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# The Antiquity of Large-Game Hunting in the Mediterranean Paleolithic: Evidence from Mortality Patterns

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## Introduction

The ability to hunt very large mammals was a significant development in the evolution of humankind. Hoofed animals (ungulates) were the main source of meat for Middle and Upper Paleolithic people across much of Eurasia and Africa (Klein 1999). These animals can be dangerous, often exceeding the body size of hunters, and aggressive in their own defense. Yet large-game hunting is a natural and nearly universal part of contemporary foraging cultures (Lee and DeVore 1968). Some nonhuman primates also hunt mammals, but they tend to focus on relatively small prey (Stanford 2001). Not only did hominids eventually master the challenges of bringing down large game, they became ecologically distinct from all other predators with respect to prey age selection (Stiner 1994).

When did hominids become the sort of ungulate predator that we see among recent foraging cultures? Here I present an updated account of evidence for the antiquity of large-game hunting in the Mediterranean Basin, presenting archaeological data from the late Middle Pleistocene through early Holocene. The evidence is principally from the age structures of artiodactyl (even-toed) ungulate death assemblages – mortality pat-

terns inferred from dental eruption and wear. Information on bone fusion and sex ratios in prey is also considered where available.

The evidence lays to rest any suggestion that meat acquisition by early Mousterian humans was confined to scavenging. To date, the caves of Hayonim (Bar-Yosef and Goren 1973; Meignen et al. 2006) and Qesem (Barkai et al. 2003; Gopher et al. 2005) provide some of the earliest, best-preserved examples of large-game hunting, the implications of which reach beyond the Near East. But there is more to the findings than this. Considerable variation is apparent in Paleolithic foraging habits and flexibility (e.g., Gaudzinski 2006; Jaubert et al. 1990; Speth and Clark 2006; Stiner 1994). General equivalence in one dimension of foraging does not promise equivalence in others. Both Middle and Upper Paleolithic peoples hunted, gathered, and at times scavenged for food. There were significant differences in dietary breadth between the two periods (Stiner 2001; Stiner et al. 2000) as well as in humans' probable impact on prey population densities between periods. This presentation concentrates on merely one dimension of Paleolithic foraging behavior – prey age selection.

### **The Three-Cohort Method: A Brief Review**

The three-cohort method and models used in this study were developed more than a decade ago (Stiner 1990). Since then, the three-cohort approach has been applied widely in research on Paleolithic faunas (e.g., Enloe 1997; Gaudzinski 1995; Pike-Tay et al. 1999; Speth and Clark 2006; Speth and Tchernov 1998; Steele and Weaver 2002; see also Lyman 1994). Interestingly, and reassuringly, the results are fairly consistent among studies, at least in the larger patterns observed. Detailed descriptions of the method can be found elsewhere (Stiner 1994:271–295), and only a brief review is undertaken here.

The dental wear stages for deer, cattle/bison, and sheep/goat documented by Payne (1973) and others (see Hillson 1986) are the foundation of the ageing criteria. Because there is less precedent for mountain gazelles, age criteria for them are based on a combination of Payne's (1973) and Davis's (1980b) systems and Stutz's (2002) study of known-age individuals in the comparative collections of Tel Aviv University and the Hebrew University of Jerusalem. Only eruption and wear observations are used, but good agreement generally exists between crown-height measurement data for high-crowned (hypsodont) species and occlusal-wear stage data. Regardless, no simple correspondence exists between dental condition and age in real years due to the nonlinear pace of occlusal wear (Gifford-Gonzalez 1991; Hillson 1986; Severinghaus 1949).

The three-cohort system – consisting of juvenile, prime adult, and old adult age groups – is divided according to the principal life stages through which long-lived individuals pass. The three cohorts correspond

to the differing susceptibilities of individuals to attritional factors such as disease, accidents, and malnutrition, as well as to significant changes in body composition. Prior to the late stages of development, juveniles are generally poor in fats because so much of their energy is devoted to growth.

Because few age categories are involved, the three-cohort system handles small assemblages better than most and accommodates isolated teeth as well as those in intact dental rows. The technique targets the deciduous fourth (or third) premolar followed by the fourth premolar or, alternatively, the third molar, with crosschecks to adjacent dental elements. The dP4–P4 or dP3–M3 sequence in artiodactyls has three attractions: these teeth are easily distinguished from other cheek teeth, they track a lifetime of food intake and occlusal abrasion, and the fourth premolar can be completely worn away in advanced age (and the third molar nearly so). These dental sets collectively represent the full potential lifetime of an ungulate.

Juveniles are individuals younger than the age at which the fourth deciduous premolar is normally shed and replaced by the permanent fourth premolar. A permanent premolar, however, must show some evidence of occlusal wear in order to be counted, as this is the only reliable indicator that the permanent tooth was “exposed” in the jaw at the time of death. The prime-adult stage begins at the deciduous-permanent boundary and continues up to the point when half of the crown is worn away. The latter point corresponds to about 65 percent of the maximum potential life span. Old adults are indicated when more than half the height of the P4 or M3 crown has been worn away. The maximum potential life span

(MPL) theoretically ends when the crown is destroyed, which happens to the P4 in advanced age. At this point, feeding becomes difficult or compromised, and the animal soon perishes.

#### **Juvenile Mammals and Preservation Bias**

Young ungulates often seem too few relative to adults in archaeofaunas, including those dating to the Paleolithic. Interestingly, juvenile ungulates and carnivores are often plentiful in assemblages created by hyenas in other layers of the same sites (Stiner 1994:299, 328–329; Wrinn n.d.). Is underrepresentation of juveniles the result of poor preservation, or does it reflect human prey choice? Considerable debate has taken place over this question. However, only some of the concerns about biases against juvenile cohorts in mortality data are justified by the structural biology of teeth.

Fully formed, healthy teeth are very dense structures and for this reason resist all decomposition forces much better than bone does. Teeth that are only partly formed at the time of death are a good deal less resistant, and their potential for preservation is on par with or inferior to that of compact bone. Thus, it is the state of development of a tooth, and specifically the degree of mineralization that has been achieved by the time of death, that determines its potential to be preserved. The size of a tooth, and whether it is permanent or deciduous, is far less important in determining its preservation potential.

Mammalian enamel is very porous during formation, but only briefly in relation to the full potential use-life of the tooth. The mineral fraction in a developing tooth may be as low as 37 percent (about half that of mature bone), the organic fraction 19 per-

cent, and water as high as 44 percent (Wainwright et al. 1976:224). The proportions of the three components change radically with maturation, when enamel is composed of about 94–97 percent mineral, 2 percent organic matrix, and 4 percent water. In addition to a very high inorganic/organic ratio, the apatite crystals of fully developed tooth enamel are roughly 10 times larger (about 40 nm across) than the apatite crystals of bone (about 4 nm on average) (Currey 1984; Weiner and Traub 1992). The lower ratio of surface area to volume of the fully formed crystalline structure of enamel makes it denser, less porous, and much less soluble than bone is. These points apply to both permanent teeth and many deciduous teeth.

The enamel cap of a mature cheek tooth is backed by dentin, forming a remarkably resilient structure. The enamel cap is brittle and susceptible to crushing prior to the development of the backing. Of concern for mortality analysis is the amount of time during which a particular element is vulnerable to destruction, should the animal die young. A number of zooarchaeologists have suggested that the “visibility” of juveniles in death assemblages suffers disproportionately under suboptimal preservation conditions, particularly in carnivore-ravaged faunas, because juvenile teeth are, as a rule, more fragile (Binford and Bertram 1977; Levine 1983; Marean 1995; Munson 1991, 2000). By this reasoning, some argue, the apparent absence or scarcity of juveniles in archaeofaunal mortality patterns is a product of differential preservation, not of selective hunting by prehistoric humans (Marean 1995). Specifically, small numbers of juveniles in the mortality patterns are taken to represent missing data rather than as an indication of

the original age structure of a death population. Although this assessment can be defended in some instances (e.g., Hoffecker et al. 1991; Stiner 1998), it is inappropriate in a great many other cases where prime-adult biases or other distinctive mortality patterns are observed. Suffice it to say, the mortality patterns discussed below are largely or wholly a product of prey choice by predators based on the methods of age scoring and taphonomic study of assemblage formation processes.

### **Mortality Models**

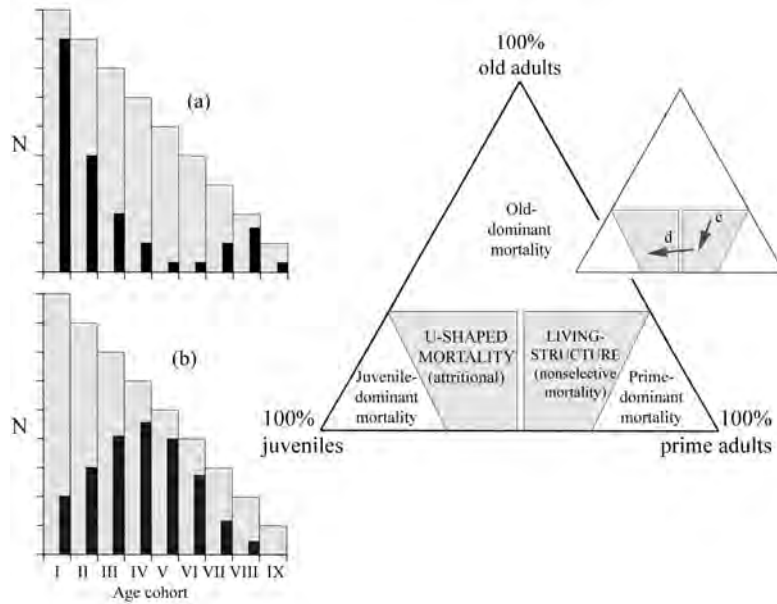
The traditional format for depicting mortality patterns is the two-dimensional bar chart, and descriptive terms in the zooarchaeological literature reflect this (Figure 6.1a–b). Alternatively, the proportion of individuals in only three age cohorts can be plotted on tripolar graphs. Areas of the tripolar graph in Figure 6.1 represent different classes of mortality patterns and the range of variation associated with each. The most common mortality patterns in nature occupy the two lower-center panels: these are U-shaped, or attritional, mortality on the left; and the “living structure” of populations and nonselective mortality on the right (Stiner 1990). The three corners of the graph correspond to biases toward each of the three designated age groups; the prime-adult zone of the graph is of particular interest with respect to human ecology. The range of variation for each mortality pattern is defined on the basis of empirical comparisons of living structures and death patterns from nonviolent causes in recent contexts.

The structures of living mammal populations, encompassed by the “living structure” panel of the tripolar graph, normally

vary between stable, growing, and declining states (Caughley 1977). A prey population may be pushed into sustained growth mode by hunting pressure. Under these conditions, the reproductive prospects for young adults may improve in spite of their having less life experience (see Caughley 1977), and a signal of this effect in tripolar format is a decline or “compression” on the old-adult axis (c) in Figure 6.1). Extreme hunting pressure theoretically may trend toward the lower part of the “attritional” (U-shaped) area of the pattern map (d) (Wolverton 2001). Hunting pressure is not the only or most common cause of U-shaped mortality patterns in nature, however, and other potential explanations must also be taken into account, including the sex ratio of the adult animals hunted (Beaver 2006).

### **A Comparison Predator Niches**

How do the ungulate mortality patterns caused by recent and Pleistocene humans compare to those generated by the big carnivores? And when did prime-adult-focused hunting, a behavior commonly discussed in the zooarchaeological literature, emerge during the Pleistocene? Figure 6.2 summarizes the main tendencies of nonhuman predators and recent humans in various world regions, and of Paleolithic humans of the Italian peninsula. The points represent broad averages of multiple cases, and they are framed against natural variation in living-prey population structures and from nonviolent (attritional) causes. Spotted hyenas, wolves, cheetahs, and African wild dogs are cursorial hunters capable of long or fast chasing of prey, and the mortality patterns that they generate overlap completely with the death patterns resulting from disease, malnutri-

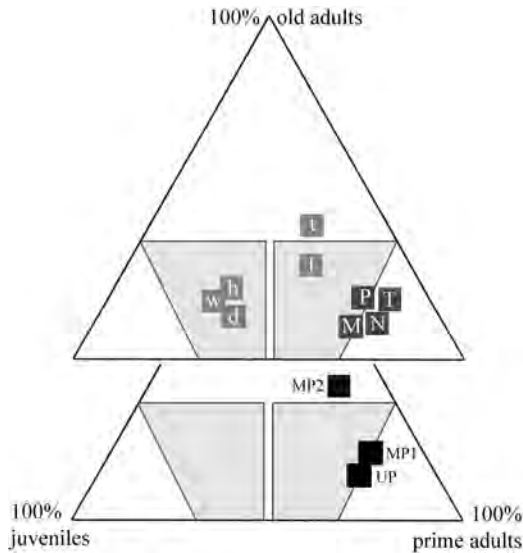


*Figure 6.1. Idealized stable living structure of a mammalian population (large gray bars) contrasted with U-shaped mortality pattern (a, black bars) and prime-dominant mortality pattern (b, black bars). Living-structure and mortality models in tripolar format are shown on the right: shaded panels represent natural variations in the age structures of living ungulate populations and thus also nonselective mortality patterns and mortality patterns caused by attritional factors such as disease, accidents, and malnutrition. Each corner of the diagram represents a strong bias toward the designated prey age group. The inset shows expected trends caused by moderate levels of hunting pressure (c) and a projection for extreme hunting pressure (d) but only if accompanied by a significant bias to males.*

tion, and senescence. Lions and tigers are more inclined to ambush their prey, and selection is less biased to age, unless the quarry is exceptionally large or small. The mortality patterns created by these ambush specialists tend to resemble the age structures of the living prey populations. This is why taphonomic evidence is needed to tie predators to mortality patterns in prehistoric

sites. Scavenging for ungulate carcasses pushes the mean value higher on the old-age axis for cursorial and ambush predators alike, exemplified for Indian tigers in this comparison (see Stiner 1990:299 Pleistocene spotted hyenas).

The mortality patterns produced by predators exhibit a fundamental division according to whether the animal is predomi-



*Figure 6.2. Models and averaged values for observed ungulate mortality patterns created by various human and nonhuman predators. Ambush predators are tigers (t) and lions (l); cursorial, or long-chase, predators are spotted hyenas (h), wolves (w), and African wild dogs (d). Holocene human predators are Paleoinidian-Archaic (P), Mississippian farmers (M), Nunamiut Eskimo (N), and trophy hunters in modern game parks (T). MP<sup>1</sup> is the mean for most Middle Paleolithic hunted faunas from Italy (100–33 ka); it closely resembles that for the Upper Paleolithic (UP). MP<sup>2</sup> represents a handful of cases from coastal Italy dominated almost exclusively by head parts from old-adult prey. (Data from Stiner 1990.)*

nantly a chaser or a stalk-and-ambush hunter. The distance between these behavioral categories in the tripolar plot is quite significant ecologically. Typically, only two or three, or at most four, large predators will coexist in a given region, and this behavioral

divide is maintained from one continent to the next. Though largely fixed in predator adaptations today, the distinct manner by which the two strategic classes interact with the same kinds of prey reduces the risk of interference competition among the predators. A theoretical outcome of interspecific competition is ecological differentiation, or character displacement, which relieves the stresses of conflict between consumers that coexist in an ecosystem (MacArthur and Levins 1967; Pianka 1978:189–199, 260). The differences in the mortality patterns that cursorial predators, classic ambush hunters, and humans produce in ungulate prey testify to a long legacy of natural selection.

A minor feature of the Middle Paleolithic data is attributed to scavenging in two sites from coastal Italy (MP2 in Figure 6.2). These are head-dominated assemblages representing small amounts of meat, probably from winter-killed carcasses. These and certain other sites are also rich in the remains of collectable (slow-moving) small game animals, such as shellfish and tortoises (Stiner 1994, 2005). Even without the MP2 group of cases, the Middle Paleolithic mean from Italy is situated somewhat higher on the old-adult axis than is the Upper Paleolithic–Epipaleolithic mean from the same region.

The mean values for human cases dating from the Middle Paleolithic through historic periods straddle the boundary between non-selective and prime-biased pattern areas of the figure. The averaged patterns for the four “recent” human cultures are remarkably similar to one another, yet they are from very different parts of the world and involve diverse species and weapons systems ranging from bows and arrows, atlatls, and spears to

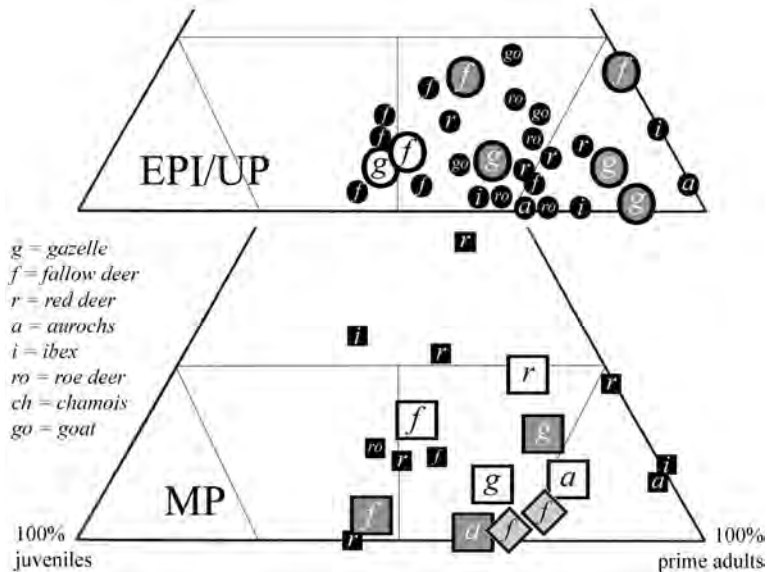


Figure 6.3. Observed mortality patterns in artiodactyl prey from Mediterranean Upper Paleolithic–Epipaleolithic and Mousterian assemblages from Israel, Lebanon (Ksar ‘Akil), Turkey (Üçağzlı Cave), and Italy. Large symbols represent Galilee sites: Hayonim Cave and Meged Rockshelter in the Wadi Meged (gray infill); Kebara Cave on Mount Carmel (white infill). Italian sites are Riparo Mochi in Liguria and Grotta Polesini, Grotta Palidoro, Grotta Breuil, Grotta di Sant’Agostino, Grotta Guattari, and Grotta dei Moscerini in Lazio. Two cases from Qesem Cave appear as diamonds.

firearms (Stiner 1990). The distance between the human and big-cat clusters is similar to that which separates the big cats from the long-chase hunters. Here, we have a fundamental, if rather monolithic, characteristic of the human hunting niche that applies to recent and prehistoric periods and that is an evolutionary outcome of hominids’ long-standing membership in ungulate predator guilds.

Only subtle differences are apparent for the Middle Paleolithic versus the Upper Paleolithic mean values. Human prey-selec-

tion patterns typically span the entire living-structure and prime-dominant areas of the pattern map for both periods (which on average indicates a mild bias toward prime-adult prey). Figure 6.3 presents the full gamut of variation in mortality patterns in Middle Paleolithic, Upper Paleolithic, and Epipaleolithic assemblages from Israel, Italy, Turkey, and Lebanon (Table 6.1), with the Central Levantine cases highlighted apropos this volume in tribute to Ofer Bar-Yosef: Hayonim Cave, Meged Rockshelter (Bar-Yosef 1998; Bar-Yosef and Goren 1973;

**Table 6.1 Three-cohort system results for artiodactyls in the time-ordered Mediterranean faunal assemblages, based on the dP- P<sub>4</sub> or dP-M<sub>3</sub> dental eruption-wear sequence.**

| Central Levant region                                    |           |             |                |              |                |              |
|--|-----------|-------------|----------------|--------------|----------------|--------------|
| Assemblage (and site)                                    | Total MNE | % juveniles | % prime adults | % old adults |                |              |
| <b>Gazelle</b>   |           |             |                |              |                |              |
| Late Natufian (HT)                                       | 31        | 42          | 39             | 19           |                |              |
| Early Natufian (HC)                                      | 18        | 50          | 39             | 11           |                |              |
| Kebaran (HC)   | 18        | 28          | 61             | 11           |                |              |
| Early and pre-Kebaran (MR)                               | 8         | 12          | 88             | 0            |                |              |
| Aurignacian (HC)   | 128       | ~11         | ~79            | ~10          |                |              |
| Early Upper Paleolithic (KC, all cuts)                   | 85        | 46          | 46             | 8            |                |              |
| Late Mousterian (KC, all cuts)                           | 316       | 30          | 62             | 8            |                |              |
| Early Mousterian (HC)                                    | 36        | 16          | 64             | 19           |                |              |
| <b>Fallow deer</b>                                       |           |             |                |              |                |              |
| Kebaran (HC)   | 4*        | 25          | 50             | 25           |                |              |
| Early and pre-Kebaran (MR)                               | 4*        | 0           | 75             | 25           |                |              |
| Early Upper Paleolithic (KC, all cuts)                   | 95        | 45          | 46             | 8            |                |              |
| Late Mousterian (KC, all cuts)                           | 114       | 38          | 47             | 16           |                |              |
| Early Mousterian (HC)                                    | 16        | 56          | 44             | 0            |                |              |
| Acheulo-Yabrudian, Upper (QC)                            | 24        | 29          | 71             | 0            |                |              |
| Acheulo-Yabrudian, Lower (QC)                            | 21        | 24          | 71             | 5            |                |              |
| <b>Red deer</b>  |           |             |                |              |                |              |
| Late Mousterian (KC, all cuts)                           | 40        | 18          | 55             | 27           |                |              |
| <b>Aurochs</b>   |           |             |                |              |                |              |
| Late Mousterian (KC, all cuts)                           | 46        | 20          | 67             | 13           |                |              |
| Early Mousterian (HC)                                    | 8         | 37          | 62             | 0            |                |              |
| Other Mediterranean regions (Italy, Turkey, and Lebanon) |           |             |                |              |                |              |
| Shelter site (and source country)                        | Layers    | Prey        | Total MNE      | % juveniles  | % prime adults | % old adults |
| <b>Terminal Epipaleolithic</b>                           |           |             |                |              |                |              |
| Polesini (Italy)   | 1-12      | red deer    | 784            | 33           | 51             | 16           |
|  | 1-12      | aurochs     | 19             | 0            | 95             | 5            |
|  | 1-12      | wild ass    | 111            | 25           | 59             | 16           |
|  | 1-12      | horse       | 120            | 22           | 36             | 42           |
|  | 1-12      | roe deer    | 202            | 21           | 66             | 13           |
|  | 1-12      | chamois     | 79             | 48           | 27             | 25           |
|  | 1-12      | ibex        | 13             | 0            | 85             | 15           |
| Ksar 'Akil (Lebanon)                                     | I         | fallow deer | 20             | 80           | 15             | 5            |
| <b>Epipaleolithic</b>                                    |           |             |                |              |                |              |
| Palidoro (Italy)   | 33-34     | red deer    | 10             | 20           | 70             | 10           |
|  | 33-34     | aurochs     | 7              | 29           | 71             | 0            |
| Ksar 'Akil (Lebanon)                                     | I-V       | wild goat   | 43             | 14           | 56             | 30           |
|  | II        | fallow deer | 21             | 48           | 38             | 14           |



Table 6.1 continued

| Shelter site (and source country)                  | Layers  | Prey        | Total MNE | % juveniles | % prime adults | % old adults |
|--|---------|-------------|-----------|-------------|----------------|--------------|
| Ksar 'Akil (Lebanon)                               | III     | fallow deer | 20        | 55          | 40             | 5            |
|  | IV      | fallow deer | 17        | 35          | 41             | 23           |
|  | V       | fallow deer | 33        | 48          | 42             | 9            |
| Upper Paleolithic<br>Mochi (Italy)                 | C-D     | red deer    | 22        | 27          | 64             | 9            |
|  | C-D     | ibex        | 11        | 36          | 64             | 0            |
|  | C-D     | roe deer    | 7         | 29          | 71             | 0            |
| Early Upper Paleolithic<br>Üçağızlı (Turkey)       | C-I     | roe deer    | 15        | 27          | 73             | 0            |
|  | C-I     | wild goat   | 42        | 22          | 64             | 14           |
|  | C-I     | fallow deer | 18        | 44          | 50             | 6            |
|  | B-B3    | roe deer    | 10        | 20          | 60             | 20           |
|  | B-B3    | wild goat   | 9         | 33          | 56             | 11           |
|  | B-B3    | fallow deer | 16        | 31          | 63             | 6            |
| Mochi (Italy)                                      | F-G     | red deer    | 8         | 13          | 75             | 12           |
|  | F-G     | ibex        | 5*        | 20          | 80             | 0            |
| Mousterian (Late Pleistocene through Interglacial) |         |             |           |             |                |              |
| Sant'Agostino (Italy)                              | S0-3    | red deer    | 46        | 41          | 44             | 15           |
|  | S0-3    | fallow deer | 13        | 35          | 50             | 15           |
|  | S0-3    | roe deer    | 9         | 44          | 39             | 17           |
| Breuil (Italy)                                     | Br      | aurochs     | 48        | 1           | 87             | 12           |
|  | Br      | red deer    | 42        | 0           | 71             | 29           |
|  | Br      | ibex        | 16        | 37          | 26             | 37           |
|  | B3/4    | red deer    | 18        | 55          | 44             | 1            |
|  | B3/4    | ibex        | 30        | 0           | 87             | 13           |
| Moscerini (Italy)                                  | M2-4,M6 | red deer    | 39        | 10          | 38             | 52           |
| Guattari (Italy)                                   | G4-5    | red deer    | 25        | 24          | 44             | 32           |
|  | G4-5    | aurochs     | 13        | 15          | 62             | 23           |

Notes: (Total MNE) Minimum number of dental elements that could be age-scored, right and left sides combined. (HC) Hayonim Cave; (HT) Hayonim Terrace; (KC) Kebara Cave; (MR) Meged Rockshelter; (QC) preliminary results from on-going study at Qesem Cave; (\*) sample is too small for reliable calculation. (-) The data for the Hayonim Aurignacian are estimated from Davis (1989:59); source for Kebara Cave is Speth and Tchernov (1998:231); Epipaleolithic for Ksar 'Akil from Kersten (1987); Natufian from Hayonim Cave and Hayonim Terrace from Munro (2001:294); Upper and Middle Paleolithic sites in Italy from Stiner (1990, 1994); early Upper Paleolithic from Üçağızlı Cave from Stiner (n.d.). Equid dental sequence uses the P2 rather than P4.

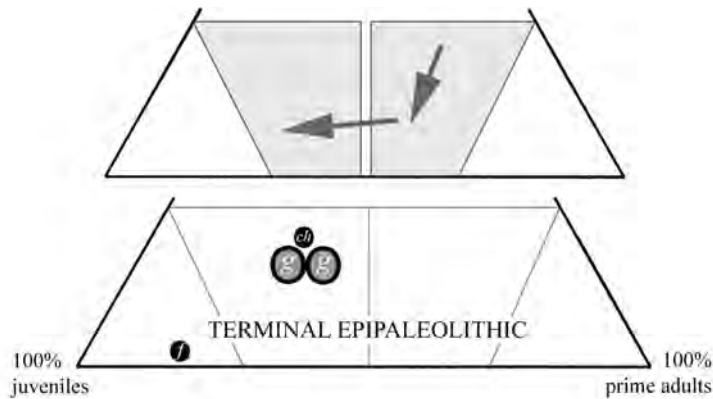
Kuhn et al. 2004; Meignen et al. 2006; Stiner 2005; Tchernov 1998), and Kebara Cave (Bar-Yosef et al. 1992; Speth and Tchernov 1998) in the Galilee. Other cases are from Riparo Mochi (Kuhn and Stiner 1998; Stiner 2005), Grotta di S'Agostino, G. dei Moscerini, G. Guattari, and G. Breuil in Italy (Kuhn 1995; Stiner 1994); Üçağızlı Cave on the Hatay coast of Turkey (Kuhn et al. 1999; Kuhn et al. 2003; Stiner n.d.); and Ksar 'Akil in Lebanon (Kersten 1987). Although equid species are present in some of these faunas, they generally are too rare for their mortality patterns to be considered. There are no major differences between the total distributions of the Epipaleolithic–Upper Paleolithic and Middle Paleolithic cases. There are no substantive differences, moreover, between the early Mousterian cases from Hayonim Cave and Speth and Tchernov's (1998; see also Speth and Clark 2006) results for the late Mousterian from Kebara Cave.

Mesopotamian fallow deer are the dominant prey animal in the upper and lower Acheulo-Yabrudian deposits of Qesem Cave (near Tel Aviv, Israel; Barkai et al. 2003; Gopher et al. 2005). The mortality patterns of the deer are consistent with mortality patterns for the later Paleolithic periods (diamond-shaped symbols in Figure 6.3) and therefore indicate that the prime-adult hunting niche pre-dates the early Mousterian. The Acheulo-Yabrudian occupants carried limb parts, in addition to many cranial elements, to the site and processed these parts with the aid of fire (Lemorini et al. 2006; Karkanas et al. n.d.). It is clear that late Lower Paleolithic hominids at Qesem Cave obtained high-quality animal tissues with some regularity.

### **Hunting Pressure in the Late Pleistocene**

The Middle Paleolithic cases in Figure 6.3 display greater total variation than those of the Upper Paleolithic do. This difference between periods might be explained by the longer duration of the Middle Paleolithic period, but it could also suggest less overall pressure on artiodactyl prey populations. The Upper Paleolithic (UP) cases in Figures 6.2 and 6.3 are positioned slightly lower on the old-age axis than the Middle Paleolithic cases, even when the cases interpreted as scavenged are excluded from consideration (MP1 in Figure 6.2). The more compressed Upper Paleolithic distribution may indicate an increase in human hunting pressure on ungulates (model c in Figure 6.1). In two-dimensional format, this distribution would correspond to a steeper age structure in which a somewhat larger proportion of individuals is taken up by younger adults or juveniles. Evidence from small-game use more clearly supports the idea that human populations were quite small prior to the Middle–Upper transition (Stiner et al. 2000). The ungulate mortality evidence on this question is far more subtle, if significant at all. This phenomenon is manifest in the Italian Paleolithic (Stiner 1994); there are no discernible trends in the *mean* values by Paleolithic period and subperiod in the Levantine sites examined by this author. However, Speth and Clark (2006) propose on the basis of a variety of indicators that mild hunting pressure obtained in the rich and detailed late Middle Paleolithic sequence at Kebara Cave, and they include mortality patterns as a critical line of evidence.

A more robust anomaly is found in the three-cohort mortality data (Figure 6.4) for the late Epipaleolithic, which display much



*Figure 6.4. Mortality patterns in artiodactyl species from Mediterranean assemblages dating to the terminal Epipaleolithic: Natufian in Hayonim Cave and Hayonim Terrace (gray infill), late Epipaleolithic Grotta Polesini (Italy), and Ksar 'Akil (Lebanon). Symbols are as in Figure 6.3.*

stronger biases toward juveniles than expected. These are the Natufian gazelle assemblages from Hayonim Cave and Hayonim Terrace (from Munro 2001), one Epipaleolithic chamois assemblage from Grotta Polesini (10 ka, Stiner 1994), and one Mesopotamian fallow deer assemblage from Ksar 'Akil (Kersten 1987). This effect is consistent with the modeled consequences of excessive hunting pressure (model d in Figure 6.1) but requires careful qualification with sex-ratio (Beaver 2006) and seasonality data (Munro 2004).

Detailed information is available for the Natufian cases, which are distinctive for their remarkable emphasis on fawns (Munro 2001; Davis 1983; Davis et al. 1994) in comparison with earlier gazelle assemblages from the Galilee. This effect in the early Natufian of Hayonim Cave does indeed seem to be explained, at least partly, by excessive hunting pressure (prediction d in

Figure 6.1). However, seasonal procurement in ethnographic contexts is also known to produce extreme juvenile biases, such as when Nunamiut caribou hunters seek out spring calves for their exceptionally soft hides (Binford 1978; Stiner 1990). But these episodes yield only a small portion of the total number of animals the Nunamiut procure in a year, and the consequences of the practice are invisible in the averaged value for this culture. Time averaging is nearly inevitable in the earlier archaeological cases, but the Natufian occupation of Hayonim is thought to represent a largely sedentary community (Bar-Yosef and Belfer-Cohen 1989; Belfer-Cohen 1988a, 1988b, 1991; Belfer-Cohen and Bar-Yosef 2000; Munro 2001). Interestingly, the adult sex ratio of gazelles in Hayonim Cave remains at about 65 percent males from the early Mousterian through the Natufian (Munro 2001, 2004; Stiner 2005).

In the case of residentially mobile foragers, a seasonal focus on juvenile prey may be evidenced at one site but not at another. Such a scenario could be proposed for the exploitation of highland chamois at Grotta Polesini in Italy, since an extreme juvenile bias is not apparent in several other artiodactyl species from the same site. The situation is less clear for Mesopotamian fallow deer in the final Epipaleolithic layer of Ksar 'Akil, although this assemblage contrasts markedly with fallow deer assemblages in all of the earlier Epipaleolithic layers also recorded by Kersten (1987).

The marked juvenile biases in the ungulate faunas of these Mediterranean series appear at about the same time as a precipitous drop in the total ungulate biomass acquired by Paleolithic foragers (Stiner 2005), not long before a transition to Neolithic or Mesolithic lifeways, depending on the region. The biomass data lend credence to the idea that the juvenile biases in some terminal Epipaleolithic cases, particularly but not exclusively the large Natufian sites in the Levant, are about more than seasonal episodes of specialized hunting. Some of these cases must signal a fundamental shift in human foraging ecology, probably linked to chronic territorial circumscription.

Comparisons of bone-fusion states across limb elements can offer detailed information on juvenile age structures (e.g., Horwitz and Goring-Morris 2001; Kersten 1987; Zeder and Hesse 2000), because element fusion follows a fixed order during development. A comparison of fusion frequencies (MNE) across six major leg elements of gazelles from Hayonim Cave (Figure 6.5) – the proximal epiphysis of the first phalanx; the distal tibia; the distal calca-

neum (tuber calcanei); the proximal head of the femur; the distal metapodials; and the distal radius (Davis 1980a) – reveals some important differences in the exploitation of juvenile mountain gazelles among the Mousterian, Kebaran, and Natufian periods. Very few fetuses or fawns occur in the Mousterian or Kebaran assemblages. The situation is quite different for the early Natufian (white area of Figure 6.5), mainly because of hunters' remarkable emphasis on very young gazelles (Munro 2004). Many of the first phalanges of gazelles from the Natufian are unfused, composed of porous immature bone, or both, indicating that a third or more of these individuals were fawns or even near-term fetuses. The early and late phases of the Natufian from Hayonim Cave and Hayonim Terrace are similar to each other, but the Natufian as a whole differs greatly from both the Kebaran and the Mousterian in terms of gazelle assemblages. Because individuals just one year older than fawns are present but not abundant in the Natufian assemblages, the emphasis on fawns cannot be explained simply by seasonal differences in site occupations.

A final look at mortality trends in the mountain gazelles uses the ratio of juveniles to adults as determined by both metapodial fusion (which occurs between 10 and 16 months of age) and the deciduous-permanent dental boundary discussed above (Figure 6.6). Data are available for a wider range of Galilee sites (Davis 1983; Davis et al. 1994; Munro 2004; Rabinovich 1998; Speth and Tchernov 1998; Stiner 2005). Davis et al. (1994) noted a gradual increase in the proportion of juvenile animals hunted with time. Davis (1981, 1983) has also argued that increased culling of juveniles

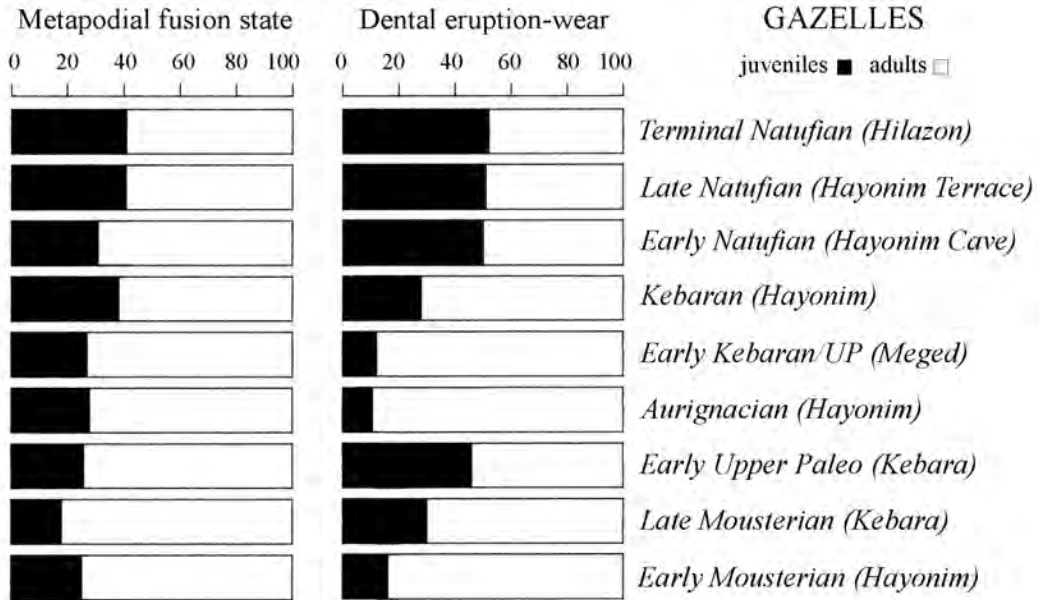


Figure 6.5. Percentages of unfused (immature) specimens for six limb elements of gazelles from the Natufian, Kebaran, and Mousterian layers of Hayonim Cave. The elements fuse over the course of 6 to 16 months, beginning with the proximal first phalanx and ending with the distal radius (Natufian data from Munro n.d.)

began early in the Natufian period as the result of the human occupations coinciding with the spring birthing peak, apparently the result of greater overall sedentism, new hunting methods, or both. The results for Hayonim Cave are in general agreement with Davis's results. The trend seems less gradual than previously described (Figure 6.6), and the proportion of juveniles is somewhat higher in the dental data than in the bone-fusion data, perhaps because milk teeth preserve better than immature bone does, but the results from bone fusion and dental replacement are similar.

There seems, then, to have been a net increase in juvenile off-take with time, con-

sistent with the observations of other authors working in the Galilee (Davis et al. 1994; Munro 2001; but see Bar-Oz et al. 1999). Though these changes may have begun with slightly increased exploitation of yearlings during the Kebaran, a conspicuous number of fawns or very young juveniles had been added to the death assemblages in the Natufian. The trend toward greater exploitation of young animals could be the result of increased harvesting intensity. All told, the early Middle Paleolithic pattern represents the lightest effect on mountain gazelle populations, and the Natufian, the severest. In addition, gazelles became progressively more important than other ungu-

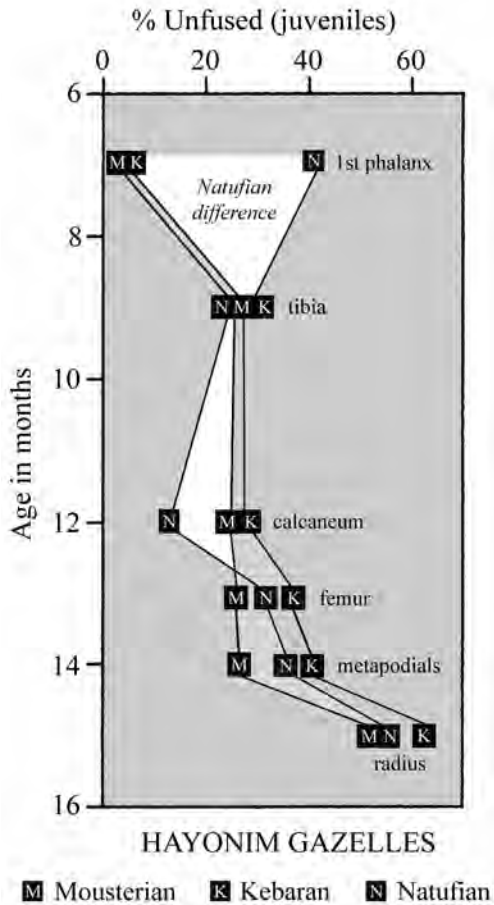


Figure 6.6. Trends in ratios of juvenile to adult gazelles for the Early Mousterian through Terminal Natufian periods at various Galilee sites, based on metapodial fusion and dental eruption and wear data.

lates in the Galilee region (Speth and Clark 2006; Stiner 2005).

### Concluding Discussion

The mortality patterns of artiodactyl prey in Paleolithic cave sites speak to questions about the hunting capabilities of early

humans and the early development of prime-age-focused hunting, a uniquely human predator-prey relationship. The methods employed in this study ensure that the patterns were not substantially biased by poor preservation or analytical oversights. Human emphasis on prime-adult prey was, in fact, geographically and temporally widespread from the Middle Paleolithic through Holocene periods. The Acheulo-Yabrudian assemblages from Qesem Cave extend the history of this niche characteristic back to at least 200,000–400,000 years ago, at least in the Levant. Just how pervasive the behavior was in the Lower Paleolithic of other Old World regions remains to be understood. Comparisons to the earliest archaeofaunas of East Africa, for example, are hampered by the low incidence of head parts in many cases, which in itself may testify to important differences in predatory tactics in earlier phases of the Lower Paleolithic (see Brantingham 1998; Bunn and Kroll 1986; Klein 1999:243; Potts 1984). Given what is known at present, other transitions in predator niche are expected between 1 million and 500,000 years ago. Testing the idea awaits, however, the discovery of large, well-preserved assemblages of the right periods.

What are the behavioral implications of prime-dominant mortality patterns in artiodactyl ungulates? Humans' place in large-predator guilds seems to have been shaped long ago by periodic competition with large carnivore genera such as *Panthera*, *Lupus*, *Lycaon*, and *Crocuta*, well before the early Mousterian. This aspect of predator-niche segregation is surprisingly consistent across ecosystems and culture periods, wherever and whenever humans, big cats, canids, and hyenas have coexisted.

More remarkable still is the fact that prime-focused hunting evolved long before stone- or bone-tipped hunting weapons came into regular or widespread use. The earliest hunting technology for capturing large hoofed animals seems to have been confined to hand-held wooden lances (e.g., Thieme 1997). Though elegantly crafted in some cases, the very simplicity of these weapons underscores the fundamental and necessary role of cooperation among hunters. Cooperation allows predators such as lions, wild dogs, wolves, and spotted hyenas to bring down prey whose body weight greatly exceeds that of the individual hunter.

Of course, mortality patterns tell us only so much about hominid behavior and ecology. Mortality patterns are largely about prey choice as mediated by a predator's "approach" to live quarry – whatever it takes to contact, grab, and overwhelm it. Other zooarchaeological data tell us that Middle Paleolithic hominids maintained exceptionally narrow diets – at least where meat was concerned – that centered on large herbivores (Stiner et al. 2000). Meat supplements to this diet were confined to easily gathered small animals, such as tortoises or shellfish, in contrast to later cultures of the region (Klein and Scott 1986; Stiner 1994, 2005). Hominid diets began to broaden with the MP-UP transition roughly 45–50,000 years ago. This development may coincide with the earliest indications of hunting pressure on large game, but more studies are needed. Certainly, the Mousterian samples are the most variable overall with respect to the old-adult age axis, suggesting that artiodactyl populations had ample recovery times. Prime-age-focused hunting might have begun reducing the mean age at first repro-

duction in prey populations sometime in the Upper Paleolithic, but this is less clear. In the central Levant, only the Epipaleolithic associates *conspicuous* increases in human population densities with greater pressure on ungulate resources. Analogous developments may be evidenced around the time of the Pleistocene–Holocene boundary in certain other Mediterranean regions, although the necessary background data are less complete.

Prime-focused ungulate hunting can be a relatively fragile predator–prey relationship, because human hunters disproportionately seek adults. Prime-age-focused hunting is ecologically complementary to the patterns of prey age selection by cursorial predators and, to a lesser extent, to those of nonhuman ambush predators. However, habitual prime-focused ungulate hunting may be feasible only for omnivorous predators, who can switch to other foods when the densities of favored prey decline (Stiner 1994; Winterhalder and Lu 1997).

Subtle age compression of ungulate populations during the Upper Paleolithic does not indicate a high risk of extinction. It merely suggests that human hunters were a major source of mortality for these ungulate populations and that hunting was sufficiently heavy to push populations into growth mode for greater lengths of time. The strong juvenile biases in the late Epipaleolithic Mediterranean cases are exceptional by contrast, and they occurred around the same time as a precipitous drop in total ungulate biomass acquired. The biomass data lend credence to the idea that radical shifts in human ecology took place around this time, perhaps resulting ultimately in the demise of Paleolithic hunting and gathering ways of life in some areas.

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