Gazelle bone marrow yields and Epipalaeolithic carcass exploitation strategies in the southern Levant

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Abstract

We measure the bone marrow yields of mountain gazelle (*Gazella gazella*) carcasses to reconstruct gazelle exploitation strategies during the Epipalaeolithic periods in the southern Levant. We present experimentally derived data on the bone marrow content of seven fresh gazelle carcasses, determine the range of marrow yields among individuals of different sexes and seasons of death, and compare the new data to gazelle skeletal element abundances from five Epipalaeolithic assemblages from Israel. We found extensive variation in marrow fat content among individual gazelles. Animals with the highest marrow yields were killed in the spring while animals killed in the early autumn had lower fat contents. Nevertheless, our results suggest that gazelle marrow provided a reliable, albeit small fat resource for prehistoric foragers in all seasons. Strong relationships between bone fragmentation and marrow content demonstrate that Epipalaeolithic people preferentially processed bones with high marrow yields.
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1. Introduction

The mountain gazelle (*Gazella gazella*) was the most common ungulate prey species captured and consumed by humans throughout much of the Epipalaeolithic and pre-Pottery Neolithic periods in the Levant (Bar-Oz, 2004; Davis, 1987; Horwitz, 1996; Munro, 2004). Although several taxa have been experimentally butchered to estimate the caloric value of their bone marrow (Binford, 1978; Blumenschine and Madrigal, 1993; Lupo, 1998; Madrigal and Capaldo, 1999; Outram and Rowley-Conwy, 1998) no marrow indices currently exist for the mountain gazelle. Here, we present experimentally derived data on the bone marrow content of seven gazelle carcasses and examine variation in marrow yields among individuals of different sexes and seasons of death. Our aims are to identify potential sources of variability in marrow yields and to contribute to the current body of work on marrow extraction by providing the first measures for gazelle. Previous studies of gazelle transport and processing in the southern Levant have relied on bone marrow derived from domestic sheep (following Binford, 1978). Gazelle marrow yields will be of value to researchers working in a wide range of cultural periods in Southwest Asia.

Despite the excess abundance of consumable fat in the modern world, fat was once a limited commodity eagerly sought by human foragers to ensure adequate nutrition (Speth, 1983, 1997; Speth and Spielmann, 1983). In temperate environments the availability of fat varies tremendously across the annual cycle − fat is more plentiful in wet and warm seasons than in less productive dry or cold seasons. Most mammals store fat when food is abundant and metabolize it when food is scarce. Fat is stored in four major areas of the mammalian body: beneath the skin, in muscle tissue, in the kidney and in bone medullary cavities. Of these, the medullary marrow is the smallest, and the last to be mobilized in times of

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stress (Brooks et al., 1977; Cheatum, 1949; McCullough and Ullrey, 1983; Ransom, 1965; Sinclair and Duncan, 1972). Mammalian marrow cavities thus not only provide key fat reserves for the animals that possess them, but a crucial source of fat for past human foragers, especially in lean seasons when fat is scarce in nature. Because the exploitation of bone fats by past foragers is ubiquitous, identifying bone marrow extraction strategies can provide valuable insight into the intensity of carcass use and the level of subsistence stress experienced by human groups (Binford, 1978; Munro and Bar-Oz, 2005; Outram, 2001).

It is widely acknowledged that human hunters strongly prefer fatty body parts when processing and transporting prey carcasses [e.g., Binford, 1978, 1981; Blumenschine and Madrigal, 1993; Enloe, 1993; Madrigal and Capaldo, 1999; Speth, 1983, 1987, 1989, 1990; Speth and Spielmann, 1983]. Furthermore, in lean seasons humans are known to selectively target the fattest animals in the best physiological condition, while ignoring and even abandoning complete carcasses of fat depleted animals (Speth, 1983; Speth and Spielmann, 1983). Medullary marrow is thus an important resource that must be considered when modeling transport and butchery patterns of past human decisions. Given the central role of bone marrow, it is essential to understand the yield, distribution and seasonal variation in marrow fat for the key prey species used in prehistory. In particular, comparisons between elemental representation and marrow indices allow archaeologists to determine whether bones were preferentially transported or butchered with the goal of obtaining bone marrow, and if element selection coincided with seasonal cycles of fat availability.

The experimental data on gazelle marrow yields presented here is thus, designed not only to add a new taxa to the current repertoire of marrow indices, but to expand available data so that current hypothesis on prehistoric subsistence stress, transport and butchery behaviors and past human foraging decisions can be refined. As such, this study represents one important facet of a broad-based gazelle project in which the authors are currently engaged. The gazelle project combines ecological, biological, taphonomic and zooarchaeological methods to build a comprehensive picture of human hunting impacts on gazelle populations. It explores both variation in hunting impacts across time and space, and the potential influence of human hunting on the early stages of the domestication process.

2. Mountain gazelle physiology and ecology

Although no studies exist on the body condition of mountain gazelles, data on food availability and seasonality in the Mediterranean zone and gazelle reproduction are plentiful. These data are drawn on below to construct a model for male and female gazelle body condition throughout the annual cycle (Fig. 1; Table 1). The model provides a baseline for predicting prehistoric human hunting decisions during different seasons of the year.

The fat content and quantity of an animal's bone marrow varies according to a variety of factors including season, sex,

age and an animal's physical condition [e.g., Blumenschine and Madrigal, 1993; Fong, 1981; Lupo, 1998; Ratcliffe, 1980; Speth, 1983]. Seasonal differences in marrow fat content are determined by changes in food availability and an animal's annual reproductive cycle [e.g., Fitzgibbon and Fanshawe, 1989]. When food is abundant animals store fat as a risk aversion strategy and in preparation for energetically demanding reproductive activities such as pregnancy, lactation, and procuring mates.

Israel is home to a highly seasonal Mediterranean climate characterized by wet, cool winters and dry, hot summers, as well as constrained periods of vegetal growth. Precipitation falls nearly exclusively between October and April — the first heavy rains fall in December and precipitation peaks in January and February. The peak dry season is between July and September (Horowitz, 1979). Mountain gazelles are predominantly grazers and preferentially forage in grassland habitats, which are richest between December and mid-May. When the grasslands dry up in mid-May, gazelles shift to browse in mixed Mediterranean woodlands through November (Baharav, 1983a). Peak food availability for gazelles thus coincides with the wet season.

Available data on gazelle foraging behavior and reproductive season originates from two distinct modern gazelle populations inhabiting the Galilee of northern Israel — Ramat Yissakhar (eastern Lower Galilee) and Ramat Qedesh (eastern Upper Galilee). The Ramat Yissakhar population inhabits a very different landscape from past gazelle populations — one that often includes year round availability of food and water inadvertently created by human settlements and agricultural activity (Baharav, 1983b). The seasonal fluctuations in food and water availability at Ramat Yissakhar are thus less pronounced in comparison to the conditions that gazelle populations would have been exposed to in the past. To minimize the effects of modern conditions, the data on gazelle reproductive cycles presented here are derived from the Ramat Qedesh population, which had minimal exposure to standing water in the dry season.

The reproductive cycle of mountain gazelles from Ramat Qedesh corresponds clearly with peaks of favorable vegetative conditions (Baharav, 1983b). The mating season is at its height during the late autumn and early winter (December—January). Most does are pregnant by January and fawns are born six months later at the beginning of the dry season in late May and June (Baharav, 1983a). On average, lactation lasts for 75 days until August (Table 1). Seasonal fluctuations in the fat content of male and female gazelles are related to differences in their reproductive demands. Males expend more energy in the late autumn rut, while females expend most energy during pregnancy and lactation in the spring (Baharav, 1974, 1983a,b; Fig. 1).

The compounding effect of the dry season and the prolonged expenditure of energy on both pregnancy and lactation means that female gazelles should be in their worst physiological condition during the late summer and fall. In contrast, they should reach peak condition between January and March after they have had a few months to fatten up on rich vegetation and

	J	F	M	A	M	J	J	A	S	O	N	D
CLIMATE	Peak rains		Rainy	Dry						Rainy		
GAZELLE FORAGE	Predominantly grazing (grasses and forbs)							Browsing (leaves and shrubs) and grazing				
MALE REPRODUCTION											Rut	Mating
FEMALE REPRODUCTION	Pregnancy						Lactation					Mating
MALE CONDITION	Good	Excellent			Good			Poor			Good	
FEMALE CONDITION	Excellent			Good			Poor			Good		

Fig. 1. Predicted male and female gazelle body condition across the annual cycle based on known climatic, forage, and gazelle reproductive data from Israel.

before pregnancy has taken a toll on fat reserves. Unlike females, males invest tremendous energy in the rut — particularly due to inter-specific competition with other males. Although males lose some fat stores during the rut, the ensuing wet season with its abundant food resources enables males to regain top physical shape before the dry season begins. Like females, males likely reach their poorest physical condition at the end of the dry season in the late summer and early autumn. In an average year, male body condition likely fluctuates less dramatically than that of females since males have the opportunity to regain good physical condition after the rut and do not experience the combined effect of lactation and low resource availability in the dry season (Fig. 1).

Age-related variation in the fat content of mammalian marrow is linked to the changing function of the marrow cavity. As the animal grows the function of the marrow cavity gradually shifts from red blood cell production to fat storage (Blumenschine and Madrigal, 1993; Hanks et al., 1976). The age at which fat storage begins varies by ungulate species, and young animals may start depositing fat in marrow cavities as early as one month of age (Ballard and Whitman, 1987).

Nevertheless, the marrow cavity continues to play a role in red blood cell production up until the animal reaches full body size (Hanks et al., 1976). The marrow found in bone cavities engaged in red blood cell production is typically red and gelatinous due to its low fat content and can easily be confused with the marrow of an animal in poor physical condition.

Variation in the fat content of bone marrow in a mature animal is related to the animal's stage in the process of fat mobilization and storage. Because the medullary marrow is the last fat reserve to be used during times of stress, the fat should not be metabolized unless an animal is already in poor physical condition. The metabolism of marrow fat begins in the limb elements closest to the body (femur and humerus), proceeds to the elements in intermediate positions (radius and tibia) and ends with the most distal elements (metacarpal and metatarsal). Fat deposition occurs in the opposite direction from distal to proximal elements. The relative fat content in different bones in the skeleton thus indicates an animal's physiological condition (Brooks et al., 1977; Neiland, 1970; Ransom, 1965). If proximal elements have the highest fat

Table 1
Summary of key life history and anatomical characteristics of mountain gazelle based on studies of extant and recent populations [Data from Baharav, 1974, 1983a,b; Mendelssohn and Yom-Tov, 1999; Mendelssohn et al., 1995; Simmons and Ilany, 1975–1977]

Characteristic	Female	Male	
Size/dimorphism			
Adult head and body length (mm)	920–1040	1000–1140	
Adult hind foot height (mm)	320–340	320–354	
Mean adult weight (kg)	18.09 (16.25–25.0)	24.86 (17.10–29.50)	
Horns	Small, short and thin	Large, long and thick	
Reproduction			
Sexual maturity	18 months	3 years	
Mating	Early winter: December/January		
Births (gestation)	1 offspring in May/June (180 ± 5 days)		
Male competition	Polygamous interaction with territorial males		
Population structure			
Sex ratio	100 adult females per 81 males		
Social units	Females and young herds	Young male herds (0.5–2) Adult male herds	Territorial males
Territories	None	Seasonal, May–October	
Mean annual population density	23 per square km		
Life expectancy	8 years		

content, then an animal has not begun to metabolize its fat and is likely in reasonable condition. However, if the most distal elements have higher fat contents than proximal elements an animal is likely in poor condition.

3. Sample and methods

Seven mountain gazelle carcasses were collected by officials from the Israel Nature and Parks Authority and donated for this study. Only adult animals were included in the sample because most mammals do not reach their full capacity for marrow production until they reach adulthood. Carcasses were collected on the same day of the animal's death and immediately frozen until the experiment began. State of dental wear and eruption, sex, date killed, body weight, and general condition was recorded for each animal (Table 2). Six of the gazelles originate from the Mediterranean region of Israel and one is from an unknown locality in the Judean desert of southern Israel. Of the seven individuals, five were road kills (4 males, 1 female) and two (males) were confined animals (fed year round) from the Chai-Bar, a wildlife reserve on Mount Carmel, Israel. The latter two animals died after becoming entangled in the fence while trying to flee from competing males. The gazelle sample is composed exclusively of prime adult animals that were killed between October 2004 and September 2005. The female was killed during early pregnancy (first third of pregnancy, based on fetus size). Because of its skewed distribution, this sample is not ideal to investigate sex differences in marrow fat distribution. It does, however, provide the opportunity to examine variation amongst gazelles killed in different seasons – autumn (September– October), winter (December–January) and early spring (March).

The effects of modern agriculture, in particular increased availability of water and fresh agricultural forage in the dry season, can dampen the effects of seasonal variability on mountain gazelle physiology. This is an unfortunate consequence of experimentation in the modern age and cannot be entirely avoided. Nevertheless, some of the animals sampled here (males 1010 and 1011) originate from areas in the Mediterranean zone and the Judean desert where agriculture is more limited than in other habitats of Israel. It is impossible to find animals exposed to identical conditions as those in prehistory, and this sample still enables us to explore general patterns in the variation of gazelle marrow yields.

Prior to butchering, the gazelle carcasses were removed from the freezer and allowed to thaw for 24 hrs. Butchering was performed on two different days (July 12 and December 5, 2005) by an experienced butcher (G. Hallun) and three student assistants using metal knives. The butchers removed the mandible, scapula, humerus, radius, ulna, metacarpal, femur, tibia, metatarsal, calcaneum, first phalanx and second phalanx from one side of each animal carcass. The side that was butchered was randomly chosen for each animal. After cleaning the flesh and ligaments from each element, the fresh bones were weighed.

One of each of the following paired elements was selected from each animal for marrow extraction: humerus, radius, metacarpal, femur, tibia, and metatarsal. For four specimens (1000, 1002, 1005, 1007) one side of the mandible, the scapula, pelvis, two first phalanges, two second phalanges, and the calcaneum were also sampled. Each of the long bones was cut transversely with a jigsaw at the distal and proximal ends of the shaft and across the midshaft. The mandible was sliced horizontally approximately 1 cm from the base. The phalanges and calcaneum were sliced transversely through the midshaft. Marrow was extracted from each medullary cavity using a metal probe. The marrow from each element was then placed in an individually marked, pre-weighed Petri dish, and weighed to the nearest 0.01 g using an electronic balance. This weight minus the Petri dish is referred to as the marrow wet weight following Blumenschine and Madrigal (1993), see also Madrigal and Capaldo (1999). Dry marrow weights were obtained by heating the Petri dishes in an oven set at 50–60 °C. Every 30 min the samples were removed from the oven and reweighed, until the weight remained constant for three consecutive readings. The final reading minus the weight of the Petri dish is the dry marrow weight

Table 2
Characteristics of experimentally butchered gazelles

ID number	HA-1000	HA-1002	HA-1005	HA-1007	HA-1009	HA-1010	HA-1011
Sex	Male	Male	Male	Female (pregnant)	Male	Male	Male
Month killed	Oct-04	Dec-04	Jan-05	Mar-05	Mar-05	Sept-05	Sept-05
Live body weight (kg)	20.90	16.70	15.40	19.90	21.78	10.20	23.69
State of tooth eruption	All teeth erupted P2–P4 moderate wear	All teeth erupted M2–M3 light wear	All teeth erupted and in wear	M3 half erupted	All teeth erupted M2–M3 light wear	All teeth erupted and in wear	All teeth erupted and in wear
Age and age rank	Prime adult 2	Prime adult 3	Prime adult 5	Prime adult 1	Prime adult 3	Prime adult 5	Prime adult 5
Region of death	Mount Carmel	Mount Carmel	Mount Carmel	Judean Foothills	Judean Foothills	Southern origin	Judean Foothills
Locality	Chai-Bar	Bat-Shlomo	Chai-Bar	Latroun	Bet-shemesh	Unknown	Shoresh
Cause of death	Entangled in fence	Car accident	Entangled in fence	Car accident	Car accident	Car accident	Car accident

Age ranks are numbered from youngest to oldest based on stage of tooth wear and eruption.

(fat and non-fat residues; cf. Blumenschine and Madrigal, 1993).

The fat content and the energetic value (in Kcal) of each marrow sample were calculated to define the range of variation in marrow quality among carcasses and elements in our sample. Marrow is composed of fat, water and non-fat residues. The amount of fat is inversely proportional to both the amount of water and non-fat residues (Neiland, 1970). Heating the wet marrow evaporates the water leaving only the fat and the non-fat residues in the dry marrow sample. Percent dry marrow weight is highly correlated with fat content in a variety of temperate (Neiland, 1970) and tropical East African ungulates (Brooks et al., 1977; Sinclair and Duncan, 1972). Mountain gazelle marrow has not previously been evaluated, but given the universality of the trend for a wide range of bovid species, the relationship is likely to be the same.

The %fat content of the bone marrow is calculated as the percentage of dry marrow weight in relation to wet marrow weight minus a constant of 7% that accounts for the average percentage of non-fat residues in ungulate bone marrow (%fat content = [(dry weight/wet weight)100] − 7; Neiland, 1970; Sinclair and Duncan, 1972). The constant value was derived from a range of African ungulate species in varying physical conditions. The energetic value of each sample was calculated by multiplying %fat content by marrow wet weight (g) to obtain fat weight (g) and then multiplying by 9 Kcal (Energetic value = [%fat content × marrow wet weight] × 9 Kcal/g; see also Blumenschine and Madrigal, 1993; Madrigal and Capaldo, 1999). Previous bomb calorimeter tests on a wide variety of species show that the average energetic value of mammalian bone marrow clusters around a value of 9 Kcal/g for a variety of ungulate species (Blumenschine and Madrigal, 1993; McCullough and Ullrey, 1983 and references therein).

The energy content of gazelle marrow was determined for a subset of 16 samples of dry marrow (∼0.2 g per sample) from three of the sampled animals (1000, 1002 and 1007). Energy content was measured using a Gallenkamp Ballistic Bomb Calorimeter at the Laboratory of Physiology, Department of Zoology, Tel-Aviv University. After weighing each sample, the marrow was burned and the released energy was measured in microvolt units. This measurement was used to calculate the amount of calories in each gram of marrow.

Visual assessment of the texture and color of bone marrow in mature animals is widely used by wildlife biologists to estimate an animal's fat content and its overall body condition in the field (Cheatum, 1949). The color and texture of bone marrow are directly related to its fat content − marrow with high fat content is white and firm while marrow with low fat content is red and watery (Neiland, 1970). Marrows from animals in intermediate condition are pink and translucent. The color of the marrow fat is used here as an additional line of evidence to assess the marrow fat content and hence the overall body condition of the gazelle carcasses butchered in our experiment.

4. Results

The wet and dry weights from the seven mountain gazelles sampled here show substantial variation amongst individuals. Wet weights range from between 21.57 and 45.53 g for the combined sample of six long bones (one side each from the humerus, radius, metacarpal, tibia, femur, metatarsal), while dry marrow weights range between 3.82 and 36.02 g (Table 3). The distribution of wet and dry marrow across the six long bones is similar for each of the seven animals with the exception of 1002 (Table 4). On average the tibia has the highest wet marrow yield followed by the femur, humerus, radius, metatarsal and metacarpal. The first and second phalanges, the mandible, and the scapula have significantly lower marrow yields, while the wet marrow in the pelvis and calcaneum is negligible. Rank reversals in marrow wet weights occur in three gazelles in our sample (1000, 1002, 1005). In one case the rank of the metatarsal and radius are reversed, in another the humerus and radius exchanged positions and in the third the metatarsal has moved above both the humerus and the radius. It is significant that the three animals with rank reversals have the lowest average fat contents in the sample. This is confirmed in our calculations of %fat content in the marrow samples (Table 5). Again, %fat content varies considerably amongst individuals and in most cases among elements from the same individual.

The rank order of the average dry marrow weights from individual elements is the same as for wet marrow, except for one shift − unlike the wet marrow rankings, the dry marrow weight of the metatarsal ranked higher on average than the radius. Deviation of individuals from the average rank order is more common for dry marrow weights than wet weight values − all specimens with the exception of 1009 have at least one element rank reversal and the ranking of nearly all of the elements from 1002 differ from the average pattern (Table 4).

Correlation analysis of both the wet and dry marrow contents of individual elements from the seven carcasses shows a strong and significant coefficient in most cases ($r_P > 0.90$; Table 6). Similarly, the wet and dry marrow weights of all animals are significantly correlated with each other. An exception to this pattern is specimen 1002, which has low dry marrow weights that are not correlated with its wet weights or the dry and wet weights of any other animals.

Sixteen marrow samples from three animals were selected for bomb calorimeter analysis. Due to cost restrictions,

Table 3
Total wet and dry marrow weights (in grams) and Kcal values for a combined sample of six long bones (one side only) from the studied gazelle carcasses

ID number	Wet weight	Dry weight	Total Kcal
HA-1000	31.39	9.15	62.6
HA-1002	32.83	5.52	29
HA-1005	34.55	3.82	12.6
HA-1007	45.53	33.93	276.7
HA-1009	38.17	36.02	300.1
HA-1010	21.57	14.71	118.8
HA-1011	30.62	25.89	213.7

Table 4
Wet and dry marrow weights (in grams) by element

Element	HA-1000		HA-1002		HA-1005		HA-1007		HA-1009		HA-1010		HA-1011	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Tibia	9.81	2.76	12.28	1.39	9.03	**1.00**	14.37	11.32	11.97	11.52	6.37	5.80	11.17	9.85
Femur	6.77	2.44	7.10	1.05	7.70	**1.02**	9.52	7.90	10.95	10.38	6.25	3.82	7.56	5.48
Humerus	**4.59**	1.51	4.06	**0.49**	5.32	0.62	7.29	5.33	6.55	6.16	2.86	**1.22**	3.75	3.02
Radius	**4.69**	**0.90**	**2.78**	**0.25**	**4.25**	**0.33**	6.14	4.36	4.02	3.71	2.26	**1.15**	3.11	2.90
Metatarsal	3.34	**1.10**	**3.78**	**1.74**	**4.94**	**0.55**	4.85	3.23	2.98	2.72	2.19	**1.62**	3.00	2.79
Metacarpal	2.19	0.44	**2.83**	**0.60**	3.31	0.30	3.36	1.79	1.70	1.53	1.64	1.10	2.03	1.85
Mandible	0.55	0.13	0.73	**0.03**	**0.16**	**0.03**	0.90	**0.04**						
Phalanx 1	0.52	0.13	0.36	**0.13**	**0.39**	**0.08**	0.80	**0.34**						
Phalanx 2	0.26	0.05	**0.09**	0.02	0.13	0.02	**0.02**	0.04						
Scapula	Negligible		**0.14**	0.00	0.11	0.01	**0.08**	**0.09**						
Calcaneum	Negligible		Negligible		Negligible		Negligible							
Pelvis	ND		Negligible		Negligible		Negligible							

Rank reversals from the average pattern are shown in bold. ND, no data.

samples were selected to maximize variability. Animals from both sexes were selected as were animal in both good and poor condition. Bomb calorimeter analysis of the 16 samples indicates substantial variation from the average value of 9 Kcal/g provided by animal fat (McCullough and Ullrey, 1983; Table 7). The marrow from 1002 yielded low energetic value (6.23 Kcal/g on average), while the marrow from 1007 and 1000 yielded energetic values similar to the average for many ungulate species (9.22 and 8.76, respectively). ANOVA tests show that the caloric values of the bones from the three animals differ significantly ($F = 12.27$, $P < 0.001$). However, a Student's t-test indicates no significant difference between 1007 and 1000 ($t = 1.83$, $P = 0.10$), but significant difference between 1007 and 1002 ($t = 6.15$, $P < 0.001$) and 1000 and 1002 ($t = 3.80$, $P < 0.05$). The results indicate that the dry marrow from specimens 1000 and 1002 yielded lower average values (8.76 and 6.23 Kcal) than 1007 (9.22 Kcal). The low energetic values indicate that the dry marrow residues from specimens 1000 and 1002 contained high proportions of non-fat residues and low proportions of fat in comparison to the sample from 1007.

5. Gazelle marrow and the Epipaleolithic record

The modern gazelle bone marrow data are applied to the archaeological record to examine human carcass utilization strategies during the Epipalaeolithic period (21,000−11,000 cal. years BP) in the southern Levant. Five Epipalaeolithic assemblages are considered here (Table 8). Previously, we applied a multivariate taphonomic approach to assess the role of bone fat processing in these assemblages (Bar-Oz and Munro, 2004; Munro and Bar-Oz, 2005). We concluded that Epipalaeolithic foragers intensively processed gazelle bones for marrow and possibly grease.

The average marrow yields from the gazelle sample are used to explore variation in bone fragmentation and survivorship of gazelle in the Epipalaeolithic assemblages. First, we examine the relationship between bone marrow yield (Kcal) and the minimum number of gazelle animal units (MAU) to evaluate human transport decisions. Only those elements that store bone marrow are considered (long bones, mandible, first and second phalanges). We also compare the average Kcal yields of bone marrow with the fragmentation index for each marrow bearing bone to determine whether humans selectively processed bones according to their marrow yields. The fragmentation index was derived by dividing the number of identified specimens (NISP) by the minimum number of elements (MNE). Finally, %completeness values are provided for gazelle long bones and foot bones to estimate the point of diminishing returns beyond which foragers were not willing to access marrow except perhaps under stressful conditions.

Table 5
Fat content and Kcal values of bone marrow from six limb bones (one side only) from the sampled gazelles

Element	HA-1000		HA-1002		HA-1005		HA-1007		HA-1009		HA-1010		HA-1011	
	%Fat	Kcal	%Fat	Kcal	%Fat	Kcal	%Fat	Kcal	%Fat	Kcal	%Fat	Kcal	%Fat	Kcal
Tibia	21.1	18.7	4.3	4.8	4.1	3.3	71.8	92.8	89.2	96.1	84.1	48.2	81.2	81.6
Femur	29.0	17.7	7.8	5.0	6.2	4.3	76.0	65.1	87.8	86.5	54.1	30.4	65.5	44.6
Humerus	25.9	10.7	5.1	1.9	4.7	2.2	66.1	43.4	87.0	51.3	35.7	9.2	73.5	24.8
Radius	12.2	5.1	2.0	0.5	0.8	0.3	64.0	35.4	85.3	30.9	43.9	8.9	86.2	24.1
Metatarsal	25.9	7.8	39.0	13.3	4.1	1.8	59.6	26.0	84.3	22.6	67.0	13.2	86.0	23.2
Metacarpal	13.1	2.6	14.2	3.6	2.1	0.6	46.3	14.0	83.0	12.7	60.1	8.9	84.1	15.4
Average %fat	22.1		9.8		4.1		67.5		87.4		61.2		77.6	
Total Kcal		62.6		29.0		12.6		276.7		300.1		118.8		213.7

Table 6

Pearson product-moment correlation matrixes for wet and dry marrow weights of six long bones from the studied gazelles

		HA-1000		HA-1002		HA-1005		HA-1007		HA-1009		HA-1010		HA-1011	
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
HA-1000	Wet	1.00													
	Dry	0.94	1.00												
HA-1002	Wet	0.94	0.91	1.00											
	Dry	**0.31**	**0.43**	**0.50**	1.00										
HA-1005	Wet	0.95	0.99	0.95	**0.50**	1.00									
	Dry	0.85	0.98	0.86	**0.52**	0.97	1.00								
HA-1007	Wet	0.99	0.94	0.96	**0.32**	0.96	0.86	1.00							
	Dry	0.99	0.96	0.95	**0.32**	0.97	0.89	1.00	1.00						
HA-1009	Wet	0.94	0.99	0.88	**0.28**	0.97	0.95	0.94	0.97	1.00					
	Dry	0.94	0.99	0.89	**0.28**	0.97	0.95	0.95	0.97	1.00	1.00				
HA-1010	Wet	0.92	0.97	0.90	**0.38**	0.97	0.96	0.91	0.94	0.98	0.98	1.00			
	Dry	0.93	0.91	0.98	**0.52**	0.95	0.88	0.93	0.94	0.89	0.90	0.93	1.00		
HA-1011	Wet	0.98	0.95	0.98	**0.43**	0.98	0.90	0.98	0.98	0.94	0.95	0.95	0.99	1.00	
	Dry	0.97	0.90	0.99	**0.45**	0.94	0.83	0.97	0.96	0.88	0.89	0.89	0.98	0.99	1.00

Insignificant correlations are marked in bold.

The average Kcal value of dry marrow from the sampled animals was compared against gazelle MAU values from five Epipalaeolithic bone assemblages using a Spearman's rank order correlation (Table 9). All assemblages show insignificant correlations. In contrast, the relationship between dry marrow yield (Kcal) and the fragmentation indices (NISP/MNE) of long bone shafts and first and second phalanges from each of the Epipalaeolithic sites show positive and significant correlations (Table 10). Fragmentation indices should increase with marrow yield, because humans are expected to preferentially process bones that contain the most marrow. Likewise, an increase in the frequency of marrow extraction will result in the fragmentation of more bones and will thus increase the NISP/MNE ratio. The significant correlations between NISP/MNE ratios and marrow yield in the Epipalaeolithic

Table 7

Marrow weight (in grams) and Kcal yields of samples used for bomb calorimeter analysis

	Sample	Marrow weight	Microvolt	Microvolt/g	Kcal/g	Average
HA-1007	Combined long bone sample	0.375	844	2249	10.22	
		0.098	200	2052	9.33	
		0.134	275	2049	9.31	
		0.129	265	2055	9.34	
		0.147	302	2055	9.34	
		0.147	270	1841	8.37	
	Femur	0.166	332	2000	9.09	
		0.157	314	1997	9.08	
	Tibia	0.173	348	2013	9.15	
		0.188	371	1971	8.96	9.22
HA-1000	Combined long bone sample	0.093	187	1997	9.08	
		0.074	146	1972	8.96	
		0.103	194	1888	8.58	
		0.168	311	1848	8.40	8.76
HA-1002	Tibia	0.093	106	1147	5.22	
		0.294	468	1593	7.24	6.23

assemblages indicate that Epipalaeolithic humans were preferentially breaking those bones with the most marrow.

Compact gazelle hind foot bones require effort to crack despite low returns, and thus specify how far humans were willing to go to access even small marrow stores. Of the three gazelle phalanges, the first and second contain marrow – the first phalanx holds as much as five times as much as the second. The calcaneum also contains marrow stores, but our experiments showed these to be negligible. A rough measure of extraction intensity is provided by comparing the %completeness of the first and second phalanges, and the calcaneum against the non-marrow bearing compact bones of the lower leg (the astragalus and third phalanx). In the Epipalaeolithic assemblages, the first phalanx has the lowest completeness index on average (40.2%). The completeness index for the second phalanx is much higher (62.3%), but exceeds the calcaneum although the calcaneum contains less marrow (49.8%). Both the astragalus and third phalanx have significantly higher completeness ratios than the other elements (74.6% and 81.6%; Table 11). With the exception of the calcaneum, the completeness ratios for the compact elements correspond directly to bone marrow yields. The low rate of completeness for the first phalanx indicates that though small, this source of bone marrow was usually tapped, while effort consistent with lower medullary content was invested into cracking the second phalanx and calcaneum less than half the time. While Epipalaeolithic foragers intensively exploited marrow stores in gazelle carcasses, as attested by the fragmentation of nearly all marrow bearing bones including the first phalanx, they stopped short of thorough exploitation at the smallest of marrow stores.

6. Discussion

6.1. Variation in fat content among individuals

Our results document extensive variation in marrow fat content amongst individual gazelles. The fat content of the dry marrow corresponds well with the color and texture of

Table 8
Epipalaeolithic faunal assemblages studied. Sites are arranged in chronological order

Site	Cultural phase	Time range (cal. years BP)	Reference
Nahal Hadera V	Early Kebaran	21,000–17,000	Bar-Oz (2004), Bar-Oz and Dayan (2002)
Hefzibah 7–18	Geometric Kebaran	17,000–14,500	Bar-Oz and Dayan (2003)
Hayonim Cave	Early Natufian	14,500–13,000	Munro (2001, 2004)
Hayonim Cave	Late Natufian	13,000–11,500	Munro (2001, 2004)
el-Wad Terrace	Late Natufian	13,000–11,500	Bar-Oz et al. (2004)

See also Munro and Bar-Oz (2005) Table 1, for a summary of taphonomic and zooarchaeological variables for each site.

the samples. Marrows with low fat content (1000, 1002 and 1005) were blood red and runny, while marrows with higher fat contents (1007, 1009, 1010 and 1011) were white to pink and solid. These observations are supported by the bomb calorimeter analyses.

The low fat content and the red and runny texture of the marrow from specimens 1000, 1002 and 1005 indicate that these animals were in poor physiological condition when they died. In other studies (Brooks et al., 1977; Cheatum, 1949; Klein, 1968; Madrigal and Capaldo, 1999; Neiland, 1970; Nieminen and Laitinen, 1986; Ratcliffe, 1980; Sinclair and Duncan, 1972) animals with equivalent marrow fat contents were typically ill, injured or on the verge of starvation. None of the animals in the sample died of natural causes, so it is not clear how physical condition influenced death. Specimens 1000 and 1005, however, died in captivity after getting caught in the fence surrounding their enclosures. Both of these animals are prime adult males who were placed in enclosures with another dominant adult male. In the wild, male gazelles often live in bachelor herds, but vie to become dominant and possess their own territory. Territorial males are solitary and vigorously defend their territory (Mendelssohn, 1974; Mendelssohn and Yom-Tov, 1999; Mendelssohn et al., 1995). The death of the two prime adult males in captivity indicates that they attempted to flee their enclosures, most likely to avoid competition with the dominant male. It is quite likely that competition and the agonistic behavior of the dominant male led to the poor health of these two individuals. Specimen 1002 the animal in the poorest physiological condition was

killed by a car, as were all animals in good condition. It is not known why 1002 was in such terrible condition, or if his poor health made him more susceptible to death on the road.

Unfortunately, because of the unsystematic nature of the carcass collection strategy, the sample is dominated by males and only one female is represented. The lone female (1007) was killed in the early spring (March) during her first trimester of pregnancy when she was in good physical condition and had consistently high marrow fat content across all elements. Because she is the only female in the sample, it is impossible to assess whether her condition is related to the season of death, her pregnancy, her sex, or a combination of these. Specimen 1009 has the highest marrow weight and fat content of the sampled animals. Like 1007 this male was killed in March, when he was expected to be in peak condition.

Finally, the two wild males (1010, 1011) killed in the early autumn (September 2004) had intermediate fat contents. Although they were killed at the end of the dry season after a long period of reduced food quality and likely had less total body fat than in other seasons, they should not have been on the brink of starvation unless forage had been exceptionally poor. The geographic origin of 1010 and 1011 suggest that they were minimally impacted by modern agricultural activity. Specimen 1011 derives from the Judean desert where agriculture is rare, while specimen 1010 inhabited the Mediterranean hills in the central part of Israel where grape and olive production dominate agricultural activities. Olive trees and grape vines do not constitute regular forage for gazelles. Although the impact of the dry season is evident in their marrow fat

Table 9
MAU of gazelle marrow bearing bones from the Epipalaeolithic assemblages

Element	Dry marrow (g)	Kcal	MAU				
			NHV KEB	HEF G-KEB	HAYC EN	HAYC LN	EWT LN
Tibia	6.23	49.36	60	25	17	5	13
Femur	4.58	36.23	48	45	9	4	14
Humerus	2.62	20.50	60	32	18	18	14
Radius	1.94	15.03	41	24	7	11	5
Metatarsal	1.96	15.41	29	13	12	8	5
Metacarpal	1.09	8.26	23	14	8	7	4
Phalanx 1	0.17	3.02	118	43	15	12	13
Mandible	0.06	0.52	60	25	8	4	7
Phalanx 2	0.03	0.55	111	37	13	12	12
MAU vs average Kcal							
Spearman's r			$r_s = 0.32$	$r_s = 0.02$	$r_s = 0.33$	$r_s = 0.20$	$r_s = 0.47$
P value			$P = 0.40$	$P = 0.94$	$P = 0.38$	$P = 0.60$	$P = 0.21$

Table 10
Average Kcal yields of gazelle bone marrow and fragmentation indices (NISP/MNE) of gazelle marrow bearing bone shafts from the Epipalaeolithic assemblages

Element	Kcal	NHV KEB			HEF G-KEB			HAYC EN			HAYC LN			EWT LN		
		NISP	MNE	NISP/MNE	NISP	MNE	NISP/MNE	NISP	MNE	NISP/MNE	NISP	MNE	NISP/MNE	NISP	MNE	NISP/MNE
Tibia	49.36	62	9	6.9	34	4	8.5	94	23	4.1	43	7	6.1	18	2	9.0
Femur	36.23	45	4	11.3	15	2	7.5	43	11	3.9	18	6	3.0	20	1	20.0
Humerus	20.50	54	5	10.8	24	3	8.0	40	20	2.0	46	27	1.7	25	3	8.3
Metatarsal	15.03	50	5	10.0	14	2	7.0	72	19	3.8	49	13	3.8	5	2	2.5
Radius	15.41	22	3	7.3	22	3	7.3	44	13	3.4	48	18	2.7	14	2	7.0
Metacarpal	8.26	35	9	3.9	24	3	8.0	37	12	3.1	37	12	3.1	5	2	2.5
1st phalanx	3.02	1611	940	1.7	647	339	1.9	234	120	2.0	151	89	1.7	211	99	2.1
2nd phalanx	0.55	1308	888	1.5	507	293	1.7	145	103	1.4	122	92	1.3	158	93	1.7
NISP/MNE vs average Kcal																
		$Y = 0.13X + 3.96$			$Y = 0.10X + 4.13$			$Y = 0.04X + 2.11$			$Y = 0.06X + 1.57$			$Y = 0.23X + 1.65$		
Spearman's r		$r_s = 0.76$			$r_s = 0.75$			$r_s = 0.85$			$r_s = 0.69$			$r_s = 0.93$		
P value		$P = 0.03$			$P = 0.03$			$P < 0.001$			$P = 0.06$			$P < 0.001$		

content, the animals that died in autumn still provided reliable and exploitable marrow fat yields.

Our marrow extraction experiments suggest that except in cases where animals were in particularly poor condition due to disease, injury or nutritional stress, mountain gazelle marrow provided a reliable source of fat that could have been tapped by prehistoric humans in all seasons. Even the marrow of animals that were killed at the end of the dry season was in good condition, even if the quality of the fat was not at its peak.

6.2. Variation in marrow content among bone elements

Although the rank order of the wet and dry marrow weights from marrow bearing elements are highly correlated amongst individuals, most of our experimental animals show at least one rank reversal in comparison to the average pattern. Reversals are more common for dry than wet marrow weights. Wet marrow weight rankings are likely less variable because marrow wet weight is significantly correlated with the volume of the marrow cavity (Emerson, 1990), which varies proportionally with body size. Not surprisingly, dry weights show greater variability because they more accurately reflect the %fat content of the marrow sample, which varies according to a number of previously discussed factors (season, age, sex and body condition). Body condition, in particular, may impact element rankings, because fat mobilization does not affect all elements equally, but proceeds from proximal to distal elements, causing rank reversals between distal and proximal bones (Blumenschine and Madrigal, 1993; Brooks et al., 1977; Lupo, 1998; Sinclair and Duncan, 1972; Speth, 1987, 1989). Animals with low fat contents are thus more likely to show rank reversals in bone elements than those in good condition. The rankings of the bone elements from specimen 1002, the animal in the poorest condition in our sample, differ the most from the other sampled animals, while specimen 1005, also in poor physical condition, follows closely behind. Interestingly, however, although the pattern of distal to proximal fat mobilization is borne out in specimen 1002 (i.e., distal elements replace the proximal elements in rank order), this pattern is not repeated in specimen 1005. The percentage of fat in the marrow from specimen 1005 is so low that relative rankings of elements are no longer informative.

Like the wet and dry marrow weights there is substantial variation in the fat content among elements within each gazelle carcass. Again, some animals display clear patterns of fat mobilization, while others do not. The classic pattern of fat depletion shown for specimen 1002 is repeated in its fat content, confirming the poor physical condition of this animal. Specimen 1005, which has a very low percentage of

Table 11
Percent completeness of gazelle foot bones from the Epipalaeolithic assemblages

Site		Phalanx 1	Phalanx 2	Calcaneum	Phalanx 3	Astragalus
Nahal Hadera V	Comp/MNE	165/840	451/882	70/173	518/663	402/535
	%Completeness	29.7	51.1	40.5	78.1	75.2
Hefzibah	COMP/MNE	40/170	171/311	26/69	162/226	79/201
	%Completeness	23.5	55.0	37.7	71.7	79.2
Hayonim Cave EN	COMP/MNE	70/120	86/103	24/36	69/81	27/31
	%Completeness	58.3	83.5	66.7	85.2	87.1
Hayonim Cave LN	COMP/MNE	55/89	71/92	15/24	49/65	21/24
	%Completeness	61.7	77.2	62.5	75.4	87.5
el-Wad Terrace	COMP/MNE	23/83	41/92	5/12	30/48	50/64
	%Completeness	27.7	44.6	41.7	62.5	78.9
Average %completeness		40.2	62.3	49.8	74.6	81.6

COMP/MNE = number of elements that are at least 90% complete divided by MNE for that element.

fat in all of its marrow cavities, again appears to be even worse off, and has already metabolized even the last stores of fat in its metacarpal and metatarsal. The other animals are not severely fat depleted and have less patterned values – some of those with high average marrow contents (1007, 1009) exhibit great consistency in fat content across elements indicating that their fat has not been mobilized and that they are in good physical condition.

Prehistoric foragers seeking fat from gazelle carcasses are expected to have targeted those elements with the highest fat content for marrow extraction. In healthy animals these include the tibia, femur and humerus, in particular. The radius, metacarpal and metatarsal also provide sufficient fat to make them worthy of the labour required to breach them. Given the pattern of fat mobilization from proximal to distal elements, however, it is possible that the elements that humans selected for marrow processing may have shifted if animals were in poor physical condition. Although several other elements contain marrow, the results of our experiment showed them to be substantially smaller than the yields from the six limb bones and thus these elements are not expected to have been tapped as regularly as the limb bones, except under stressful conditions.

Gazelles are small-bodied ungulates, and compared to other big game animals do not provide a tremendous amount of marrow fat in any season. Nevertheless, gazelles comprise over 85% of the fauna in most Epipaleolithic and pre-Pottery Neolithic assemblages in the southern Levant, and larger animals were rare. Gazelle marrow would therefore have constituted a common and valuable source of fat in Mediterranean environments especially in the dry season.

6.3. Implications for Epipalaeolithic foraging

Non-significant relationships between fat content and elemental representation (MAU) in five Epipaleolithic assemblages suggest that gazelle bone abundance in each of the assemblages was not affected by selective transport decisions. Gazelle body-part patterns from these same sites indicate that human foragers carried carcasses back to the site complete, likely due to the fact that gazelles are small-bodied and were hunted reasonably close to habitation sites (Munro and Bar-Oz, 2005).

In contrast, significant correlations between the fragmentation (NISP/MNE) of long bone shafts and the energetic yields of gazelle marrow presented here clearly demonstrate that bones from the Epipalaeolithic sites were preferentially accessed according to their energetic yield. The similar positive slopes of the regression lines (Table 10) suggest that Epipalaeolithic people intentionally selected and processed high yielding marrow bones. Such preferential exploitation of rich marrow bones might indicate that animal food was abundant, and/or that the availability of other fat resources was high. Nevertheless, it must be noted that all zooarchaeological assemblages studied here represent large time-averaged accumulations, and are thus products of numerous

multi-seasonal hunting episodes and complex accumulative processes (Lupo, 2001).

Despite the relatively low marrow yield from a single gazelle carcass, the fragmentation of the Epipalaeolithic assemblages indicates that humans routinely opened gazelle long bones for marrow. Virtually no long bones, with the exception of some juvenile elements, were recovered complete (Munro, 2004; Munro and Bar-Oz, 2005). These results indicate that gazelle marrow was a desired commodity with a value that exceeded its extraction costs in all seasons of the year. Elements with smaller marrow stores show a different exploitation pattern from the long bones. The phalanges, which contain small, but measurable sources of fat even in lean times, are also frequently broken for marrow extraction, but only about half as often as the long bones (Munro and Bar-Oz, 2005). The small size of these marrow stores (less than half gram of dry marrow) and the fact that Epipalaeolithic people invested in extracting them even half of the time suggests an intensive gazelle carcass butchering strategy.

The substantial gap in the frequency of breakage of the long bones and the phalanges might indicate a point of diminishing marrow returns [see Burger et al., 2005]. The frequency of marrow extraction from phalanges would thus be an informative indicator of particularly intensive carcass use (Binford, 1978). The extraction of marrow from phalanges may reflect a seasonal pattern, in which phalanges are breached only in the lean season. Unfortunately, because Epipalaeolithic occupations represent complex, often multi-seasonal accumulation processes it is difficult to test this hypothesis. Nevertheless, the percent completeness of first and second phalanges in comparison to the six long bones has the potential to provide a useful comparative index of the intensity and seasonality of marrow exploitation amongst sites and time periods.

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