

Carnivory, Coevolution, and the Geographic Spread of the Genus *Homo*

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This review traces the colonization of Eurasia by hominids some 1,700,000 years ago and their subsequent evolution there to 10,000 years ago from a carnivorous perspective. Three zooarchaeological trends reflect important shifts in hominid adaptations over this great time span: (1) increasing predation on large, hoofed animals that culminated in prime-adult-biased hunting, a predator-prey relationship that distinguishes humans from all other large predators and is a product of coevolution with them; (2) greater diet breadth and range of foraging substrates exploited in response to increasing human population densities, as revealed by small-game use; and (3) increased efficiency in food capture, processing, and energy retention through technology, and the eventual expansion of technology into social (symbolic) realms of behavior. Niche boundary shifts, examined here in eight dimensions, tend to cluster at 500 thousand years ago (KYA), at 250 KYA, and several in rapid succession between 50 and 10 KYA. Most of these shifts appear to be consequences of competitive interaction, because high-quality, protein-rich resources were involved. Many of the boundary shifts precede major radiations in the equipment devoted to animal exploitation. With a decline in trophic level after 45 KYA, demographic increase irreversibly altered the conditions of natural selection on human societies, from a largely interspecific competitive forum to one increasingly defined by intraspecific pressures. Regionalization of Upper Paleolithic artifact styles is among the many symptoms of this process.

KEY WORDS: carnivory; colonization of Eurasia; hominid evolution; Paleolithic; zooarchaeology.

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INTRODUCTION

Predation is a many splendored thing—so much so that only a few overarching generalizations can reasonably be made about the carnivorous habits of larger mammals. It is the multidimensional nature of predatory adaptations in general that promises insights on the evolutionary history of human beings in particular. Hominids evolved into large-game (ungulate) hunters of some sort by at least the late Middle Pleistocene. Their relationships with prey populations nonetheless were tempered by the availability and digestibility of a wide range of other foodstuffs. We can be sure as well that these early hunters differed from recent hunter-gatherers in a number of important ways.

Hominids colonized two new continents and many more ecosystems by 1.5 million years ago (MYA), an interesting forum for examining the role of carnivory in human evolution. Colonizing populations experienced true winter in northern Eurasia and, during that season, encountered fewer plant and animal species on which to subsist. These hominids also came into contact with new kinds of meat eaters and large-bodied omnivores, the latter of whom may have competed for not only meat but also energy-rich plant parts. Here I review some of the dimensions of carnivory most relevant to paleoanthropological research and then discuss changes in Middle and Late Pleistocene hominid predatory behavior primarily from a zooarchaeological perspective. Hominid taxonomic terms are avoided as much as possible, since most of the evidence for carnivory does not occur in the same sedimentary contexts as classifiable hominid skeletal remains. Suffice it to say, Middle Pleistocene and later hominid populations should have had high dispersal capabilities just to keep themselves in food and thus considerable opportunity to exchange genes (*sensu* Wobst, 1974; for another large-bodied predator, Wayne, 1993).

This review capitalizes upon my experience with Paleolithic faunas of the northern and eastern Mediterranean Basin (Fig. 1), supplemented extensively by the knowledge gathered by other researchers. Direct observations are worth thousands of words when it comes to the taphonomic issues surrounding early sites, and here is an opportunity to make some global points with something other than the usual examples. My view is interspecific and population-oriented. It gives equal press to small and large game, as well as to the pre- and postacquisition behaviors associated with meat eating. The ultimate challenge is to understand how human carnivory and its evolution were conditioned by the use of plant resources. There will be no direct answers to this question, but one may glimpse through zooarchaeological data some of the rules by which ancient consumers shifted among resource classes, and perhaps even some social dimensions of time allocation, land use, and ways of managing risk through social networks and technology. Although these aspects of human existence changed tremendously over the course of the Pleistocene, surprisingly mundane aspects of subsistence are responsible for increasing the carrying capacity of some environments occupied by human ancestors. These behaviors also had consequences for children's nutrition

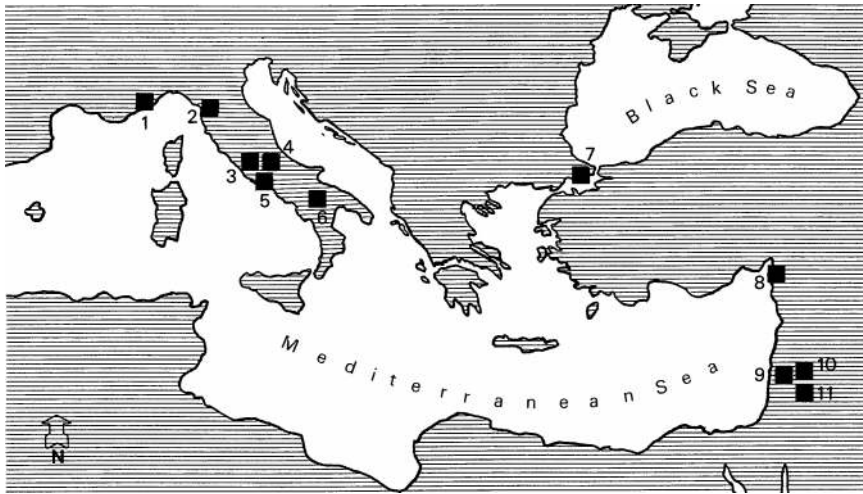


Fig. 1. Locations of Mediterranean sites mentioned in text: 1 – Grimaldi Caves in the Balzi Rossi (Italy), including Riparo Mochi; 2 – Buca della lena and Grotta di Gosto (Italy); 3 – Torre in Pietra, Castel di Guido, Polledrara, Rebibbia-Casal de’Pazzi, Grotta Polesini; all northeast of Rome (Italy); 4 – Fontana Ranuccio and Isernia (Italy); 5 – Monte Circeo and Gaetan coastal sites (Italy), including Grotta Breuil, Grotta Guattari, Grotta di Sant’Agostino, Grotta dei Moscerini; 6 – Venosa, Basilicata (Italy); 7 – Yarımburgaz Cave near Istanbul (Turkey); 8 – Üçagizli Cave, Hatay (Turkey); 9 – Hayonim Cave and Kebara Cave in western Galilee (Israel); 10 – Gesher Benot Ya’aqov and Ubeidiya, Jordan Valley (Israel); 11 – Qafzeh Cave, Jezrael Valley (Israel).

and survivorship, rates of individual contact and interaction, and the potential for spreading or pooling resource risk. Only a fraction of these behaviors have analogs among modern nonhuman primates, an observation essential for modeling the evolution of carnivorous behavior in hominids.

I begin by exploring the nature of human carnivory relative to other living primates and then review the archaeological and paleontological evidence of hominid colonization and adaptations in Eurasia. Three trends in particular are exposed by the faunal record: (1) niche diversification among ungulate predators; (2) small game use and its ramifications for paleodemography; and (3) the expanding roles of technology in Paleolithic cultures. The final section of this review focuses on the apparent shift from interspecific to largely intraspecific forums of evolution and its effects on human existence in eight niche dimensions.

A WORKING DEFINITION OF CARNIVORY

Modern humans cannot serve as direct models for extinct hominids. Neither can other living species. However, comparisons of living species that seek predictable relations among behavioral and/or physical traits and common responses to environmental variation can yield useful models. Two very different sources

of information have revolutionized research on Paleolithic subsistence and the evolution of predatory behaviors among hominids. The first of these is the wildlife literature on nonhuman primates (see Isaac, 1978; Rose and Marshall, 1996; Tooby and DeVore, 1987) and various members of the order *Carnivora* (see Binford, 1981; Blumenschine, 1986; Blumenschine *et al.*, 1994; Brain, 1981; Kortlandt, 1965; Schaller and Lowther, 1969; Stiner, 1990, 1991a; Turner, 1984). Although some researchers may feel obliged to dismiss nonhuman primates for the purposes of modeling human evolutionary processes, or alternatively to dismiss carnivores, it is likely that we need to consider both.

Nonhuman primates provide a wealth of information about primate-style predation (Boesch and Boesch, 1989; Butynski, 1982; Hamilton and Busse, 1978; Harding, 1973, 1974; Harding and Strum, 1976; Hausfater, 1976; Morris and Goodall, 1977; Stanford, 1995; Stanford *et al.*, 1994; Strum, 1981; Wrangham, 1977), social and communication systems (de Waal, 1989; King, 1994), and some of the circumstances in which simple tool use behavior may have evolved (e.g., Boesch and Boesch, 1984; McGrew, 1987, 1992; Teleki, 1974; Wynn and McGrew, 1989). Information on the carnivores—canids, felids, hyaenids, and ursids—is equally critical, because, although these mammalian lineages are only remotely related to humans, they are close neighbors in the food web. Thus the relevance of the nonhuman primate literature for modeling aspects of hominid evolution is assured by the close phylogenetic history we share with them. Information on the carnivores instead provides a backdrop for investigating why certain dimensions of hominid predatory niches expanded and shifted as they did through time. This backdrop clarifies the probable circumstances of hominids' ecological divergence from the primates as a group, including the competition that hominids likely faced when acquiring animal resources and, equally important, their ways of maximizing the nutritional yields of those resources.

A second, distinct area of information that has enlightened Paleolithic research is the faunal record reexamined through the lens of taphonomy. Though not the focus of this presentation, taphonomic data testify to considerable resource overlap between hominids and large carnivores in their need for ungulate (hoofed) prey, shelter, and foraging territory. Most ungulates weigh more than the human beings, hominids, or carnivores that have hunted them, and therefore represent enormous concentrations of complete protein and (often) fat. Common interest in these high-quality resources is one of the most likely forums for periodic competition in the animal world and likely shaped the evolutionary histories of all large predators (e.g., Binford, 1981; Foley, 1984; Potts, 1984; Stiner, 1990, 1994; Turner, 1992; Van Valkenburgh, 1989).

How Unique Are Human Beings?

From the viewpoint of nonhuman primates, human predatory behavior is nearly unique (Stiner, 1993a). Some terrestrial monkeys and apes are known to

hunt vertebrates, and a few primate species consume mammals in appreciable quantities (e.g., Boesch and Boesch, 1989; Stanford *et al.*, 1994). Nonhuman primates that hunt generally avoid prey that approach or exceed the size of their own bodies (McGrew, 2001; Rose, 2001; Stanford, 2001). Baboons' and chimpanzees' methods of processing game are inefficient in comparison to those of many members of the order Carnivora, as well as to recent human beings—at least for carcasses that are too large, and bones too robust, to be eaten whole. In stark contrast to modern nonhuman primates, humans and many carnivores frequently (a) cooperate in the care and stashing of infants, (b) transport food over long distances, (c) cache food, (d) share food well beyond the boundaries of propinquity, and (e) systematically process large bones for the soft tissues they enclose. The predatory behaviors of nonhuman primates have absurdly few dimensions if compared to the ways of wolves, wild dogs, spotted hyenas, and certain other carnivores. The interactions fostered by predation among chimpanzees and baboons are interesting, perhaps especially for their social implications, but they do not explain many of the postacquisition behaviors that have evolved among hominids during the Paleolithic nor, for that matter, recent humans' remarkable compatibility with carnivorous pets.

Many of the behavioral differences among predators are about processing, monopolizing, and in some cases sharing of animal resources. The foraging models of population ecology formalize these observations by considering both search and handling costs in equations of risk and gain (e.g., Maynard Smith, 1974; Pianka, 1978; Stephens and Krebs, 1986). Yet even these elegant approaches have only begun to touch upon how much predators differ in their techniques for extracting food value from prey. Barring processing costs, most modern predators are as interested in the soft tissues inside bones as they are in the external tissues. Some species are just better at getting at bone-locked nutrients, thanks in large part to hyperdeveloped dentitions (e.g., Van Valkenburgh, 1989; Van Valkenburgh and Hertel, 1993). Cats, for example, excel at soft tissue feeding (Kitchener, 1991; Leyhausen, 1979), at least where large prey are concerned, whereas hyenas readily transport, consume, and digest large bones in quantity (Kruuk, 1972; Sutcliffe, 1970). The procedures for extracting bone-locked yellow marrow, red marrow, or brains are time consuming, and some predators will move prey parts over long distances just to reduce the risk of interference and gain processing time. One of the most striking aspects of early hominid foraging behavior was the tendency to reconcentrate food and stone tools in space (Isaac, 1978, 1984; Potts, 1984; Toth, 1987), transporting meat or bones in lieu of defending them at acquisition sites. The scale of this behavior, as measured by the density of archaeological concentrations, increased by at least one order of magnitude from the Early to Late Pleistocene, suggesting radical restructuring and increasing sizes of consumer groups.

If a balanced consideration of predation behavior must include what transpires before and following the death of a prey animal, it also begs consideration of density-dependent effects (Pianka, 1978, p. 199). Exploitation of prey by social predators can be quite open-ended, for example, allowing participation of

individuals in several capacities, provided the species exists at relatively high densities and prey are large enough to permit group feeding. Food dispersion reduces the rates of intraspecific and interspecific contact, as well as any potential benefits of sharing food, as it raises the costs of searching for and transporting food (Stiner, 1991a). Hominid population densities certainly increased in some regions and periods (Ambrose, 1998b; Binford, 1999; Klein, 1989; Relethford, 1998; Sherry *et al.*, 1994; Stiner *et al.*, 1999), and this must have influenced the need for controlling the outcomes of personal interactions, food availability, and hominids' potential for degrading key elements of their food supply (see also Layton *et al.*, 1991; Winterhalder and Goland, 1993; Winterhalder and Lu, 1997). Let us now turn to the last one-plus million years of archaeofaunal evidence for hominid game use with an eye to Eurasia.

ECOLOGIC BACKGROUND, 2.5–1.5 MYA

African hominids began eating flesh from large herbivores more than 2 MYA, and some investigators infer a strong evolutionary link between hominid brain expansion and increased carnivory (Aiello and Wheeler, 1995). Meat from large mammals may first have been obtained by scavenging carcasses at natural death sites and robbing other predators of their kills (e.g., Binford, 1981, 1987; Blumenschine, 1986; Blumenschine *et al.*, 1994; Bunn and Blumenschine, 1987; Bunn *et al.*, 1980; Isaac, 1984; Isaac and Crader, 1981; Potts, 1984; Shipman, 1986). Some hunting of smaller prey also seems likely on ecological grounds, since it is widespread among modern terrestrial primate species, as a supplement to tubers and nuts (Sept, 2001). However, much of the early evidence (> 1 MYA) of hominid-modified bone involves large mammals (Bunn, 1981; Potts and Shipman, 1981), species that would have been challenging to kill with Oldowan or early Acheulean technology. The fact that some of the same or spatially associated prey bones were modified by large carnivores suggests that hominids put themselves at risk to obtain ungulate parts (Bunn, 1981; Potts, 1984).

Large cats, hyenas, and canids were well established in the African ecosystems where hominids first introduced themselves to the virtues of large-game products (Binford, 1981; Blumenschine *et al.*, 1994; Brantingham, 1998; Bunn *et al.*, 1980; Isaac, 1978, 1984; Isaac and Crader, 1981; O'Connell *et al.*, 1988; Potts, 1984; Rose and Marshall, 1996; Shipman, 1986; Speth, 1989; Tappen, 1995). Hominids eventually invaded novel predator guilds of Eurasia as well (Arribas and Palmqvist, 1999; Martínez-Navarro and Palmqvist, 1995, 1996; Palmqvist *et al.*, 1996; Stiner, 1990, 1994; Turner, 1984, 1986, 1992; Van Valkenburgh, 2001). Ecologically, these are remarkable developments, since "guilds" founded on high-stakes resources such as ungulate prey are thought to be major arenas of coevolutionary change, even under relatively stable environmental conditions (compare Ehrlich

and Raven, 1964; Jaksic, 1981; Pianka, 1978; Root, 1967; Schoener, 1974, 1982; Van Valkenburgh, 1989). The paths by which Pleistocene hominids invaded these guilds are subjects of intense investigation, in recognition that ungulate tissues became increasingly important resources to hominids thereafter.

Carnivory and hominids' colonization of Eurasia more than 1.5 MYA are best considered in community context, for, although these were unique developments in human evolutionary history, hominid populations were not alone in their expansions north- and eastward. Turner (1984, 1992) and Tchernov (1981, 1992, 1994) argue that early hominid incursions in Europe and Asia around the Early–Middle Pleistocene boundary were made possible by climate change and major turnover in the membership of animal communities. Recent paleontological finds in Spain, Italy, Georgia, and China suggest a late Lower Pleistocene date of entry for hominids, accompanied by a suite of large mammals that included the primitive hyena, *Pachycrocuta brevirostris*, and the saber-toothed cat, *Megantereon whitei* (Arribas and Palmqvist, 1999; Martínez-Navarro and Palmqvist, 1995).

It has been suggested more than once that warm periods in the earth's climate history (oxygen isotope stages 5, 7, 9, 11, 15, and 19, following Shackleton and Opdyke, 1973) were also the times of greatest penetration into the northern reaches of Europe and Asia by early hominids (e.g., Gamble, 1995; Turner, 1984). In Italy, Germany, and the southern British Isles, warmth-loving hippopotami spread into river valleys with each interglacial (Blanc, 1937; Stuart, 1982), then retreated south with the return to glacial conditions. Crucial ecological differences among subtropical species can be seen from which populations withdrew from northern fringes of their range as climate deteriorated and which did not. Oddly, hominids and spotted hyenas stayed put. The extinction of several archaic carnivores (Eisenberg, 1981; Turner, 1986) apparently left room for new niches in Eurasia, soon filled by spotted hyenas (*Crocuta*), hominids, and other versatile opportunists.

Successful colonization of Eurasia by African hominids likely hinged on their ability to obtain flesh (see also Foley, 2001), since access to plant foods is intensely seasonal throughout much of temperate and periglacial Eurasia. As omnivores, however, hominids were not simply joining the ranks of Eurasian flesh eaters—also present in Eurasia were two groups of large-bodied omnivores, bears (*Ursus*) and pigs (*Sus*). The ecological links between humans, pigs, and bears may always have been weak (e.g., Stiner, in press), because all are dietary generalists (*sensu* Cachel and Harris, 1998; Foley, 1984; Pianka, 1978, pp. 253–256) that normally switch to alternative food types when the abundance of a preferred type declines. Winter food scarcity is a particular problem for omnivores, once the ground is concealed by snow, plants have withered, and the autumn glut of fruits and nuts has already been consumed. Brown and black bears cope with this hiatus in food availability by piling on remarkable amounts of body fat in autumn and hibernating through winter. Interestingly, bears may depend upon scavengable meat most in spring, as winter-killed carcasses emerge from snow melt and

when plant growth is limited and calorie-poor (Clevenger and Purroy, 1991). Pigs also store subcutaneous fat in preparation for winter, when the remnants of their food supply lie under ground or snow, although they continue to dig out whatever they can. Hominids could not have bypassed the problem of winter food limitations, as they clearly lack the physiological requirements for hibernation. One likely solution was greater carnivory, particularly that involving large mammals, that also would have brought them into periodic competition with social canids (wolves and wild dogs), spotted hyenas, and large cats (leopards, lions, and tigers).

COLONIZATION OF EURASIA

The earliest occupations of Europe and Asia by premodern *Homo* are incompletely known, and virtually every discovery constitutes a surprise. The history of colonization nonetheless reveals a coarse distinction between earliest hominid presence in lower latitude areas of Eurasia and occupations of the north. The glacial and steppic conditions of northern Eurasia, particularly the rigors of subzero temperatures, no doubt explain why hominids were late in penetrating cold-temperate and subarctic environments, although they eventually succeeded at even this. Several questions about the colonization process can be addressed with available archaeological and human fossil evidence:

1. When did premodern humans first arrive in Eurasia?
2. How permanent were these early incursions in relation to glacial–interglacial cycles (the problem of “effective latitude”)?
3. How far north did these incursions extend?
4. How did the colonizing hominid populations cope with winter? Specifically, what role did carnivory play in subsequent adaptations to environments that experience winter?

Western Asia is assumed to have been the bridge by which populations of *Homo ergaster* expanded from Africa. Because temperature ranges there were not very different from those to which hominids were already accustomed (Tchernov, 1992), their spread across southern Asia may have been rapid (Foley and Lahr, 1997; Klein, 1989).

Early hominid populations in Eurasia were thinly spread such that our perceptions of their presence are minimal prior to about 0.5 MYA. The oldest archaeological horizons outside Africa occur over the entire length of southern Europe and Asia. Ubeidiya in the Jordan Valley of Israel (Stekelis, 1966) dates to about 1.4 MYA (Bar-Yosef and Goren-Inbar, 1993; Tchernov, 1981, 1994). The Dmanisi hominid fossils from Georgia in the Caucasus may be as old as 1.7 MYA (Gabunia and Vekua, 1995; Gabunia *et al.*, 2000). Of course, early hominid fossils (*H. erectus*) also are known from river deposits of what was once

mainland Southeast Asia (Java), dating between 1.0 and 1.7 MYA (Sémah *et al.*, 2000; Swisher *et al.*, 1994), and possible early artifacts (>1.9 MYA) are reported from Riwat in Pakistan (Dennell, 1998; Dennell *et al.*, 1988). Hominid fossils of roughly similar form and antiquity occur in southern Europe (Gibert, 1992; Gibert *et al.*, 1994; Mallegni, 1992), as do early artifact assemblages (e.g., Oms *et al.*, 2000). Although attempts to establish the antiquity of these sites are troubled by a number of technical concerns, one cannot escape the sense that hominid populations ventured from Africa quite early, not long after the first appearance of the genus *Homo* as presently classified by human paleontologists, and perhaps by more than one geographic route. Once the process was set in motion, hominids quickly spread throughout southern Eurasia.

Several authors in Roebroeks and van Kolfschoten's edited volume, *The Earliest Occupation of Europe* (Roebroeks and van Kolfschoten, 1995a), document the concentration of fossils and artifacts in the lower latitudes of mainland Europe and Asia prior to 500 thousand years ago (KYA). Fossils and artifacts dating to the early Middle Pleistocene have been found in Spain (Carbonell *et al.*, 1995; Carbonell and Rodriguez, 1994; Parés and Pérez-González, 1995; Raposo and Santonja, 1995; Villa, 1991), Italy (Ascenzi *et al.*, 1996; Mussi, 1995; Piperno, 1992; Villa, 1991), southeast and east-central Europe (Bosinski, 1995; Valoch, 1995), and the Balkans (Darlas, 1995; on Dmanisi, see Gabunia and Vekua, 1995; Ljubin and Bosinski, 1995). In Italy, where the paleontological and archaeological records are generally rich (Barker, 1981), hominid presence is weakly registered prior to about 450 KYA (Palma di Cesnola, 1996; Piperno, 1992), but a few earlier sites are known. Isernia la Pineta is said by some investigators to be as old as 700,000 years (Peretto, 1991, 1992, 1994). Ceprano is the source of a late *Homo erectus* calvarium >700,000 years (Ascenzi *et al.*, 1996), and certain other sites lacking fauna may prove to be older still (e.g., Monte Peglia and Monte Poggiolo; Piperno, 1992), the pitfalls of using Oldowan-like artifacts as type fossils notwithstanding (Arribas and Palmqvist, 1999). Coeval and older examples are known from adjacent areas of western Asia, at Ubeidiya (<1.4 MYA; Bar-Yosef and Goren-Inbar, 1993; Tchernov, 1981, 1992) and Gesher Benot Ya'aqov (600–700 KYA; Goren-Inbar, 1992).

Most early hominid fossils in Eurasia are highly fragmentary and usually occur in water-lain sediments, often in association with taxonomically diverse faunas (e.g., Mallegni, 1992, 1996; Manzi and Passarello, 1989; Radmilli, 1984; Segre and Ascenzi, 1984; Tagliacozzo, 1992). Notable exceptions may be some of the recently discovered sites in the Orce Basin of southern Spain (Gibert, 1992; Gibert *et al.*, 1994; Martínez-Navarro, 1991; Raposo and Santonja, 1995; Tixier *et al.*, 1995; but see Palmqvist, 1997). The earliest unambiguous cases in Germany instead date to about 350–400 KYA (Mania, 1995), southern Britain to 500 KYA (Roberts *et al.*, 1995), and north-central Europe to about 600 KYA or less (Tuffreau and Antoine, 1995). Scandinavia was not part of hominids' world until the late Upper Paleolithic at the earliest (Holm and Larsson, 1995).

Roebroeks and van Kolfschoten (1994, 1995b) are extreme in their claim that the first reliable traces of hominids appear only after 500 KYA in Europe. However, it is true that cases older than this age are remarkably few and lie closer to the lands bridging Asia and Africa, where we expect to find them. Taken together these observations suggest that hominids were neither abundant nor well established in animal communities above about 50° N latitude prior to 500 KYA (Dennell, 1983; Dennell and Roebroeks, 1996). Their apparent absence from high-latitude environments is paralleled by their absence from high elevations at lower latitudes. Steinheim in Germany and Zhoukoudian in northeastern China pose interesting exceptions to the first observation; however, Steinheim is thought to date to a short interglacial phase (Weinert, 1936), and the cultural layers of Locality 1 of Zhoukoudian range anywhere between 500 and 200 KYA (reviewed in Weiner *et al.*, 1998). One must also recognize that a few seemingly exceptional cases are bound to arise, quite independently of what climate extremes early hominids were able to withstand, due to relatively poor time resolution for the Lower Paleolithic and repeated climate oscillations over this great span of time.

By 500 KYA hominids clearly were able to survive in a wide variety of northern habitats despite the climatic severity of some (Roebroeks *et al.*, 1992; Rolland, 1998). Fire was almost certainly a part of late Lower Paleolithic technology and may have enhanced hominids' ability to survive Eurasian winters. Oddly, solid cases for controlled use of fire before 250 KYA in Eurasia are very few, although fire features as old as 350 KYA may exist at Vertesszollós (Kretzoi and Dobosi, 1990). Unambiguous hearth areas dating to roughly 170–200 KYA are abundant and well preserved in Hayonim Cave, however (Fig. 2) (e.g., Stiner *et al.*, 2001b).



Fig. 2. Layer upon layer of wood ash lenses preserved in early Mousterian deposits of Hayonim Cave, ca. $\leq 200,000$ years before present.

Evidence for fire features in coeval and older layers of Zhoukoudian Cave in China is less clear-cut than previously thought, since some burned bones are present but wood ash and charcoal are lacking (Binford and Ho, 1985; Weiner *et al.*, 1998). It is strange that traces of fire are common in archaeological records only by the later Middle Paleolithic (e.g., Meignen *et al.*, 1989, in Kebara Cave, Israel; Stiner, 1994, pp. 46–53, in Grotta dei Moscerini, Italy), becoming a regular part of Middle and Upper Paleolithic peoples' lives thereafter (cf. James, 1989).

A Closer Look at Italy, Israel, and Turkey

After 500 KYA, traces of early hominids on the Italian peninsula are fairly common. The spatial associations between artifacts and animal bones in the earliest sites, most of which occur in open fluvial, lacustrine, or marsh deposits, are difficult to interpret (cf. Anzidei *et al.*, 1984; Caloi and Palombo, 1978, 1988; Cassoli, 1978; Cassoli *et al.*, 1993; Piperno, 1992; Tagliacozzo, 1992). In fact, the great majority of them are better classified as localities than archaeological sites. Especially peculiar about the early cases that preserve bone is the relatively high frequency of megafauna remains in conjunction with the simplest of stone tools. The fauna of Isernia, for example, contains in descending order of abundance *Elephas (Paleoloxodonta) antiquus*, *Dicerorhinus hemitoechus*, *Bison* sp., *Ursus deningeri*, *Hippopotamus amphibious*, *Megaceros* sp., *Sus scrofa*, *Hemitragus* sp., *Dama* sp., and *Panthera leo*. Few of these taxa are within the normal prey body size range favored by modern hunter-gatherers possessing far better equipment (compare Kelly, 1995; Kuhn and Stiner, 2001). Fontana Ranuccio, the earliest cultural layers of which are potassium-argon-dated to 458 KYA, contains small clusters of artifacts within a monumental scatter of bones (Biddittu *et al.*, 1979). This bone bed is rich in megafauna, ungulates, carnivores, and diverse small vertebrates, along with a few hominid skeletal fragments (Segre and Ascenzi, 1984). Venosa (Notarchirico), which dates to about 500 KYA (Belli *et al.*, 1991), also contains elephant and red deer (*Cervus elaphus*) bones in general association with stone tools (Cassoli *et al.*, 1993; Piperno, 1992, pp. 167–169; Piperno *et al.*, 1990). Casal de'Pazzi (ca. 200 KYA; Anzidei *et al.*, 1984; Bietti, 1985; Passarello *et al.*, 1984/1985), Castel di Guido (Radmilli *et al.*, 1979), and Torre in Pietra (Blanc, 1958; Caloi and Palombo, 1988) are thought to be somewhat younger on the basis of geological evidence, but they are similar with respect to the prevalence of megafauna and large ungulates among the faunal remains. The examples from Italy resemble those from Middle Pleistocene open settings elsewhere in Europe (e.g., Gaudzinski and Turner, 1996) and western Asia (Bar-Yosef, 1994; Tchernov, 1992).

Arguing that hominids had a great deal to do with the formation of many of these Middle Pleistocene bone accumulations is an awkward stretch. Some of the bone beds are vast, yet contain minuscule to modest numbers of stone

artifacts. Some artifacts and bones were rolled by water or polished by waterborne sands and silts; others lying beside them were not (see also Villa, 1991). The water-lain context of these early sites likely is an important key to understanding the circumstances of assemblage formation. Elephants, hippos, and to some extent rhinos have high water requirements for drinking and wallowing. In compromised health, these animals gravitate to permanent water, where they also may die, generation after generation (Haynes, 1991). Thus the megafaunal bone aggregations at the Middle (and some Late) Pleistocene localities may best be explained by the behavioral ecology of megafaunal species and could have accumulated in a manner that was largely independent of hominids' foraging interests.

My and others' analyses (Caloi and Palombo, 1978; Cassoli, 1978; Segre and Ascenzi, 1984) of the faunas from Fontana Ranuccio and Torre in Pietra indicate that a remarkably diverse range of vertebrate body sizes are represented. A few of the medium-sized and smaller ungulate bones display traces of marrow processing, probably but not certainly made by hominids; other items were gnawed by large or small carnivores, and some were rolled by water and abraded by waterborne sediments. A wide range of biological and geological agencies clearly contributed to the bone concentrations, and accumulation histories were protracted and complex. Hominid components at these localities generally are thin, localized overlays on a larger paleontological background. That hominids may occasionally have helped giant mammals to their deaths, or scavenged their carcasses, is possible or even likely at some localities in Italy and elsewhere (compare Callow, 1986; Gaudzinski and Turner, 1996; Mania, 1995; Santonja and Villa, 1990; Scott, 1986a,b; Villa, 1990, 1991). The argument that early hominids regularly hunted giant mammals is not well supported by the available evidence. More to the point, it is very unlikely that hominids added significantly to the mortality factors that operated on megafauna populations of this period.

One strange but certain connection between artifacts and elephant remains exists in a few of the Italian cases, due to hominids' deliberate working of elephant cortical bone fragments into large bifaces and unifaces (Villa, 1991). At Castel di Guido more than 100 unambiguously worked specimens were found (Radmilli, 1984), and one bifacially worked specimen was recovered at Fontana Ranuccio (Segre and Ascenzi, 1984). The elephant bone fragments were flaked as if they were stone, quite unlike the bone-working techniques of the Upper Paleolithic.

After about 250 KYA the archaeological record of early humans expands to a more diverse array of settings, and faunal associations undergo some distinct shifts. Here we are essentially into the times of what some paleontologists call archaic *Homo sapiens* and others call *Homo helmei* (Foley, 2001). The late Middle Pleistocene was a volatile phase in the evolutionary history of humankind, marked by considerable encephalization. Archaeofaunal assemblages are more clearly

centered on ungulates, contain many fewer megafaunal remains, and, in many cave sites, intercalate with large carnivore den occupations.

Cave sites are not a major part of Lower Paleolithic records, at least not until quite late, but cave sites are very much a part of the Middle Paleolithic record, beginning about 200–250 KYA in western Asia and Europe. What hominids were doing in these caves is another matter (Brugal and Jaubert, 1991; Gamble, 1986; Stiner, 1991b, 1994; Straus, 1982). In Yarimburgaz Cave in Turkey (ca. 250,000, Arsebük and Özbasaran, 1994; Farrand, 1992; Farrand and McMahon, 1997; Howell and Arsebük, 1989), Paleolithic artifacts (Kuhn *et al.*, 1996) occur in the same late Middle Pleistocene layers as a fauna dominated by cave bears (*Ursus deningeri*). Ungulate bones occur in very small quantities, and taphonomic analyses reveal little if any connection to human activities in the cave (Stiner *et al.*, 1996); scant remains of wolves and spotted hyenas are also present. The close spatial proximity of stone artifacts, ungulate bones, and carnivore bones in Yarimburgaz Cave prove to be overlays of isolated biogenic events. The shelter was visited at different times by hominids, cave and brown bears, wolves, and spotted hyenas, and the hominid components there are particularly ephemeral. Regardless of how ungulate bones arrived in Yarimburgaz Cave, their low frequency ($N = 151$) relative to stone artifacts ($N = 1674$) raises questions about the economic focus of tool use there. In fact, few if any bones have cut marks on them, suggesting that the tools were put to other purposes.

As documented previously by Gamble (1986), alternating use of caves by hominids and large carnivores, such as hyenas, bears, and wolves, was common in the Mediterranean Basin. Broadly similar situations are evidenced in Italy between 110 and 35 KYA at Grotta dei Moscerini, Grotta Guattari, Buca della Iena (Stiner, 1991b, 1994), Grotta del Gosto (Tozzi, 1974), and also in France (Brugal and Jaubert, 1991) and Germany (Gamble, 1999); in some cases, the association of artifacts and carnivore-collected materials resulted from the slope wash of artifacts into natural traps (Villa and Soressi, 2000), but others involve primary disposal by both agencies at different times. Where hominid components are thin and appear ephemeral, carnivore components often are thick and easily recognized. Some of the types of taphonomic evidence that guide these inferences are illustrated in Figs. 3, 4, and 5.

Other late Middle Pleistocene sites instead are dominated by hominid-generated debris, thick with the remains of large, medium, and some small ungulate species. One of the earliest examples of an obviously hunted ungulate fauna, mostly fallow deer (*Dama mesopotamica*), mountain gazelle (*Gazella gazella*), and aurochs (*Bos primigenius*) is from Hayonim Cave in the Galilee of northern Israel (Stiner, 1998a; Stiner and Tchernov, 1998). Modification of the few carnivore remains in this cave is entirely attributable to hominids. Preliminary thermoluminescence (Valladas *et al.*, 1998) and electron-spin-resonance results (Schwarcz and Rink, 1998) indicate an average age of 170 KYA for the 2.5-m-thick early Middle



Fig. 3. Hallmarks of marrow-processing behavior: (a) Deer metapodial shafts split by Middle Paleolithic hominids, with relatively clean fracture edges and displaying herzian cone fractures (arrows indicate contact points). Cone fractures can be produced by direct impact (percussion) from a rounded stone hammer or by compression in the jaws of a large carnivore; the former action is much more efficient mechanically, and thus hominids tend to generate cone fractures at high frequencies while processing bones for marrow. Large carnivores, such as hyenas, tend to generate much fewer per assemblage (Stiner, 1994, pp. 103–157). (b) Deer metapodials gnawed by captive Minnesota wolves; note the generally ragged edges of these specimens and less efficient exposure of marrow cavities (from G. Haynes' comparative collection, U. Reno, Nevada).



Fig. 4. Superficial bone damage caused by Paleolithic stone tools: (a) Axial scraping or grooving on ungulate long bone shaft fragment, Middle Paleolithic, Grotta Breuil (specimen length is 2.3 cm); (b) Cut mark on ventral face of leopard first phalanx, Kebaran layer, Hayonim Cave (4 cm); (c) Cut marks on vulture bone tube (11 cm) from Aurignacian layer, Hayonim Cave, probably occurred during skin or feather removal for some nonculinary use; (d) The distal ends of two gazelle humeri of Natufian age, Hayonim Cave (3 cm, 4 cm); (e) Repeated impact depressions on anterior face of complete horse first phalanx (9 cm), probably used as soft hammer or anvil for flint knapping, La Quina, France.

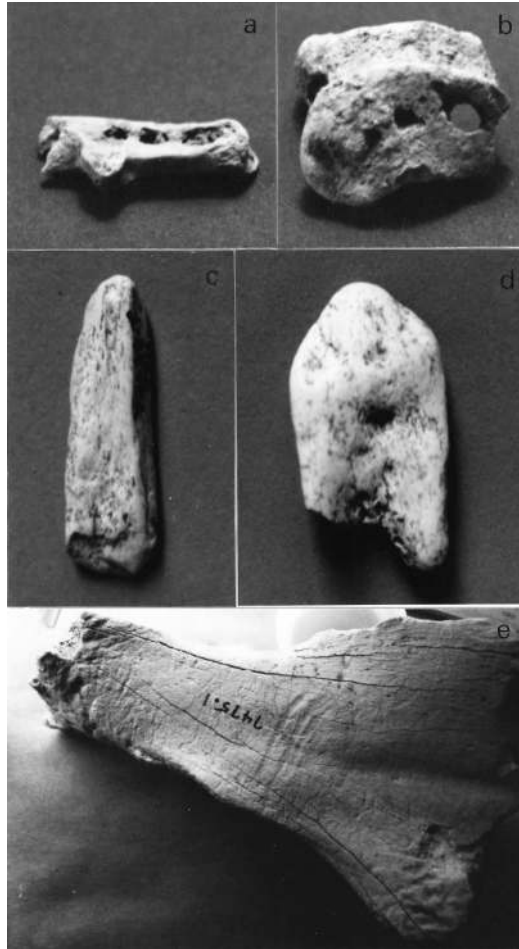


Fig. 5. Carnivore gnawing damage in the form of (a, b) tooth punctures, made by a fox or small cat on lagomorph hind limb fragments, Riparo Mochi, Italy (specimen lengths 1.8 cm, 1.6 cm); (c, d) Compact bone “tablets” smoothed by salivary enzymes or gastric erosion of large carnivore, Yarimburgaz Cave, Turkey (3.4 cm, 3.2 cm); (e) Crenelation, rounding, and tooth drag marks made by spotted hyenas on large ungulate innominate from La Quina, France (14 cm).

Paleolithic deposit (Meignen, 1998), but the oldest bone-bearing cultural layer of this cave is estimated at 200 KYA, based on faunal associations and tortoise mean size variation (Stiner *et al.*, 2001a).

Later Middle Paleolithic (Late Pleistocene) examples of ungulate hunting in Israel include assemblages from Kebara Cave (Bar-Yosef *et al.*, 1992; Speth and

Tchernov, 1998) and Qafzeh Cave (Rabinovich and Tchernov, 1995). Comparable situations are reported for Grotta Breuil and Grotta di Sant'Agostino in Latium, Italy (Stiner, 1990, 1990/1991, 1991a, 1994; Tozzi, 1970), as well as in France (Chase, 1986; David and Poulain, 1990; Jaubert *et al.*, 1990), Germany (Gaudzinski, 1995), Russia (Hoffecker *et al.*, 1991), and the Zagros Mountains (Marean and Kim, 1998). Indeed, half or more of the European Middle Paleolithic sites that preserve faunal remains contain impressive amounts of both ungulate bones and stone artifacts. The relative frequencies of the two materials in these kinds of sites are positively and strongly correlated where this property has been examined (Stiner, 1999; Stiner and Kuhn, 1992). The abundance of human-caused damage to the bones (cut marks, percussion fractures or cones, burning), the prime-dominated age structures of artiodactyl (even-toed) ungulate species such as aurochs (wild cattle) and red deer, and relatively complete patterns of body part representation indicate that Middle Paleolithic humans at times enjoyed uninhibited access to large game, apparently by hunting them.

Without concluding that Middle Paleolithic foraging habits were modern in every way—they certainly were not (Mellars, 1996; Stiner, 1994; Trinkaus, 1986)—the faunal record includes clear, relatively straightforward evidence of ungulate hunting. However, the faunal record also includes other facets that are less easy to interpret, because they diverge from what we expect on the basis of recent hunter-gatherers (Gamble, 1986, 1999; Kuhn and Stiner, 2001). Small prey were exploited at lower latitudes by Middle Paleolithic humans, for example, but this was largely confined to “gatherable” marine mollusks, tortoises, legless lizards, and ostrich eggs (Klein and Scott, 1986; Palma di Cesnola, 1965, 1969; Stiner, 1993b, 1994; Stiner *et al.*, 2000; Stiner and Tchernov, 1998). Occasional scavenging, primarily of ungulate head parts in spring, is associated with small-game use in the multiple layers of Grotta dei Moscerini (Italy), indicating more than anything a strong emphasis on gathered foods (Stiner, 1993b, 1994).

Many of the zooarchaeological manifestations of the Middle Paleolithic nonetheless are a good deal closer to what one would expect to see if large game animals were a regular part of human subsistence, in marked contrast to most of the Lower Paleolithic faunal records of Eurasia. This is not simply because Middle Paleolithic humans had more reliable access to ungulate prey. The products of foraging were deliberately aggregated in some Middle Paleolithic sites—processed and consumed by multiple persons, resulting in thick refuse accumulations (e.g., Speth and Tchernov, 2001; Stiner, 1994). The rising prevalence of such sites after 250 KYA associates with important changes in stone technology, including the introduction of a versatile array of core preparation techniques and flake tools (Boëda, 1986; Bordes, 1961; Geneste, 1985; Kuhn, 1995; Meignen, 1988). In summary, the site-making habits of Upper Paleolithic and later foragers resulted in rather different total patterns than is generally true for the Middle Paleolithic (Brugal and Jaubert, 1991, on sites in France; Stiner and Kuhn, 1992, Stiner, 1994,

on west-central Italy). There is, however, a notable increase in site numbers after about 70 KYA.

TRENDS IN FAUNAL EXPLOITATION IN PALEOLITHIC EURASIA

Archaeologists interested in the evolution of human carnivorous adaptations ultimately must explain diachronic variation in the complete spectrum of predatory activities, their technological correlates, and the patterns and tempo of debris accumulation on landscapes. This is a tall order, but insights on these issues are not completely out of reach. Toward this end, three faunal trends of the Paleolithic of Eurasia are discussed in detail below, based on the roles of (1) ungulate exploitation, (2) small-game use, and (3) early technologies in human societies.

Trend 1, Niche Diversification Among Ungulate Predators

Considerable overlap in the foraging interests of hominids and carnivores is apparent from the early archaeological records of Africa, Europe, and Asia. Much of this centers on the use of ungulates. In fact, ungulate remains dominate Late Pleistocene archaeofaunas nearly worldwide, especially prior to the Epipaleolithic or Mesolithic period. From ungulate faunas alone, one can trace shifts between at least three predator–prey relationships involving hominids over the last million years: itinerant scavenging, hunting, and, in a few species, domestication. These transitions were shaped, in part, by the risks of interference competition from other meat eaters for large resource packages. A theoretical outcome of interspecific competition is ecological differentiation, or character displacement, which relieves the stresses of conflict among consumers who cannot otherwise rid themselves of one another (MacArthur, 1968, 1970; MacArthur and Levins, 1967; May and MacArthur, 1972; Pianka, 1978, pp. 189–199, 260).

The first shift in ungulate exploitation appears to have been from the gathering or scavenging of isolated body parts, and occasionally whole carcasses, to regular predation of live ungulates and full access to their flesh. Meat eating by hominids in Africa included strategic transport of ungulate body parts as early as 2.5 MYA, albeit on a minute geographic scale (e.g., Bunn *et al.*, 1980; Potts, 1984; Toth, 1987). The likelihood that bony morsels were scavenged from carnivore kill sites, or the natural deaths that also attract predators, is thought by some archaeologists to explain the need for transport to safer locations, where these items could be processed without interference (Potts, 1984). Oddly, limb bones are particularly abundant in the early African cases (Brantingham, 1998), and this is not a common outcome of nonconfrontational scavenging in nonhuman predators (Bunn, 2001; Stiner, 1991a). An interpretive difficulty of these cases concerns the relative frequency of meat acquisition relative to other resources, since scavenging can on

occasion involve great returns (Bunn, 2001) but is not expected to be a reliable source of food in terrestrial ecosystems (Houston, 1979).

Processing of transported ungulate parts by early hominids amounted to rough removal of external soft tissues and cracking open the medullary cavities of large bones to reach the marrow inside. The energetic advantage gained by using stone hammers is absurdly simple (Leakey, 1971) yet may represent one of the most important early pathways into the Plio-Pleistocene predator guilds of Africa (Brantingham, 1998). The behavior could be a derivation of nut-cracking routines of the sort seen among modern chimpanzees (Boesch and Boesch, 1984; McGrew, 1992). Oddly, chimpanzees do not transfer this skill to bone-marrow processing (at least not yet). The adoption of stone hammers for marrow extraction, as opposed to the universal dependence on dental and digestive apparatuses among the Carnivora, arguably was a major dietary breakthrough for early hominids. This behavior could antedate the practice of reshaping stones by hard-hammer percussion. On the other hand, sharp flakes are efficient tools for cutting meat from bone, and stone-on-stone percussion could simultaneously permit the discovery of a useful tool and how to make it (Keeley, 1982).

Considerably more archaeological and actualistic research has been carried out on early hominid carnivory in the last two decades. In response to potential equifinality in the signatures of marrow processing by predators, an issue raised by the works of Sutcliffe (1970), Potts (1982), Haynes (1982), and Brain (1981), refinements have been made in the criteria for distinguishing hammer-induced percussion (cone) fractures on bone by hominids (Blumenshine and Selvaggio, 1991; see O'Connell's 1995 review). As well, more information has been gained on the full range of potential scavenging opportunities hominids may have encountered on African (Blumenshine, 1986; Bunn *et al.*, 1988; Cavallo and Blumenshine, 1989; O'Connell *et al.*, 1988) and Eurasian landscapes (Haynes, 1982; Stiner, 1994; Turner, 1992), the potential marrow yields of various ungulate species (reviewed by Lyman, 1994), and the means for estimating body-part profiles from fragmented bone assemblages (e.g., Bunn and Kroll, 1988; see Marean and Kim, 1998, for a different opinion). Much of this research continues to focus, however, on the same limited range of materials and sites. Though seemingly forgotten, the conclusions presented by recent literature on meat eating by early hominids are not much clearer or very different than those presented in the late 1970s through 1980s. Part of the problem stems from the paucity of well-preserved assemblages to work with—a provocative observation in itself. Also contributing to the increasingly contentious nature of these debates are the contradictory results of replication experiments that, in being designed to “verify” a preferred hypothesis, cannot exclude alternative explanations (compare, e.g., Blumenshine *et al.*, 1994; O'Connell, 1995; Tappen, 1995, 2001; on later Paleolithic periods compare Klein *et al.*, 1999; Marean *et al.*, 1992; Marean and Kim, 1998; Stiner, 1998b). Because modern investigators cannot also be *Homo erectus*, and broad generalizations should not be built from single

cases, more explicit identification of controls and greater integration with lithic evidence on tool production and use are needed to clarify the benefits of replication experiments.

Fortunately, paleoanthropologists agree that hominids eventually evolved into true ungulate hunters of some kind (e.g., Cassoli and Tagliacozzo, 1991; Chase, 1986; Gaudzinski, 1995; Hoffercker *et al.*, 1991; Jaubert *et al.*, 1990; Pike-Tay, 1999; Marean and Kim, 1998; Speth and Tchernov, 1998; Stiner, 1990, 1994). As hunters, hominids appear always to have been of the ambushing sort (Stiner, 1990), not altogether surprising in light of the fact that human locomotor adaptations favor diligence over speed. The impact of hominids' hunting tactics on ungulate populations also grew more distinct from those of coeval large cats, spotted hyenas, and large canids. Specifically, humans are the only predator that preferentially targets the reproductive core (prime adults) of ungulate populations (Stiner, 1990), a strategy that may raise the net fat yield. Because spotted hyenas and large canids generally focus on the juvenile and old-adult age groups in the same prey species, and most cats apart from cheetahs tend to take prey more randomly, humans' focus on prime-adult prey is ecologically unprecedented.

Figure 6 illustrates in tripolar format this tendency in terms of averaged ungulate mortality patterns for Paleolithic humans and various nonhuman predators relative to natural variation in living prey population structure and the mortality patterns created by nonviolent causes; each corner of the tripolar graph corresponds to a strong bias toward the age group designated. The ungulate mortality patterns generated by cursorial predators, such as spotted hyenas, wolves, and African wild dogs, overlap completely with the death patterns resulting from attritional factors such as disease, malnutrition, and old age. Predators that ambush their prey, such as lions and tigers, tend to hunt nonselectively with respect to prey age unless the prey species is exceptionally large; thus they usually generate death patterns that mimic the age structure of the living prey population. The extent to which these animals scavenge for ungulate carcasses seems to push the mean value higher on the old age axis, as is the case for Indian tigers in this comparison. Middle Paleolithic, Upper Paleolithic, and more recent human cases generally fall on the ambush side of the distribution, but they also display a relatively extreme preference toward prime adult individuals in artiodactyl prey species. The effects of human hunting thus are distinct on average from those of nonhuman predators over this great time span, evidence of niche separation that evolved as a result of hominids' membership in ungulate predator guilds. Mass kill techniques were rare to nonexistent in this and most later prehistoric periods (e.g., Jaubert *et al.*, 1990; Stiner, 1990).

Hominids' tendency to harvest prime-adult bovids and cervids was well established by the Late Pleistocene, but it first emerged in the Middle Pleistocene by about 250 KYA. The emphasis on prime-adult prey is geographically and temporally widespread from the Middle Paleolithic through Holocene (e.g., Enloe, 1997; Gaudzinski, 1995; Hoffercker *et al.*, 1991; Jaubert *et al.*, 1990; Pike-Tay, 1999; Rick

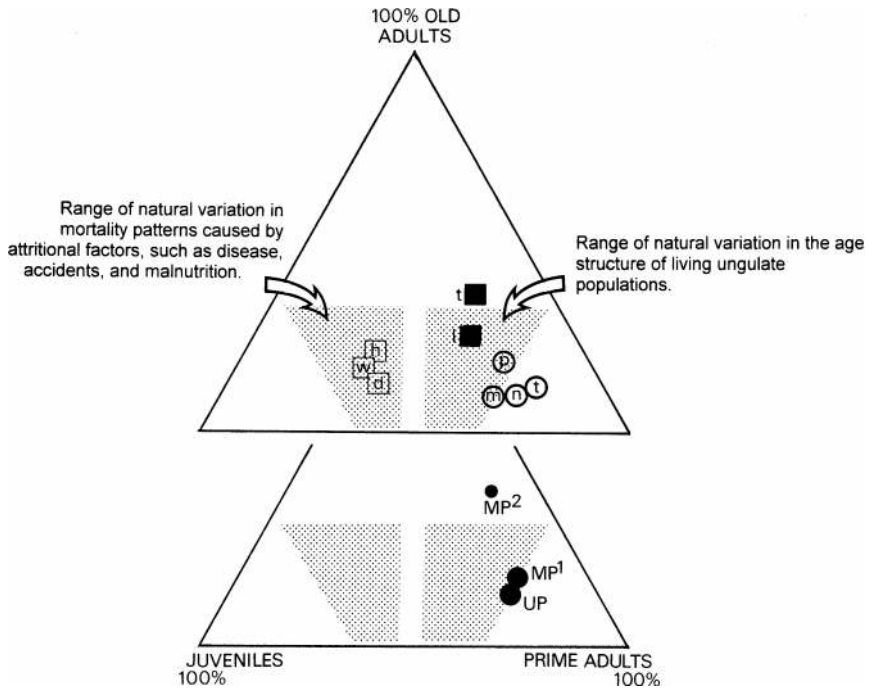


Fig. 6. Mean values for ungulate mortality patterns created by various human and nonhuman predators. Means are based on the percentage of juvenile, prime-adult, and old-adult prey in multiple death assemblages, grouped by predator agency and plotted in tripolar format (from Stiner, 1990, 1994). Shading represents natural variation in the age structure of living ungulate populations and thus also nonselective mortality patterns (right panel); and mortality patterns caused by attritional factors, such as disease, accidents, and malnutrition (left panel). Predators that ambush their prey ([t] tigers and [l] lions) tend to be unselective with respect to age. Cursorial or long-chase hunters, such as [h] spotted hyenas, [w] wolves, and [d] African wild dogs, instead tend to produce attritional mortality patterns that overlap completely with those caused by nonviolent factors. The corners of this graph represent strong biases toward the designated prey age group. Humans, from the Middle Paleolithic through recent times, tend to generate mortality patterns in ungulate prey that are slightly to strongly biased in favor of prime-adult animals. Open circles represent various Holocene human cultures (Paleoindian/Archaic [p], Mississippian farmers [m], Nunamiut Eskimo [n], trophy hunters in modern game parks [t]). MP¹ is the mean for most Middle Paleolithic hunted faunas (250–32 KYA) and closely resembles that for the Upper Paleolithic (UP). MP² refers to a handful of esoteric cases from coastal Italy, dominated nearly exclusively by the head parts of old adult prey, apparently obtained by scavenging, and coinciding with small scale marine shellfish exploitation.

and Moore, 2001; Smith, 1974; Speth and Tchernov, 1998; Stiner, 1990). Somewhat counterintuitively, this phenomenon is largely insensitive to regional and temporal variation in prevailing weapons technology (Stiner, 1990). What is more, prime-focused ungulate hunting can be a relatively fragile predator–prey relationship, because reproductive-aged adults are disproportionately sought. Seemingly

antithetical to “prudent predation” models (Pianka, 1978, p. 210), such a relationship may only be feasible for omnivorous predators that can switch to other foods when the densities of favored prey decline from hunting pressure (Stiner, 1994; Winterhalder and Lu, 1997). On the other hand, some northern Neandertal populations were as carnivorous as sympatric wolves, based on stable carbon and nitrogen isotope evidence (Richards *et al.*, 2000).

The level of ecological specialization indicated by prime-adult-biased hunting as early as 250 KYA suggests a deeper history for ungulate hunting by hominids in general. It seems likely on theoretical grounds, as well as from limited empirical evidence, that a more basic adaptation for ungulate hunting had evolved in hominids by about 500 KYA. Unfortunately, there are relatively few cases available for comparison from this time range, and most of them are subject to many more questions about site formation history.

Opportunistic exploitation of ungulates, including scavenging, did not disappear from later foraging regimens: it merely played smaller and/or different roles. Nonconfrontational scavenging is evidenced in some Middle Paleolithic cases, for example, but was obviously just one facet of a more complex array of foraging behaviors (Stiner, 1994; Stiner and Kuhn, 1992). Scavenging also is suggested by some late Upper Paleolithic cases, but involves species such as equids that were less important in the local diet (e.g., Grotta Polesini; Stiner, 1994). How these and other strategies were folded into Middle and later Paleolithic foraging systems, and the relative energetic returns of each, probably are better questions to be asking than “Could hominids hunt, or could they only scavenge?”

Selective harvesting of prime adult ungulate prey by early humans may inadvertently have set the stage for the coevolutionary relationship we call domestication (the third relationship), although it is not an automatic outcome of human hunting behavior. Prime-age-focused predatory strategies can easily reduce the mean age at first reproduction in prey populations under conditions of heavy harvesting (reviewed by Stiner, 1994, pp. 314–315). The latter criterion is, of course, common to the domestication of several mammalian species, but it must combine with a narrow range of behavioral characteristics in the subject species to produce a domesticated variant (for theoretical discussions, see Dayan, 1994; Price, 1984; Trut, 1999). In addition to greater hunting, humans’ capacities for intensive bone processing grew more sophisticated over the remainder of human evolutionary history, as did the procedures that facilitate food portage and storage (see below).

Trend 2, Small-Game Use and Paleodemography

Small-game exploitation provides a distinct view of hominid carnivory. It can reflect, for example, changes in predator–prey relationships as a function of human population density (e.g., Clark and Straus, 1983; Davis *et al.*, 1988; Klein, 1979; Klein and Cruz-Uribe, 1983; Stiner and Tchernov, 1998; Stiner *et al.*, 1999). This

potential stems from the fact that small animals differ greatly in their life history characteristics and population recovery rates, much more than ungulate species do. Small-game use at lower latitudes, such as in the Mediterranean Basin, is especially informative about density-dependent predator–prey relationships for three reasons (Stiner *et al.*, 2000): (1) some small animals have been important to human diets since at least the Middle Paleolithic (Klein and Scott, 1986; Palma di Cesnola, 1965, 1969; Stiner, 1993b, 1994; Stiner and Tchernov, 1998); (2) some of the most easily caught or collected species—tortoises and marine mollusks—also happen to be the most sensitive to harvesting pressure (Dye *et al.*, 1994; Hockey, 1994); and (3) the diversity of small vertebrates and invertebrates at low latitudes provides foragers with much variety to choose from and rank according to relative nutritional payoffs, greatly facilitating research on changes in diet breadth.

The proportion of small animals to total game intake in Italy and Israel over the last 200,000 years shows no discernible trend (Stiner *et al.*, 1999, 2000). Small animals evidently were a desirable source of supplemental protein throughout the Middle Paleolithic, Upper Paleolithic, and Epipaleolithic–Mesolithic. Varying in frequency between 5 and 50% of the total number of identified skeletal specimens (NISP), small-game animals are perhaps best viewed as backup resources. In contrast to the ratio of small to large game, the general *categories* of small animals emphasized by foragers shifted dramatically from the Middle Paleolithic to the Epipaleolithic periods. Slow-growing, comparatively sessile tortoises and marine mollusks dominate the small-game fractions of the Middle Paleolithic record, constituting as much as 46% of total game (NISP) at Grotta dei Moscerini in Italy and up to 54% in Hayonim Cave in Israel. What is more, the individuals taken were quite large on average.

Unexploited populations of tortoises and shellfish can exist at high densities, but tortoises and shellfish such as limpets and drills are easily overharvested, owing to the slow rate of individual development. Their populations may decline rapidly if too many are taken in a given year, not because of different reproductive rates so much as the fact that the time to reproductive maturity is long (Stiner *et al.*, 2000); Mediterranean tortoises require 8–12 years to reach maturity, some limpets and large drills 1–5 years. Humans' use of "low-turnover" (unresilient) species is of particular interest, as they are the proverbial "canaries in the coal mine." They are the most sensitive to hunting pressure and the first to suffer population decline as hunting pressure increases. Thus they are the species to watch if one is interested in signatures of demographic packing, the most common cause of overharvesting. It is unlikely that Paleolithic foragers viewed prey in terms of their potentials for population recovery, but foragers certainly were sensitive to declining returns for the same level of foraging effort. Because tortoises and shellfish grow throughout their life span, overharvesting also causes *diminution* or a reduction in the mean size of individuals available to foragers over time. Body-size diminution occurred early for tortoises in Israel, during the late Middle Paleolithic or earliest Upper Paleolithic (44 KYA), by 23 KYA for limpets at Riparo Mochi, Italy (Stiner *et al.*, 1999), and

well after at La Riera in Spain (Clark and Straus, 1983). In the cases from Israel and Italy, the timing and duration of diminution is independent of global climate trends and thus point to a human cause (Stiner, 1992, 1994; Tchernov, 1992, 1994). In South Africa, where this phenomenon has been examined by Klein and Cruz-Urbe (1983), tortoise and limpet diminution occurred by the Late Stone Age.

Agile, warm-blooded animals, such as partridges, hares, and rabbits, became important in human diets by the early Upper Paleolithic (Fig. 7), mainly birds at first and then lagomorphs as well. In contrast to tortoises and limpets, these warm-blooded animals mature very quickly (≤ 1 year), such that even heavily hunted populations may rebound easily. However, these quick animals are more elusive in the absence of snares and other trap technology (*sensu* Oswalt, 1976) or nets and communal drives (*sensu* Steward, 1938). They would have had a lower priority or “rank” in Middle Paleolithic foraging systems in the absence of such tools because they were more difficult to catch by hand and therefore presented lower foraging returns for the effort.

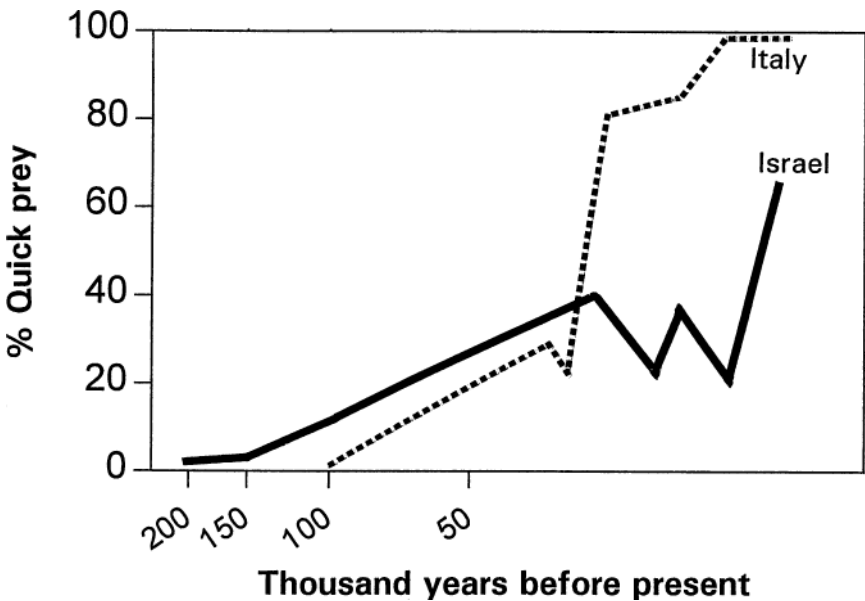


Fig. 7. Trends in the relative contribution of quick-flight (as opposed to slow-moving) prey types among the small-game remains in Pleistocene faunal series from Italy (dashed line) and Israel (solid line). “Quick” small prey types are warm-blooded and agile, and consist primarily of birds such as partridges and lagomorphs (hares and rabbits in Italy; hares in Israel). The trends in both Mediterranean regions occur at the expense of “slow” small-prey types, edible marine shellfish and tortoises in Italy, tortoises in Israel. Tortoise populations also experienced significant diminution at the hands of Paleolithic foragers by >44 KYA in Israel. Marine limpets in northwestern Italy experience significant diminution by about 23 KYA. Diminution was sustained in each kind of prey over the remainder of the Paleolithic series (Stiner *et al.*, 1999).

Predator–prey simulations by Stiner *et al.* (2000) demonstrate that hare and partridge populations can support seven to ten times the annual off-take that tortoise populations can support. Limpets and drills are only somewhat more resilient than tortoises (e.g., Dye *et al.*, 1994; Hockey, 1994; Siegfried *et al.*, 1994). Greater dependence on slow-growing animals during the Middle Paleolithic, and on larger individuals in particular, implies that early human populations were exceptionally small and thinly distributed. Paleolithic foragers' emphasis on slow (highly ranked) and quick (lower ranked) small prey grew more “even” with time, the predicted outcome of hunting pressure (Stephens and Krebs, 1986). As the availability of easily collected small animals declined, people had no choice but to focus on the quicker types. Technological aids for catching quick small animals seem to have evolved on the heels of these new foraging constraints (Stiner *et al.*, 2000).

The small-game trends described above are not confined to the Mediterranean Rim, although cases elsewhere generally postdate the eastern Mediterranean case (e.g., various authors in Bonsall, 1989; Coles, 1992). Although the quality of available faunal data varies greatly, heavy emphasis on lagomorphs develops late in virtually every sequence, appearing mainly after the Last Glacial Maximum and often closer to the Pleistocene–Holocene boundary (Kuhn and Stiner, 2001). The burgeoning importance of lagomorphs in Epipaleolithic diets is remarkably widespread, certainly including the northern interior of Europe and arid lands to the south, in open and cave sites alike. Hares were common prey at many Solutrean and (especially) Magdalenian and Epigravettian sites in southern Europe (Clark, 1987; Davidson, 1983; Hockett and Bicho, 2000; Stiner *et al.*, 1999; Straus, 1990; Zilhão, 1990), northwestern Europe (Albrecht and Berke, 1982/1983; Barton, 1999; Berke, 1984; Bratlund, 1996, 1999), southwestern Germany (Jochim, 1998), Moravia (Svoboda, 1990), the Dnestr region (Kosoutsky Layer 4; Borziyak, 1993), and even at Norgorod–Severskii on the Central Russian Plain (Soffer, 1990). The surge in lagomorph exploitation occurred somewhat earlier in western Asia (compare Byrd and Garrard, 1990; Henry and Garrard, 1988; Klein, 1995; Munro, 1999; Surovell, 1999), yet quite late in North Africa (Smith, 1998) and Iberia (Hockett and Bicho, 2000). Environmental changes brought on by global warming (e.g., Madeyska, 1999) may have expanded the habitats favored by lagomorphs and thus their numbers in Eurasia. However, paleontological evidence indicates that lagomorphs existed in most or all of these regions in earlier times but were largely ignored by humans (Stiner, 1994; Tchernov, 1994).

The findings on small-game use in southern Europe and western Asia support Flannery's Broad Spectrum Revolution hypothesis (Flannery, 1969) on expanding dietary breadth in response to demographic packing (increasing population density) during the Late Pleistocene (see also Binford, 1968; Cohen, 1977). This is not to say that local population packing was the sole cause of the cultural changes of the Upper and Epipaleolithic. Rather, it appears to have been one of several essential ingredients for cultural change (Bar-Yosef, 1995; Binford, 1999; Davis *et al.*, 1988; Keeley, 1988, 1995). Demonstration of rising human population densities

during the later Paleolithic effectively shifts paleoanthropological debates away from beliefs about the innate capacities of premodern humans and allows us to explore probable changes in the conditions of selection on their economic and social adaptations (Binford, 1999; Gamble, 1986; Jochim, 1998; Kuhn and Stiner, 1998b; Soffer, 1985; Winterhalder and Lu, 1997).

To summarize thus far, the clearest signature of rising human population densities and their effect on the availability of game in southern Europe and western Asia is the *more even dependence* on high- and low-ranked resources, corroborated by climate-independent diminution in slow-growing prey species. However, this trend appears clear-cut only if small prey are grouped according to development rates and predator escape strategies, rather than simply counting the number of species in the diet along a body-size gradient (Stiner *et al.*, 2000). Species richness and evenness, the more conventional approach, also may indicate an increase in dietary breadth during the later Paleolithic, but changes by these measures are too subtle to quell the doubts of many researchers (compare Bar-Oz *et al.*, 1999; Edwards, 1989; Grayson and Delpech, 1998; Henry, 1989; Henry *et al.*, 1985; Munro, 1999; Neeley and Clark, 1993; Simek and Snyder, 1988; Simmons and Nadel, 1998). By contrast, a radical *decline* in prey species diversity is easily demonstrated for the early Neolithic on the basis of taxonomic richness and evenness measures (Cassoli and Tagliacozzo, 1997; Davis *et al.*, 1988, 1994; Horwitz, 1996; Neeley and Clark, 1993; Tagliacozzo, 1997).

A potentially beneficial quality of small-prey populations that rebound quickly is their greater reliability wherever human population density increases. But this is only true if the work of capture can be reduced with new technology such as tended and/or untended traps and/or the manpower required for game drives (Oswalt, 1976). There is good reason to think that trap technology developed rapidly during the later Upper and Epipaleolithic periods (e.g., Adovasio *et al.*, 1996; Gamble, 1986; Gramsch and Kloss, 1989; Jochim, 1998; Kuhn and Stiner, 2001; Mordant and Mordant, 1992; Nadel *et al.*, 1994; Whittle, 1996). The tools for overcoming the quick flight strategies of birds and small mammals no doubt also permanently altered foragers' systems for ranking prey in the long run. The pressure to do so began, however, with predator-prey relationships already gone sour. This happened by the late Middle Paleolithic or earliest Upper Paleolithic in western Asia, and later in western and northern Europe. These observations raise some rather fundamental questions about what spurs technological change, specifically the relative roles of history and natural selection on Paleolithic technology and why the pace of change accelerated with time.

Trend 3, Paleolithic Technology and the Mother of Invention

The relations between technology and carnivory are integral to the story of human evolution, but that is not to say that they are easily understood. Rather than

presenting a laundry list of problems, this section identifies a few points of ambiguity and uses available information to make greater sense of them. The Eurasian Paleolithic traditionally is subdivided into three major cultural phases on the basis of stone artifact forms: Lower, Middle, and Upper Paleolithic. The hominid taxa chronologically associated with these techno-cultures vary, and there is no simple correspondence between cultural (behavioral) change and human skeletal change (e.g., Bar-Yosef and Kuhn, 1999; but see Foley and Lahr, 1997). Carnivorous behavior in hominids could be older than the practice of modifying stone; after all, modern chimpanzees and baboons hunt and consume moderately sized mammals without any tools at all. What is more, the traces of marrow extraction need not include cut marks from stone tools. Although the functions of crude early Lower Paleolithic tools are not well known (Binford, 1987; Isaac, 1984; Kleindienst, 1961, 1962; Leakey, 1971; Potts, 1984), many may have been directed to processing meat and plant foods and modifying other natural materials, few or none to game procurement (Keeley, 1982; Keeley and Toth, 1981; Sahnouni *et al.*, 1997; Toth, 1985, 1987). In fact, early examples of meat eating are rare given the time spans involved, perhaps better evidence for hominids' uncommon good luck than routine consumption of large mammals. Hunting no doubt occurred by the later Lower Paleolithic, evidenced by a few wooden spears (Thieme, 1997), but this record is largely silent on the question of habitual versus incidental meat eating.

Considerable evidence for large game hunting exists for the Middle Paleolithic period, but very few Middle Paleolithic tools can reasonably be called hunting weapons. Middle Paleolithic or Mousterian industries (ca. 250–35 KYA) are characterized principally by innovations in core preparation techniques and great flexibility in their use (e.g., Boëda, 1986; Geneste, 1985; Kuhn, 1995; Meignen, 1988). In comparison to the redundancy of Lower Paleolithic tool industries, the variety of the Middle Paleolithic is something of a relief. On the other hand, Middle Paleolithic industries are attributable to both Neandertals and the earliest anatomically modern humans after 100 KYA (at Qafzeh and Skhul; Bar-Yosef, 1989; Bar-Yosef *et al.*, 1986; Valladas *et al.*, 1988; Vandermeersch, 1989), and they persist in the archaeological record of the European Neandertals until as late as 30–28 KYA (Barroso Ruiz and Hublin, 1994; Hublin *et al.*, 1995, 1996; Straus, 1999), overlapping with early Upper Paleolithic cultures for up to 10,000 years in some areas. More startling still is the fact that Upper Paleolithic cultures appear in Eurasia (and the Late Stone Age in Africa) well after so-called “modern” human skeletal features first evolved. Rare stone-tipped weapons appeared late in the Middle Paleolithic (Müller-Beck, 1988; Shea, 1989) and are not widespread (Kuhn and Stiner, 1998b). Bone working, and bone-tipped weapons designed specifically for hunting, are confined to the Upper Paleolithic and later cultures (Fig. 8), when rapid radiations in preserved weapons and other material culture also took place (e.g., Knecht, 1997).



Fig. 8. Examples of worked skeletal materials: (a) Unidentified carved object made from a cervid metatarsal, possibly a musical rasp (7 cm long); (b) Split-based point made from deer antler (9 cm), both from the early Aurignacian, Riparo Mochi, Italy (from Kuhn and Stiner, 1998a). (c) Sagaie fragments made from deer antler, Magdalenian, Abri Dufaure, France.

There is a paradox here, in that humans routinely hunted medium-sized and large ungulates long before the undisputed appearance of the stone-tipped and bone-tipped weapons, the hallmarks of Upper Paleolithic cultures. Prime-age-focused ungulate hunting is evidenced in cases as old as 200–250 KYA (Gaudzinski, 1995; Stiner, 1998a), about the time that earliest Middle Paleolithic technologies first evolved and well before every indisputable innovation in weapons technology save the simple wooden spear (e.g., Lehringen in Germany ca. 200 KYA, Jacob-Friesen, 1956; Schönningen ca. 400 KYA, Thieme, 1997). The elaborate weapons traditions of the Eurasian Upper Paleolithic and African Late Stone Age are separated from the emergence of prime-focused hunting behavior by some 150,000 years. Even the remarkable bone points from the Middle Stone Age site of Katanda in Zaire (Brooks *et al.*, 1995; Yellen *et al.*, 1995) are much too young to close this temporal gap. The lag in technological change suggests that cooperation among hunters was essential for the capture of large game (Stiner, 1990/1991, 1994; Winterhalder, 2001), just as it is for many other social predators (Fox, 1984; Kruuk, 1972; Schaller, 1972). The evidence shows us that

the basic ability to hunt large game and shifts in the rate of technological change are relatively distinct phenomena.

So what was the evolutionary role of weapons in human carnivory, and, if this is answerable, what stimulated the rapid radiations in weapons design during the Upper Paleolithic and Epipaleolithic–Mesolithic? Was it simply a new desire for better (more efficient) mechanical performance of tools in the food quest, or did social circumstances provide new incentives for continuous redesign of weapons and other paraphernalia? Many of the technical changes described above certainly were connected to humans' dietary interest in large and small game, but less directly than one might imagine. Improvements in weapons designs and efficiency are unlikely to have raised the absolute number of large prey animals available to Paleolithic hunters. However, improvements in weapons efficiency may have reduced individual's procurement time and risk per foray, and possibly also the minimum hunting party size. This implies a change in the value of forager's time—time that could instead be allocated to other tasks (*sensu* Hames, 1992; Pianka, 1978, p. 258). If foragers could rely on larger-scale resource pooling (i.e., enough people available to cooperate and not too many cheaters), this also could favor greater individual task specialization. The benefits of personal specialization are almost certainly limited by the size of cooperative networks over which resources are most consistently pooled. Once evolved, these networks may have allowed some human groups to compete more effectively for critical resources and to reproduce more quickly than groups that cooperated less. Such networks must also set new requirements on the communication of identity.

Prehistoric hunting technology took on an additional role of visual display (*sensu* Wiessner, 1983) in the Upper Paleolithic. Many tools are decorated, and rapid generation and acceptance of new designs was fostered as never before. Thus, although weapons innovation may be driven partly by a need for greater mechanical efficiency, it may originate from the pressures of time allocation for diverse social or foraging concerns. This would have been particularly true if people were sufficiently abundant on landscapes to maintain open-ended consumer groups. Indeed there is a demonstrable positive correlation between population density and social complexity among recent hunter–gatherers (Keeley, 1995), suggesting that this also might have been true in the past (Belfer-Cohen, 1991; Mellars, 1985; Soffer, 1985).

It was also in the Upper Paleolithic that radiations in tool design and decorative traditions began to play out differently from one region to the next (compare Belfer-Cohen, 1991; Hahn, 1972; Kozłowski, 1990; Kuhn *et al.*, 1999; Newell *et al.*, 1990; Price, 1991; Reese, 1989; Stiner, 1999; Taborin, 1993; White, 1989), a process also thought to signal the emergence of visual signals of social identity (e.g., Bahn and Vertut, 1988; Gamble, 1986; Henry, 1989; Soffer, 1989; White, 1993). The earliest ornaments (>41 KYA) appeared around roughly the same time in three continents: central Europe (Bacho Kiro Cave; Kozłowski, 1982), western Asia (Üçagizli Cave, Turkey, Kuhn *et al.*, 1999, 2001), and eastern Africa (Ambrose, 1998a).

Although the apparent synchrony of these cases could be explained partly by the lower temporal limit of radiocarbon dating, other chronologic indications appear to argue against this. Exchange of decorative goods and rare raw materials also occurred. Most striking are the low volumes moved from one place to another, indicating very steep exchange gradients. Yet Upper Paleolithic ornaments share certain design features such as preferred size, shape, and probably color across regions. They vary greatly, however, in the raw materials used and manufacturing investment (compare Stiner, 1999; Taborin, 1993; White, 1993). These observations suggest some degree of shared aesthetic among foraging peoples of this period but also a tendency for token exchange rather than routine commodity transfers among groups. Perhaps ornaments were used for formalizing potential economic conduits of exchange and anticipated cooperative ties, as well as for attracting attention or making statements of identity.

Like the situation for weapons, categorical changes in the nature of social interaction networks evolved long after regular access to large prey had become a part of human subsistence systems: no earlier than the early Upper Paleolithic if preserved ornaments and art are fair indications (e.g., Bahn and Vertut, 1988; d'Errico *et al.*, 1998). The circumstances in which geographically extensive human partnerships and resource transfers evolved—hunter-gatherer insurance systems in effect—are not easily modeled. One must recognize first that history is evolution's palette, since selection acts only on existing variation. From this viewpoint, human demographic increase of the Upper and Epipaleolithic may have created feedback situations in which social networks and institutions could be exploited more efficiently to spread foraging risk over larger areas in bad times. Though provocative, these questions are among the most challenging to test with archaeological data.

A very different side of the technological record concerns carcass-processing innovations and increases in consumption efficiency. Bone cracking with stone hammers and anvils is remarkably efficient compared to the energy and time that large-jawed carnivores must spend to open the same kinds of large bones. Carcass-processing routines of the Paleolithic grew much more complex with time, including grease rendering via stone boiling, presumably in hide-lined pits (*sensu* Binford, 1978). The thick litter of fire-cracked stones in some Magdalenian (Epipaleolithic) sites in France and Germany, for example, suggests considerable antiquity to the practices known among recent foraging peoples for extracting and conserving bone grease (Audouze, 1987; Audouze and Enloe, 1991; Binford, 1993; Brink, 1997; David and Enloe, 1993; Weniger, 1987). These heat-in-liquid techniques maximize both protein and fat yields per carcass well beyond what is possible from cold extraction techniques (Binford, 1978; Lupo and Schmitt, 1997). Because fats and muscle are separated and purified to some extent by rendering, drying or smoking, they also can be stored for longer periods. These techniques are highly portable if containers are made from hide or sealed baskets.

Because more efficient harvesting of quick small game generally accompanies the changes in large-game processing, it is likely that solving resource availability problems via mobility was less of an option and that some degree of territorial circumscription was involved. Concomitant with these developments are widespread reductions in human stature in western Europe following the Last Glacial Maximum some 20,000 years ago, suggesting mild but chronic limits on humans' access to complete protein (Formicola and Giannecchini, 1999).

Still other late specializations in large-game use fostered the productivity of preferred food species and, simultaneously, depressed the productivity of competitors (also true for certain plants). These behaviors include the deliberate torching of range lands to alter vegetal structure and optimize green growth for large herbivores (e.g., Mellars, 1976, on Mesolithic Europe; Hallam, 1979, and Keeley, 1995, on recent hunter-gatherers) and, more recently, animal domestication. The latter is first indicated by anomalous geographic distributions and radical restructuring of ungulate species profiles in the early Neolithic of western Asia after 10 KYA (e.g., Davis, 1982; Davis *et al.*, 1994; Horwitz, 1996, 1999; Meadow, 1984; Redding, 1988) and human manipulation of the age and sex structures of herd animals (e.g., Zeder and Hesse, 2000). Persecution of competing predators and wild herbivores also may have intensified with the Neolithic (Diamond, 1989).

SYNTHESIS

It may be impossible to understand the evolution of hominid carnivory and its social correlates without considering the behaviors that allow predators to both obtain and assimilate animal resources. The nature of hominid carnivory changed greatly over the last 2,500,000 years, not simply in the means and frequency with which meat was obtained, but also the package sizes normally acquired and how the nutrients therein were extracted and processed in response to the limitations of the human digestive system. The fact that hominids were omnivorous greatly influenced the nature of their adaptations for carnivory, even creating possibilities not available to dedicated meat eaters. However, early hominids would probably never have arrived in Eurasia more than 1.5 MYA, much less become permanent members of animal communities there, had it not been for an already predatory lifestyle. Hominids were late arrivals to the predator guilds of Eurasia at a time of considerable species turnover in mammal communities. The African Paleolithic record indicates that they were already accustomed to competing with large carnivores and, in fact, arrived in Eurasia in the same period as certain other colonizing predators. Perhaps more challenging to the first hominids that spread into Eurasia were novel variations in seasonality, punctuated in many areas by winters of intense cold and snow-covered or frozen ground.

Hominid fossil remains and cultural debris older than 500 KYA are rare in Eurasia and are confined to the lower latitudes, suggesting only a tentative presence

at first. Hominid populations were well established in Eurasia by about 500 KYA, however, and they evidently were able to cope with cool lowland environments as far north as 50° latitude. It is likely that early hominids survived Eurasian winters with the aid of fire and some degree of large-mammal hunting, as few other foods would have been available to them during the cold season. Nuts and other large seeds, though energy-rich, long lasting, and locally common in the temperate forests of Europe and Asia, are relatively expensive to process. A blanket of snow raises the winter search costs of these resources beyond what even bears can afford. The situation for premodern hominids must have been similar, as there are no archaeological indications of stockpiled plant foods in northern sites before the Upper Paleolithic, although small numbers of burned nut hull fragments are occasionally found in Middle Paleolithic sites (Barton *et al.*, 1999). Also absent prior to the Epipaleolithic period are the tools required to process nuts or seeds in quantity. Under these early cultural conditions, meat was likely to have been the critical food source in winter.

How Lower Paleolithic hominids obtained the bulk of the meat they consumed remains an open question. Many of the early archaeofaunal accumulations are actually nested within larger, noncultural bone accumulations. Some cases suggest hunting of large mammals (i.e., felling of live prey), whereas others almost certainly involved scavenging. Oddly, megafauna are most common in the early faunal records. The contents and conditions of these faunal assemblages indicate complex, protracted formation histories only minimally connected to hominid activities. Ungulate remains (bovids, cervids, equids) dominated later archaeofaunas, especially by the late Middle Paleolithic, when the cultural associations are also more straightforward. Megafaunal species declined in the archaeofaunas of most areas long before they disappeared from Eurasian environments (Orlova *et al.*, 2000; Stuart, 1991). Some hunted ungulate faunas are biased toward prime-adult prey as early as 250 KYA, a tendency that distinguishes modern human hunting from that of all other large predators. It is likely that more generic forms of ungulate hunting by hominids existed earlier than this.

Although ungulate hunting behavior of some kind evolved long ago, early humans' foraging agendas were not equivalent to the range of variation typical of modern hunter-gatherers (Kuhn and Stiner, 2001). A number of archaeological manifestations defy explanation in these terms, such as the ways that premodern hominids kept themselves supplied with stone raw material, peculiar associations of scavenging and gathering of animal resources, and strangely liberal use of slow-moving, slow-growing small-prey populations that do not rebound easily from heavy exploitation. It is ironic as well that stone-tipped weapons surfaced only by the late Middle Paleolithic at the earliest, and that weapon heads were substantially elaborated upon only by the Upper and Epipaleolithic. Technology is often seen as the mechanism by which new lifeways became possible and doors to new niches opened. This may be true in some instances, but the faunal evidence reviewed

above indicates that many of the major radiations in hunting (and trapping) equipment evolved in response to, or at least postdate, independent shifts in hominid subsistence behavior.

Transitions in Eight Niche Dimensions

The actual role of hunting behavior in human evolution is difficult to separate from the excitement this subject normally provokes among modern scientists and lay audiences. There is considerable preoccupation with large game hunting in particular—the challenge and the equipment—perhaps because of what these phenomena mean socially to us now. Access to meat can be used to individual advantage in modern human and chimpanzee social groups. However, turning personal interactions in one's favor does not necessarily alter the rate at which individuals produce young or ensure that those young reach reproductive age. Specifically, men with meat does not necessarily translate to better nutrition for children (Hawkes, 2001; Hawkes *et al.*, 1997). The changes that our Pleistocene predecessors underwent probably did not involve the simple gain or loss of fundamental behaviors, such as hunting or scavenging, or basic responses to fluctuations in prey abundance. Evolutionary trends in hominid ecology are better expressed by the differing character and integration of gathering (some small prey are gatherable), hunting, scavenging, and food transport and processing tactics.

Several dimensions of hominid foraging niches are exposed by the archaeological evidence for carnivorous behavior. Most enlightening are the transitions or “boundary shifts” that occur in eight niche dimensions, shown in Fig. 9, and their tendency to cluster along certain time lines. The estimated timing of shifts in each of the eight niche dimensions adheres as strictly as possible to the limits currently set by the archaeological evidence. These shifts may represent ways in which competition was reduced in coevolutionary relations with other predators (following Pianka, 1978, p. 247) and, eventually, with neighboring human societies. A logged time scale is used so that the accelerated pace of behavioral change in the later periods can be viewed. Despite a dogged focus on carnivory in this review, links to technological evolution and, often, plant use are strong and widespread.

1. The *trophic level* occupied by a pure carnivore rests at the top or “end” of the food chain. Though meat is easily digested by the human body, a strict reliance on meat is the least efficient or direct way of accessing energy from primary production in an ecosystem, and thus supports proportionally few consumers relative to lower trophic levels. For this reason as much as any other, the most carnivorous Eurasian hominids were also the most highly dispersed, a situation that certainly applied to Middle Paleolithic peoples.

	TROPHIC LEVEL	CONSUMPTION EFFICIENCY	ENERGY RETENTION EFFICIENCY	PREY CAPTURE EFFICIENCY	UNGULATE AGE/SEX SELECTIVITY	NUMBER FORAGED SUBSTRATES	PREY TYPE EVENNESS	TYPE OF COMPETITION
	1	2	3	4	5	6	7	8
8 ky	plants as major protein sources	hot liquid cooking and pulverizing	permanent architecture	eliminating other predators	herd management	wetlands revolution	domesticate monoculturing	great demographic increases
10 ky				complex traps and weirs		domesticate herding		
40 ky	plant use intensifies	storage	tailored clothing portable	tools diversity further	prime-age biased ungulate hunting	fishing	BSR	more demographic pulses
70 ky	large game specialists		architecture	early radiation in weapons technology		avian prey	nearly exclusive focus on highly ranked prey	early demographic pulses
120 ky		simple tools and high cooperation	littoral shellfish	cultures regionalize/art				
250 ky	some ungulate hunting	greater hide working?			increased hunter cooperation (wood spears)	nonselective hunting?	?	competition among ungulate specialists intensifies?
500 ky			fire roasting	fire as heat source				
1 my	desultory hunting	tool assisted meat and marrow extraction	?	luck and cooperative stealing	terrestrial and low canopy foraging and gathering	mostly bits and pieces	competing carnivores pose high risks	
2.5 my	bone cracking							

Fig. 9. Threshold shifts in eight niche dimensions of carnivorous hominids on a logged time scale, from 2,500 to 8 KYA. Annotations refer to particular behavioral and trophic developments associated with each transition. ky: thousand years before present; my: million years before present.

Humans' position in the food chain dropped only with the broad spectrum revolution of the Upper Paleolithic and Epipaleolithic–Mesolithic, and, later, plant cultivation and domestication of the Neolithic, allowing them to exist at higher densities (e.g., Harpending and Bertram, 1975; Keeley, 1988).

2. *Consumption efficiency* in hominids clearly is mediated by food-processing equipment. Humble changes in feeding habits, spurred by simple needs and stresses, probably had the greatest impact on the evolution of hominids and recent humans. This is because food-processing techniques enhance the nutritional yield of a given food unit. Extending the “shelf life” of food

may even out the food supply and reduce the chances of acute malnutrition, immune system decline, and associated mortality. Oldowan stone hammers are the first, if unprepossessing, example of increased consumption efficiency in hominid adaptations. Fire is certainly another, appearing by perhaps 400–500 KYA. Both provide the footings for improvements in carcass processing, even if they were not first used in this way. This niche dimension evolved most rapidly, however, during the terminal Pleistocene, presumably in response to territorial circumscription and loss of mobility options.

Developments in storage, container, and grinding technologies revolutionized humans' ability to maximize food value from both plant and animal sources (e.g., see Keeley, 1988, and Testart, 1982, on food storage; Lupo and Schmitt, 1997, on bone grease rendering; Keeley, 1995, Miller, 1992, and Wright, 1994, on seed processing). Extracting more nutrition out of any available food package is one of the very few ways that a forager can improve upon natural patterns of food abundance. These innovations took the forms of hot-liquid cooking, pulverizing, and rendering techniques. In situations where resource exchange and pooling (*sensu* Cashden, 1985; Gould, 1980) cannot be used to damp the impact of resource lows, intensified processing solutions lent greater stability to humans' lives and thereby may have enhanced child survivorship. Although these later developments are especially vivid in archaeological records, the unique substitution more than 2.5 MYA of technology for physiological means for processing marrow and meat (Semaw, 2001) is no less remarkable for its time.

3. *Energy retention efficiency* is an elusive property of archaeological records, but a few obvious shifts were of great evolutionary importance. Fire as a source of heat must have lessened the total energy demands on the human metabolism. As evidence for fire increases in the archaeological record, so does that for extensive hide working on the basis of, for example, the proliferation of scraping tools in the early Middle Paleolithic (although micro/macrowear data are less clear on this point). Insulation mechanisms reached a new threshold in the Upper Paleolithic with portable architecture, evidenced by "tent rings" or rock alignments (e.g., Kozłowski, 1999), abandoned framing materials (e.g., mammoth bone huts, Pidoplichko, 1998; Soffer, 1990), and elaborations in hearth construction. Body insulation was perfected with tailored clothing in the northern Epipaleolithic, evidenced by needles and awls, advantages not easily surpassed even in the historic period. Permanent structures (Fig. 10) at the end of the Pleistocene represent later refinements in architectural insulation from the elements in some regions.
4. *Prey capture efficiency* is inferred partly from increasing time investments in tool manufacture and tool complexity—clearly in evidence with bone



Fig. 10. Partially preserved Natufian stone structure (ca. 12.5 KYA), Hayonim Cave, Israel, among the earliest of its kind in the world.

technology of the Upper Paleolithic and sophisticated wood working and cord craft in the Epipaleolithic and Mesolithic. Foragers generally cannot raise prey densities above environmental carrying capacity, but there is considerable room for changes in the amount of time and associated risks that people incur while hunting large prey. In the Middle Paleolithic and earlier it seems that forager cooperation in small groups overcame the limitations of simple wooden spears. Radiations of modest weapons occurred in the late Middle Paleolithic (e.g., Kozłowski, 2000; Shea, 1989), but these innovations were soon eclipsed by the appearance and rapid radiation of Upper Paleolithic technologic systems. Tools grew more complex and diversified thereafter, the designs of which apparently were more specific to task, culminating in a plethora of trapping gear in particular by the Mesolithic (nets, snares, weirs). Domestication may be an extension of this trend in capture efficiency, as herd tending and artificial enclosures reduce capture costs and losses to other predators.

5. *Ungulate age/sex selectivity* is an important indicator of changes in human predator–prey dynamics. A burgeoning emphasis on some generalized form of ungulate hunting may have evolved by 500 KYA or even earlier. This niche dimension found first clear expression, however, with the rise of prime-age–biased ungulate hunting, a strategy that distinguished

humans from all other major artiodactyl predators and may be sustainable only for an omnivore. Another shift in this niche dimension occurred at the Pleistocene–Holocene boundary with the domestication of certain ungulates, taking the form of age- and sex-specific culling at critical life stage transitions.

6. The *number of foraging substrates* exploited by hominids expanded from a terrestrial precedent, as human ancestors were principally ground foragers by 2.5 MYA. The addition of marine shellfish exploitation by 120 KYA seems almost trivial in the sense that it was practiced on a very small scale, confined to littoral habitats, and would have been a natural extension of collecting slow-moving small animals on land. It nonetheless is significant in that marine animals are part of very different food chains and energy production systems. Once part of human foraging repertoires, littoral marine exploitation appears again and again in foraging cultures, and it grew to monumental importance in some later Eurasian cases. The substantial introduction of avian prey (mostly ground and aquatic birds) by about 45 KYA in western Asia represents another new foraging substrate (since all can fly) and signals the early onset of the broad spectrum revolution. Yet another foraging substrate involves the addition of free-swimming fish in human diets after 20 KYA, e.g., Nile Valley of Africa (Peters, 1991; Stewart, 1989; Van Neer, 1986) and especially after 12 KYA, from marine, brackish, and freshwater habitats, culminating in the so-called wetland revolution by 8 KYA (e.g., Coles, 1992; Enghoff, 1991).
7. *Prey type evenness* refers to the predictions of diet breadth models in optimal foraging theory (reviewed by Pianka, 1978, pp. 256–262), specifically foragers' responses to the declining availability of highly ranked prey by taking a wider range of prey types. At relatively high latitudes ungulates clearly were preferred prey during the Paleolithic because of their potentially high food returns per foray, a standard set by 250 KYA if not before. At lower latitudes early foragers also made use of small animals that were easily caught and evidently nearly as attractive (highly ranked) as ungulates. Small quick-flight animals increasingly supplemented small-game off-take only from the early Upper Paleolithic onward. These animals are more costly to catch without special equipment, but with the rapid evolution of efficient capture devices in response to diet breadth expansion, a heavy dependence on these animals became sustainable. A new and potentially stable system seems to have grown out of this relationship by virtue of the exceptionally high population resilience of these animal taxa.

The indications of more even reliance on high- and low-ranked prey types (evenness) are greatest, however, *within* the small-game fraction of archaeofaunas, following the “slow-moving, gatherable” to “quick-moving, costlier to catch” dichotomy (Stiner *et al.*, 2000). This trend

implies that hominid populations were very small and highly dispersed prior to the late Middle Paleolithic. Human population densities increased during or just before the early Upper Paleolithic, and much more following the Last Glacial Maximum, in the Epipaleolithic and Mesolithic culture periods.

The causes of increasing human population densities during the later Paleolithic are not altogether clear. Periodic environmental circumscription provoked by climate change almost certainly stressed some populations by reducing the area of optimal human habitats (Bar-Yosef, 1995; Binford, 1968, 1999; Flannery, 1969; Keeley, 1995). Where seed exploitation was involved, dropping down a notch in the trophic pyramid is perhaps the most compelling cause of demographic increase (e.g., Harpending and Bertram, 1975; Keeley, 1995). Minor improvements in child survivorship that come with advances in food processing and storage also may have played a role (Stiner *et al.*, 2000). With resource intensification came increases in environmental carrying capacity (niche dimension 1, above), a relationship that could not easily be undone thereafter, because it also involved increased sedentism (Belfer-Cohen, 1991; Henry, 1985; Price and Gebauer, 1995; Soffer, 1985). Human diet breadth narrowed during the Neolithic because of increasing reliance on domesticates. However, human populations did not return to the levels typical of foragers because consumption of plant seeds increased further, becoming a central source of food energy. These observations lead directly into the eighth and final niche dimension recognized by this review.

8. *Interspecific competition* here is a substitution for the more standard contrast between *r*-selected and *K*-selected species discussed by population ecologists (e.g., MacArthur and Pianka, 1966; Pianka, 1978, pp. 246–247). All hominids were essentially *K*-selected organisms that exist close to environmental carrying capacity (e.g., Cachel and Harris, 1998), a condition that selects for competitive efficiency over reproductive efficiency. The rapid spread of Upper Paleolithic cultures at the expense of Neandertals, and the agricultural revolution, may represent exceptions to this generalization. In both instances demic expansion seems to have outstripped the growth rates of other, coeval societies, founded on a new ability to reproduce efficiently on a diet of lower-ranked foodstuffs (*sensu* Ammerman and Cavalli-Sforza, 1984; Harpending and Bertram, 1975; Pianka, 1978, p. 208) such as quick small game and plant seeds.

I nonetheless reserve this eighth dimension primarily for changes in the broadest *types* of competitive forces that may operate on hominid populations, specifically the declining influence of interspecific competition with time, and a corresponding increase in intraspecific competition as human populations grew and were forced to intensify their use of smaller territories. Interspecific competition with members of the order Carnivora

is responsible for the emergence of prime-adult-biased ungulate hunting by 250 KYA. Only after 20 KYA were competing carnivores conspicuously excluded from human life space (Gamble, 1986), roughly coincident with the evolution of “complex” hunter-gatherers in many areas (Bar-Yosef, 1995; Belfer-Cohen, 1991; Binford, 1968; Henry, 1989; Keeley, 1988). With Neolithic herding, extermination of competing large carnivores also grew in importance (e.g., Diamond, 1989).

The shift from predominantly interspecific to intraspecific competitive conditions is intimately connected to increases in human population density. The relative and absolute densities of predators and their prey on landscapes are known to affect the selective factors that operate on these populations (e.g., Gasaway *et al.*, 1992). Competition tends to escalate in high-density situations and where food is highly concentrated (e.g., Kruuk, 1972; Sinclair and Norton-Griffiths, 1979; Stanford, 2001). Winterhalder (1997, 2001) outlines the theoretical possibilities for evolution of intra-group resource exchange in humans, also noting the central importance of concentrated food packages and patches to this process. Although population increase does not explain every aspect of human cultural evolution, increases in human population densities do alter the rates of interspecific contact and, by extension, the potential arteries and geographic expanse over which social ties can be manipulated. Such conduits for managing resource risk are very unlikely to evolve below a certain density threshold, but, once evolved, they may persist among later populations living at low densities (e.g., Gould, 1980, on Australian aborigines).

Generally speaking, then, the archaeological record shows that hominids were more subject to the rigors of interspecific competition with carnivores early in their evolutionary history. The situation changed by the Upper Paleolithic, when most regional records were suddenly enriched with a myriad of ornaments (d’Errico *et al.*, 1998; Hahn, 1972; Kuhn *et al.*, 1999; Stiner, 1999; White, 1993; Zilhão and d’Errico, 1999) and/or decorated tools. The Upper Paleolithic is the first major period in which visual signals of “ethnicity” or individual identity are apparent (*sensu* Wobst, 1977). The marked regionalization of artifact styles in the Upper Paleolithic, and the shrinking territories of the Epipaleolithic and Mesolithic by the same kinds of criteria (e.g., Newell *et al.*, 1990; Price, 1991), tell us that the challenges to human survival came from the lay of cultural landscapes as much as from natural ones. Although food sharing and cooperative foraging must have been a part of Middle Paleolithic lifeways, and early people certainly had social lives, the demographic conditions that make large, open-ended networks numerically possible seem to have evolved quite late in the Paleolithic. Whatever the causes of demographic increase, the conditions of selection on human societies and foraging behavior shifted to a more profoundly intraspecific forum.

CONCLUSION

The earliest niche shifts involving hominid carnivory cluster at about 2.5 MYA, coincident with the beginning of the archaeological record. It is only at this point that intentionally modified or manuported stones are recognized. The next set of shifts (in Eurasia) cluster at about 500 KYA, when fire may have first appeared, and site and hominid fossil numbers increase to form an unambiguous record of human presence. A third set of shifts at 250 KYA includes the earliest appearance of prime-aged-biased ungulate hunting, an ecological development that separates the hominid hunting niche from those of other large predators. Middle Paleolithic technology also appeared around this time, likely including greater hide working and tanning. A narrower range of prey were exploited than before, nearly all of them ungulates with the notable exception of easily gathered small animals. High levels of carnivory no doubt kept hominid population densities very low. Archaeological records after about 250 KYA also differ from most earlier ones by more often fulfilling the definition of "site" as opposed to "locality," and caves came into greater use. Initial Upper Paleolithic cultures appeared between 50 and 45 KYA and spread across Eurasia like wild fire, presumably from the southcentral portion of this great land mass, replacing all Mousterian cultures by 28–30 KYA. Early population pulses seem to have preceded this transition, at least in western Asia. From the Upper Paleolithic onward the pace of change in material culture accelerated on multiple fronts, with the novel additions of body ornaments, decorated tools, and art to material culture. Indeed, the role of technology in human adaptations expanded to include visual communication and heightened manufacturing investments in some cases. The final series of shifts appear to have grown out of extreme climate changes, beginning with the Last Glacial Maximum 20 KYA and followed by rapid global warming.

Many of the changes in the eight niche dimensions listed above unfolded at exponential rates. The shifts in energy retention and consumption efficiency, and the rising importance of intraspecific competition, are linked to demographic increase, resulting from a lowering in trophic level. A series of demographic bursts, by orders of magnitude, left some parts of Eurasia more thickly populated than ever before. Evidence as diverse as reductions in human stature, increasing sedentism, and overburdened prey populations testify to the importance of these effects on Paleolithic subsistence systems. Interestingly, mass conflict among human communities is clearly evidenced only by the later Neolithic and after (e.g., Keeley, 1996; see also Boone, 1992).

Some qualitatively new niche dimensions were introduced with time (Fig. 9), indicating greater dimensionality of hominid foraging niches with time. As illustrative as this comparison of niche dimensions may be, it at best refines certain hypotheses on the basis of current evidence. These thresholds must continue to be tested with new evidence.

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