazelle was also found in the Late Natufian site of Rakefet (2:1; Ref. [55]). The high percentages of male gazelles in the Mediterranean sites

of northern Israel contrast with the high representation of female gazelles in the Late Natufian and Harifian of southern Israel, central Negev (two horn cores out of two in Rosh-Horsha and five out of six in Abu-Salem; Ref. [26]). In the Late Natufian assemblage of Upper Besor 6 from the central Negev there are equal numbers of horn core bases (three males and three females) but all four distal humeri fall clearly within the range of the recent females [65].

It would be tempting to attribute the high percentage of males to conscious culling of gazelle practiced by the Natufian people [32,96,97]. Alternatively, the high representation of males in the el-Wad Terrace assemblage may reflect targeting the better-conditioned sex at the time of year in which hunting took place (see discussion in Ref. [87]). However, the annual reproductive pattern, social structure and behavioral ecology of gazelles is highly complex (see recent review in Ref. [74]) and therefore this issue is difficult to explore. Some males defend territories for a short period during the mating season (fall), while others form bachelor herds [2–4]. At Ramat HaNadiv, southern Mount Carmel Israel, female gazelles live in permanent groups that occupy temporal territories, and various groups replace each other in the same area at different time of the day [58]. Females remain with their mother's herd possibly for life, but males leave the maternal herd when about six months old and join herds of young males [77]. In addition, male gazelle herds (bachelor, adult bachelor, and territorial adults) may form separate units at different times of the year [77].

Cope [32] claimed that although all limb bone elements studied showed some degree of diminution, some elements (in particular distal metapodials and first phalanges) seem more affected than others. Our results, which included comparisons of the breadth of both distal metacarpals and metatarsals, show a tendency of increasing size for these characters, as well as for the proximal limb-bones (i.e., distal humerus and scapula glenoid-fossa). Thus our results do not show any pronounced allometric changes in gazelle limb proportions during the Natufian. In her study, Cope [32] lumped together distal metacarpals and metatarsals, in spite of significant differences in the sizes of these bone elements ($t=6.70$, $P<0.001$ for recent females and $t=9.81$, $P<0.001$ for recent males; data in Table 5). The same holds true for her analyses of first phalanges, where no discrimination was made between those of the fore- and hindlimbs. This may have introduced a bias into her work that could account for the apparent (although not statistically significant; see [45]) diminution she describes.

The size increase of gazelles during the Natufian contrasts with the observed size reduction exhibited by the fox, gazelle, goat (*Capra aegagros*), wolf, wild boar, and probably also aurochs (*Bos primigenius*) during the Early Natufian of Israel [35]. A Pleistocene–Holocene size reduction was also noted for wildcat (*Felis silvestris*), spotted hyena (*Crocuta crocuta*), marten (*Martes foina*) [69], hare [49,80], mole rat (*Spalax ehrenbergi*) [93], hedgehog (*Erinaceus europeus*) [59], porcupine (*Hystrix indica*) [54], and jird (*Meriones tristrami*) [28]. The diminution of body size in the mammals of Israel during that time has been ascribed to post-glacial warming ([69], see also Ref. [107] and references therein for paleoenvironmental reconstruction).

However, the precise timing of morphological change differs among studies and reflects both stratigraphic resolution and the species studied. Size change in the mammals of the Levant is apparently asynchronous and may reflect a variety of biotic and abiotic selective forces ([47,48]; see also Ref. [46] for review of selective forces and size evolution of mammals). Teasing apart the complex natural selective forces is a challenging task; adding the possible role of humans further contributes to this complexity (see [35,44]). Additional high-resolution studies of gazelle size patterns through the Pleistocene and Holocene of Israel may provide valuable insight into this issue.

In sum, our data accord with the previously described Natufian shift to small game that may reflect food stress [41,90]. Mountain gazelles figure heavily in the diet of the Late Natufians of el-Wad Terrace. However, in contrast to previous suggestions, the trends observed in the size of gazelles from the Epipalaeolithic sites of the coastal plain of Israel do not demonstrate any sign of morphological dwarfism, increased variation, or allometric changes. Thus our results do not accord with Cope's [32] perception of 'proto-domestication' in Natufian gazelles. Although the concept of aborted attempts of domestication presents an exciting challenge to our understanding of the roots of this process, we find no morphological support in this particular case. We do find a high percentage of male gazelles in our sample, a pattern that could be taken as reflecting a specialized culling pattern [94] that may also reflect seasonal timing or methods of procurement, but further research is required in order to determine whether this pattern is of general significance in the Natufian of the Levant.

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