11. Paleolithic Diet and the Division of Labor in Mediterranean Eurasia

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Keywords Division of labor • hunter-gatherers • Middle trends are apparent in the technological record. Evidence of skill-intensive, time-consuming craft work that normally supports the food quest among recent forager economies also emerged in the early Upper Paleolithic, including indications

Abstract Hunter-gatherers of the recent era vary in many aspects of culture, yet they display great uniformity in their tendency to divide labor along the lines of gender and age. We argue on the basis of zooarchaeological, technological, and demographic evidence that the complementary economic roles of men and women so typical of ethnographically documented hunter-gatherers did not appear in Eurasia until the beginning of the Upper Paleolithic. The rich archaeological record of Middle Paleolithic cultures in Eurasia suggests, by contrast, that earlier hominins (Neandertals, among others) pursued narrowly focused economies, with women's activities more closely aligned to those of men with respect to schedules and territory use patterns. Hoofed animals were the principal source of meat for virtually all Middle and Upper Paleolithic foragers, but Upper Paleolithic people supplemented diets from large game with a broader spectrum of small animals, leading to considerable expansion in dietary breadth. Parallel

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skill-intensive, time-consuming craft work that normally supports the food quest among recent forager economies also emerged in the early Upper Paleolithic, including indications of dry hide scraping based on lithic micro-wear evidence and widespread use of bone tools suitable for working hide, plant fibers or both. The comparatively narrow reliance on large game animals during the Middle Paleolithic for meat would have constrained the demographic potential of these endemic populations. More broadly based economies, as indicated both by the faunal record and the increasing complexity of foraging and related technologies, appeared earliest in the eastern Mediterranean region and spread (with modification) to the north and west. The behavioral changes associated with the Upper Paleolithic record signal a wider range of economic and technological roles in forager societies, and these changes in adaptation may have provided the expanding Homo sapiens populations with a demographic advantage over other hominins in Eurasia. Middle Paleolithic human reproductive units probably were not robust at the micropopulation scale, and localized extinctions were likely to have been common. The demographic robustness of the Upper Paleolithic systems may be explained by the rise of new, diversified strategies for evening-out or sharing risk. When and where Middle and Upper Paleolithic populations first came into contact, the marginal advantages provided by collaborative economies meant that replacement of the Middle Paleolithic groups was only a matter of time.

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Any mention of the Middle and Upper Paleolithic also raises the topic of the biological and cultural transition in which Homo sapiens supplanted endemic members of the genus in Asia and Europe. An essentially African origin is widely recognized for anatomically modern human populations, and this continent is the (or at least the main) source of early behaviorally modern humans as well (Klein, 1999; Klein and Edgar, 2002). Eurasia would have posed unequal challenges for endemic and invading hominin populations because of its great environmental and climatic diversity. It is for this reason that Eurasia presents a natural laboratory for comparing some of the inferable limits of Middle and Upper Paleolithic adaptations during the Late Pleistocene. The Mediterranean Basin is particularly interesting for inter-period comparisons of human diets on account of its exceptional wealth of species and general community stability during the Late Pleistocene (Tchernov, 1998a, b).

Within Eurasia, the Upper Paleolithic period certainly earns its reputation as a revolution in human behavior. The appearance of the Upper Paleolithic, or the broader complex of behavioral characters sometimes called "modern human behavior", occurs abruptly in most Eurasian stratigraphic sequences. In contrast, elements of "modern human behavior" appear earlier and coalesce more gradually in some African Middle-Late Stone Age sequences (McBrearty and Brooks, 2000; Henshilwood and Marean 2003; Henshilwood et al., 2004). The contrasting pace of cultural change among regions and between continents is taken as evidence of an invasive expansion of behaviorally modern human populations into Eurasia at the expense of pre-existing hominins that possessed Middle Paleolithic culture.

Zooarchaeological evidence likewise testifies to important economic differences between Middle and Upper Paleolithic populations. The earliest demonstrable impacts of humans on biotic communities in Eurasia associate with early Upper Paleolithic hunter-gatherers in the eastern Mediterranean Basin roughly 45,000 years ago (Tchernov, 1992). Concomitant with the spread of anatomically modern *Homo sapiens* into Eurasia, we see the evolution of novel technological and social mechanisms for buffering or redistributing environmental risk. These behavioral developments coincide with permanent changes in human demographic potentials and the carrying capacities of environments.

Of central importance to social and economic change is the manner in which labor was divided within social groups. Human labor divided by gender and age is universal to recent small-scale societies and thus is characteristic of the modern human species. We propose that labor allocation was structured differently between the Middle and Upper Paleolithic periods. Though male and female foraging agendas differ within many higher vertebrates, this aspect of modern human behavior can be distinguished from examples of niche separation within other animals mainly in that human cultural adaptations *combine* complementary foraging roles for individuals of different ages and sexes with regular, pervasive sharing (Kuhn and Stiner, 2006). Divided, collaborative labor among recent humans is thought to confer very significant benefits in terms of foraging efficiency.

Although the so-called "division of labor" is an essential feature of the recent human condition, the circumstances in which this tendency evolved are poorly known. Criteria are needed to recognize changes in the organization of labor, and these criteria must have correlates in material culture and the dietary record if they are to serve archaeological studies. Such criteria can be developed from cross-cultural patterns in recent forager systems. This use of ethnographic information is very different from simple analogy: we are not looking for matches between present and past societies, but instead are using generalized cross-cultural patterns of recent forager systems to isolate anomalies in extinct culture systems. The anomalies must then be explained independently.

Zooarchaeologists and technologists have collected vast amounts of data on Paleolithic subsistence, far too much to review in this short essay. It is useful in light of this fact to consider how these findings might address some of the bigger questions of human behavioral evolution during the Late Pleistocene. As one small step towards this end, we propose that the typical patterns of labor division documented by ethnographic studies today emerged relatively late in human evolutionary history. With respect to Eurasia, the archaeological record of Middle Paleolithic humans (including the Neandertals, the most recent of the "non-modern" hominins) exhibits less evidence for in the array of distinct economic roles typically fulfilled by women and older children in recent hunter-gatherer groups than do the records of the Upper Paleolithic. We propose that Middle Paleolithic males, females, and juveniles all participated in a narrower range of economic activities that centered on obtaining large terrestrial game. This is not to say that every person performed identical activities or that they ate no plants; the availability of personnel to participate in some way in communal large game hunting was paramount, encouraging group members to remain in fairly close proximity to one another so as not to miss hunting opportunities. Such groups would exhibit less inter-individual variation in land use if compared to recent foragers.

We also argue that collaborative economic systems are more likely to have *first* evolved in the tropics or subtropics, where biotic diversity and evolutionary opportunities for diet diversification are greatest. This is not a matter of environmental determinism, but rather a product of repeated selection for dietary diversification as a function of low latitude and high biotic diversity. At some point in the past, cooperative economic systems may have given Upper Paleolithic humans a demographic advantage over Middle Paleolithic groups and their contemporaries, facilitating the rapid expansion of Upper Paleolithic culture throughout Eurasia.

The first part of this essay concerns observations about the division of labor by age and gender among historically

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Introduction

and ethnographically documented foraging peoples. The second part reviews Paleolithic evidence for differentiated, complementary economic roles, or the lack thereof, before the appearance of modern humans in Eurasia, based partly on data from the Mediterranean Basin. Meat use is emphasized in this essay for reasons of visibility in the archaeological record, but plant use is also addressed to the extent possible. The final part of the presentation speculates on where this unique, nearly universal human pattern might have originated, and how it contributed to the geographic spread and evolutionary success of Upper Paleolithic populations.

The Division of Labor in Recent Hunter-Gatherers

The axiomatic "division of subsistence labor" in recent foraging peoples holds that men tend to hunt large animals, and women and children tend to focus more of their efforts on gathering plants, capturing smaller animals or both. Ethnographic accounts also teach us that the boundaries between these broad economic roles are highly permeable, and that there are many individual departures from the general pattern. It is clear from some ethnographic studies, for example, that women possess the knowledge and skills needed for hunting large game, and that boys without mothers may learn to sew weatherproof clothing in regions where it is needed (Jenness, 1922; Landes, 1938; Briggs, 1970; Bailey and Aunger, 1989; Bailey, 1991; Endicott, 1999). It remains true, however, that in most circumstances individuals are prepared to cross roles mainly under duress or as temporary, rare arrangements. In addition, children at times forage for themselves (e.g., Laughlin, 1969; Watanabe, 1969), but they seldom can manage without supplementary food from parents or relatives (Blurton Jones et al., 1989, 1997; Bird and Bliege Bird, 2000; Kaplan et al., 2000; Bliege Bird and Bird, 2002; Walker et al., 2002)

Anthropologists offer at least three non-competing explanations for divided, collaborative labor among recent huntergatherers (Panter-Brick, 2002; Shennan, 2002). First, men and women may have different agendas that relate to their roles in childcare and the certainty of their genetic relationships to offspring (Hawkes and Bleige Bird, 2002). Second, avoidance of the more dangerous subsistence pursuits by women and children protects the reproductive core of population from undue risk, exposing "expendable" males more of the time. Third, the demands of childcare often cause women to favor activities that can be interrupted with minimum cost and entail relatively limited mobility (Kelly, 1995).

Certain other economic tendencies are also important to understanding the division of labor among recent foragers. These tendencies are of great interest in that they may provide archaeological criteria for identifying changes in socioeconomic patterns in Paleolithic records:

(a) Recent forager systems are very responsive to variations in the physical environment and the structure of biotie communities. It is for this reason as much as any other that large game, and meat in general, is most important to human diets in higher latitude terrestrial environments of the world, whereas gathered vegetable foods and small game tend to be more important at low latitudes (Keeley, 1988; Kelly, 1995; Binford, 2001; Marlowe, 2005). Following global patterns of biotic diversity, the range of variation in diet composition is also greater in the tropics and sub-tropics.

(b) Virtually all foragers eat fruits and greens if they are available. In circumstances where people depend on plants as major calorie sources, however, some combination of seeds, nuts and tubers almost always serve as staples (Keeley, 1988). Energy-rich seeds and nuts (and certain tubers) can be very abundant locally, but they tend to be time-consuming to collect and process (Kelly, 1995).

Staple plant resources present an extreme contrast to large game animals with respect to prevailing economic currencies (Table 11.1). Large animals generally yield high returns per unit foraging time (kJ per hour) but are unpredictable resources. Seeds and nuts give much lower net yields per increment time (kJ per kilogram acquired), but they have potentially high yields with respect to the volume obtained and the area of land utilized. Note in Table 11.1 that the returns from large and small game animals are similar to one another in terms of kJ/kg but not in terms of kJ per hour, and that all meat sources have lower returns per volume than those from intensively processed seeds and nuts.

Splitting tasks between the two broad food-getting agendas could result in a more efficient and less risky economic system, especially if the major food types have patchy and non-congruent distributions in the environment. By sharing resources at central places, a divided yet collaborative system spreads risk among individuals while getting the most from high-risk and low-risk resources in a single territory. Such a system requires, however, that the schedules, ranging patterns, and technology used by individuals differ on a regular basis and that at least some of the products of foraging are widely shared.

(c) In high-latitude environments where the options for gathering plants or small game hunting are quite limited, women and even children tend to assume responsibility for non-subsistence tasks that support the food quest, including collection of water and fuel, transport and construction of housing, and skill-intensive and time-consuming manufacture of tools, shelter, and clothing (Osgood, 1940; Balikci, 1970; Halperin, 1980; Waguespack, 2005). As important as some of these activities can be to the food quest, the workloads and daily and seasonal schedules of activity may differ greatly from those required to capture large animals.

Because many of these aspects of recent hunter-gatherer behavior are expressed in technology, it sometimes is possible to identify archaeological signatures of alternative female roles in_l circumstances where most of the food came from hunting

TABLE 11.1. Net energy yields of various food classes consumed by recent foragers, organized in terms of yield per hour (kJ/h) as oppose	ed to
yield by unit weight (kJ/kg) (From Kuhn and Stiner, 2006).	

	N cases	kJ/h		kJ/kg		
		Mean	Minimum	Maximum	Mean	SD
Large game	4	63,398ª	36,000	75,115	6,980 ^b	1,383
Small mammals	14	16,034ª	1,672	56,317	6,980 ^b	1,383
Reptiles	3	15,850 ^a	17,556	12,435	4,489 ^b	715
Birds	3	4,472ª	961	8,255	_	_
Roots and tubers	14	6,120ª	418	26,133	2,926°	1,680
Roots and tubers	13	1,882°	1,045	2,300	3,136 ^e	2,338
Seeds and nuts	34	3,520ª	380	18,538	13,188°	9,334
Seeds and nuts	9	6,508 ^d	1,203	24,933	13,188°	9,334
Seeds and nuts	6	_	_	-	19,372 ^e	6,250
Foliage	_	_	-		1,250°	819
Foliage	3	_	_	_	1,534°	186
Fruits	_	_	-	-	2,403°	1,463

^bData from Hawkes et al. (1982); Hurtado and hill (1987).

^cData from Pennington (1989).

^dData from Wright (1994, Table 11.2).

^eData from Wiessner (P. Wiessner, 2004, personal communication).

large animals – tools for craftwork – and where plant seeds and nuts served as staples - milling and grinding tools.

Division of Labor in the Paleolithic

Is there archaeological evidence for divided labor before modern humans. If so, how does it compare to known huntergatherer systems? Middle Paleolithic (Neandertals) and Upper Paleolithic humans were quasi-contemporaries in Eurasia, yet behaviorally distinct based on technological and other evidence. The Neandertals were distributed from northern Europe to the southern Mediterranean basin and well into Asia. The great expanse of this Old World geography permits systematic an examination how subsistence and technology varied across a range of environments and latitudes from 250,000 to 30,000 years ago. Neandertals and other Middle Paleolithic hominins were very intelligent, judging from the sizes of their brains, but Middle Paleolithic hunting implements were comparatively simple (Kuhn and Stiner, 2001), and modes of aesthetic expression were non-existent or are not preserved, though mineral pigments were used for purposes yet to be determined (Klein, 1999; Mellars, 1996).

Zooarchaeological Comparisons

A range of archaeofaunal studies indicate that Middle Paleolithic humans maintained exceptionally narrow foraging regimens, even in the Mediterranean Basin, with 95-99% of the animal foods procured by weight coming from large game (Fig. 11.1). Most surprisingly, Middle Paleolithic folk

behaved this way across a wide range of environments, and adjustments to variation in latitude and biotic diversity were quite limited. In the southern part of their ranges, Middle Paleolithic humans supplemented their meat intake with easily collected (gatherable) small prey animals - tortoises, marine shellfish, ostrich eggs, and large lizards. This makes sense in terms of optimal foraging models: the low handling costs of these small prey animals make up for their small size, bringing net yields closer to those of large game. It is strange, however, that small animals with higher handling costs were avoided in nearly all circumstances. Whatever flexibility existed in Middle Paleolithic foraging systems, it seldom extended to animals or plants with high capture or processing costs: this stands in stark contrast with the behavior of many recent hunter-gatherers.

Evidence for large game hunting, whether in the form of prey biomass comparisons, mortality patterns, or food transport patterns, fails to differentiate much between the economies of Middle and Upper Paleolithic societies in Eurasia, or even between the late Lower Paleolithic and the Middle Paleolithic (e.g., Adler et al., 2006; Gaudzinski, 2005; Grayson and Delpech, 2003; Stiner, 1994, 2005). One great difference between the predatory economics of these societies concerns the strategies for filling the gaps in large game availability. Upper Paleolithic foragers had more versatile methods of meat and plant food supplementation, which they used to even-out lows in the availability of highly ranked foods. This translates to permanent changes in dietary breadth, greater the inherent flexibility and internal diversity in foraging regimens, and, in some cases, increased environmental carrying capacity for some groups during the Upper Paleolithic period.

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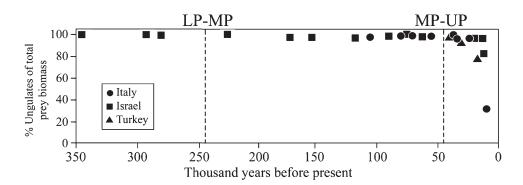


FIG. 11.1 Percentage of total prey biomass represented by ungulate prey in the assemblages of each Mediterranean faunal series. LP–MP refers to the Lower to Middle Paleolithic cultural transition; MP–UP the Middle to Upper Paleolithic transition.

Diet-breadth models suggest that the breadth or variety within forager diets depends, among other things, upon the availability of high quality, high-yield foods (Stephens and Krebs, 1986: 17-24). Narrow diets, in which low-quality prey are usually ignored, are practical only if the chance of finding more profitable prey types is high. If the encounter rates with preferred prey types decline, humans should and generally do broaden their diets by taking more lower-yield types. Dietary diversification is especially likely to occur when and where foragers put excessive pressure on preferred (i.e., highly ranked) resources, thereby forcing them into decline, and a reduction in the predator population may result (e.g., Broughton, 1997; Nagaoka, 2002). Some variation in diet breadth is reversible and to be expected within the confines of a given cultural adaptation ("adjustment") (Kelly, 1995). However, certain trends occur in forager diets over the long term, and these changes appear to represent evolutionary transitions in human adaptations (Tchernov, 1998a, b).

A major, early shift in the breadth of the meat diet coincides with the Middle to Upper Paleolithic culture boundary in southern Eurasia (Stiner, 2001). Evidence for this transition is widespread in the Mediterranean area, based on the relative exploitation of small quick animals, such as birds and lagomorphs, relative to slow-moving collectable small animals such as tortoises and shellfish. Although small animals may have served mainly as back-up resources, the highly conditional nature of small game use in the Paleolithic, along with great differences in the reproductive ecology of the species commonly hunted, reveal important changes in human ecology and demography. Small animals differ tremendously in their capture requirements, and some species - such as Mediterranean tortoises (Testudo) - are very sensitive to over-hunting and therefore represent the proverbial "canaries in the coal mine" for studying shifting human predator-prey interactions (Stiner, et al., 2000; Stiner, 2001).

The relative emphasis that humans placed on small prey types as grouped by predator defense traits – slow-moving or "sessile" animals, fast-running hares and rabbits, and quick flying game birds – implies significant reorganization in foraging economics in the Mediterranean region. It is striking that

Oxygen isotope cycle W C W С W types, 2.8 based on defense traits ness among small prey Italy Israel 2. Turkey 2.0 100 50 200 Thousand years before present

FIG. 11.2. Comparison of the degree of evenness across three small game categories in Paleolithic faunal assemblages, based on prey defense mechanisms (slow game, quick running terrestrial mammals and quick flying birds) (3 = most even, 1 = least even). Symbols are for assemblages from Italy (circle), Israel (square), and Turkey (triangle). Time is expressed on a logged scale, as are oxygen isotope climate cycles; (C) cold stage (W) warm stage (From Stiner, 2001).

Middle Paleolithic foragers seldom pursued small prey unless the animals could be collected with little effort. The situation changed abruptly around 45,000–50,000 years ago in the eastern end of the Mediterranean basin. Though archaeologists may differ in their proposed explanations, the pattern spread or emerged repeatedly in adjacent areas over the remainder of the Upper Paleolithic (consult, for example, various authors in Brugal and Desse, 2004).

An index of "evenness" (the Inverse of Simpson's Index; Simpson, 1949) in the small prey types collected by foragers summarizes the abrupt expansion in Paleolithic diets in Mediterranean contexts (Fig. 11.2). Much of the expansion in diet took place during a phase of climate cooling (Oxygen Isotope Stage 2; following Martinson et al., 1987). Had it occurred only in conjunction with global warming (OIS 3), the trend would be difficult to distinguish from natural shifts in the natural diversity and structure of humans' food supply. Instead, the evidence points to a categorical change in how 1



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humans interacted with small animal populations around the time of the Middle-Upper Paleolithic cultural transition. As noted above, the burgeoning importance of small quick prey in Upper Paleolithic diets is also detectable in the northern interior of Europe as well as in the warmer, arid lands to the south. Not every Upper Paleolithic forager group made use of costly small prey, but many did, in contrast to a nearly uniform lack of this behavior in the Middle Paleolithic in the same regions.

Differences in prey species productivity are a key to interpreting the economic trends for Paleolithic demography. An important quality of small prey animals that reproduce quickly is their greater potential reliability as a food source. Warm-blooded small animals, mainly partridges, hares, and rabbits, mature in 1 year or less and their populations rebound easily from heavy hur (Stiner et al., 2000). Predator-prey simulation modeling results show major differences in the scale at which humans could possibly hope to depend on tortoises, hares, and partridge-like birds for meat. Other things being equal, hare populations can support up to seven times greater off-take of adults and sub-adults by predators than tortoises can support, and partridges can support up to ten times greater off-take than tortoises. This means that humans' reliance on tortoises is only sustainable if human population densities are very low. Human's reliance on partridges and hares is sustainable in both low- and high-density conditions.

It is odd that Middle Paleolithic foragers in the Mediterranean region focused on slow-growing prey types so consistently, to the extent they pursued small animals at all. Where tortoises were an important food source in the Levant, there is no evidence for over-harvesting of the tortoises (i.e., no reduction in the mean body size of individuals or skewed age structures) until the very end of the Middle Paleolithic. At the threshold of the Middle-Upper Paleolithic cultural transition, when fast reproducing but difficult to capture small animals were added to human diets in significant numbers, the mean sizes of tortoises declined and unnatural skewing is evidenced in the age (size) structure of the harvested animals (Stiner, 2005: 139–147). Taken together, these observations imply that human populations of this particular region had first exceeded the availability or potential of high-ranked, high-return resources to support them as early as 50,000 years ago (but see Speth and Clark, 2006). The zooarchaeological evidence testifies to further demographic growth in the Mediterranean basin over the remainder of the Late Pleistocene, accelerating particularly 15,000 years ago (Binford, 1968; Flannery, 1969; Bar-Yosef, 1981; Keeley, 1988).

Technological Comparisons

Recent hunter-gatherers supplement their meat intake from large game with a variety of small animals and plant foods. Seed and nut hull fragments are found in a few Lower and Middle Paleolithic sites (e.g., Barton et al., 1999; Goren-Inbar et al., 2002; Madella et al., 2002), but there are no indications of stockpiled nuts or seeds. Of course, preservation of organic remains is rare for reasons of sediment chemistry and great time depth, but the kinds of large durable artifacts needed to grind or crush seeds and nuts are also absent, or exceedingly rare, in the Middle Paleolithic toolkit. Another potential complication is that many Middle Paleolithic groups occupied relatively cool, high-latitude environments, where a dietary bias towards large game is to be expected in recent foragers as well. Here, ethnographic experience would predict that females and other non-hunting members living at high latitudes would have taken on the role of technology specialists. The ethnographic record fails to predict Middle Paleolithic's low level of technological elaboration.

European Neandertals almost certainly wore simple skin garments of some kind. However, the types of artifacts commonly used by recent hunter-gatherers to manufacture tailored, weather-resistant clothing - bone needles and awls - did not become a regular part of the archaeological record until the Upper Paleolithic. Edge damage on stone tools from meat cutting and wet/fresh hide is relatively common in Middle Paleolithic assemblages, but evidence of working dry hide (cured leather) in the form of micro-wear traces on stone artifacts is comparatively scarce (e.g., Beyries, 1987; Anderson-Gerfaud, 1990; Lemorini, 2000; Martínez-Molina, 2005). Taken together, the archaeological evidence suggests that Middle Paleolithic females and juveniles did not undertake a suite of economic roles equal in the diversity to that within recent hunter-gatherer groups living in similar environments.

A different side of the technological record concerns innovations in the tools and techniques for increasing the digestibility of plant seeds and squeezing more nutrition out of animal carcasses. Food processing grew much more complex in the late Upper Paleolithic (<30,000 years ago) and especially during the Epi-Paleolithic. Significant increases in carcass processing efficiency were gained by the practice of bone grease rendering. Spongy bone parts were broken into small pieces, put in water, and the mixture was heated by adding fire-warmed stones. In this way pure fats could be skimmed off as they rose to the surface and the fat stored for months in this purified form. Grease rendering is evidenced in a variety of late Upper Paleolithic sites (ca. 26,000–14,000 years ago) in Portugal, France, Germany, and the Czech Republic by the combined presence of worn anvil stones, distinctive patterns of bone fragmentation, and thick litter of fire-cracked rocks (Audouze, 1987; Weniger, 1987; West, 1997; Stiner, 2003). Though heat-in-liquid techniques are labor-intensive, ethnoarchaeological studies show that people can raise the protein and fat yields per carcass well beyond what is possible from simpler extraction techniques (Binford, 1978; Lupo and Schmitt, 1997). This hard work can be worthwhile provided that it does not interfere with getting another carcass, or if the natural availability of large prey is

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limited. Only simpler "cold-marrow extraction" techniques were practiced during the Lower and Middle Paleolithic periods, which focused on the most concentrated marrow reserves in large medullary cavities (e.g., Bunn et al., 1980; Potts, 1984; Stiner, 1994; Speth and Clark, 2006).

Women's Work in the Middle Paleolithic

The marked skeletal and muscular robusticity of the Neandertals indicates high levels of activity among both males and females (Trinkaus, 1983, 1986). Recent experimental work suggests that activity levels during childhood development were high as well (Lieberman et al., 2001). Thus there is little reason to think that females were simply reproductive vessels.

Some paleoanthropologists have proposed that Middle Paleolithic women and their children were economically independent of mature males (Binford 1984; Soffer, 1994), perhaps consuming small resources in the field rather than carrying them to base camps. This hypothesis would predict a class of archaeological evidence - field consumption stations - that currently is not known for the Middle Paleolithic, in contrast to some Holocene archaeological records (e.g., Great Basin, Elston and Zeanah, 2002) and some recent aboriginal populations of Australia. The archaeological evidence instead points to a third hypothesis in which women, children, and men all participated actively in the exploitation of large animals. This third model assumes that the archaeological record is representative of Middle Paleolithic diets, and women and juveniles somehow participated in large game hunting more extensively, more consistently, and more directly than is generally seen among recent foragers. This is not to deny the importance of large game hunting among many recent foragers. Nor should we assume that social and economic roles in Middle Paleolithic societies were identical among age groups or by gender. Rather, it is the narrowness of the large game focus during the Middle Paleolithic and its associated search requirements that constitute an important difference in behavior and in labor organization in particular.

Hunting large animals is a rough and dangerous business, all the more so if the hunters were equipped with thrusting spears to be used at close range (Churchill, 1993; Shea, 1997). Like other social carnivores, humans can gain advantages over prey if some members of the hunting party act as artificial surrounds or funnels for directing the movement of quarry toward the killers. Evidence for healed fractures is common on Neandertal skeletons, although the sex distribution for these injuries is unclear (Berger and Trinkaus, 1995). Individual roles in hunts can vary according to several categories of risk, from direct physical contact to the more generalized challenges of frequent moves and foraging on rough or unfamiliar ground. We can be sure that those individuals who came in closest contact with large prey generally incurred the greatest risks. Other individuals ean take the more circumspect 161

meat and still can be essential to the pay-off of a hunt. A vast zooarchaeological literature shows us that large amounts of ungulate meat and bone often were carried back to base camps during the Middle Paleolithic. Body parts of prey were processed and apparently shared at these camps, so the close proximity of group members was not simply about keeping hungry hunters honest. Still, the fates of Middle Paleolithic women and children would have been very closely allied to male hunting with respect to activity schedules and ranging patterns.

Top-level carnivores can only exist at very low population densities in terrestrial environments for at least two reasons. First, a heavy dependence on large game for food energy implies an ecological position high in the trophic pyramid where entropy effects are extreme. Second, large game animals can yield high average return rates, but these resources are unpredictable as staple food sources (Hawkes, 1996; Bliege Bird, 1999; Wrangham et al., 1999; Kaplan et al., 2000). In humans, the high day-to-day variance in protein and fats available to children and pregnant or lactating women will limit the reproductive potential of a highly carnivorous population. While the long existence of Middle Paleolithic lifeways across the Old World indicates that adult females in these societies enjoyed reasonable levels of reproductive success, women's fertility would have remained very low due to the unpredictable diet and the necessity of women's cooperation and ready proximity for hunting operations. Middle Paleolithic populations seldom attained large sizes and were subject to frequent crashes (Semino et al., 2000; Pennington, 2001; Richerson et al., 2001; Boone, 2002; Shennan, 2002).

To summarize thus far, Middle Paleolithic society must have been constrained by the combined influences of high risks of injury all around, frequent residential moves, and economies based on a high quality but unpredictable nutrient supply subject to boom and bust cycles. The demographic consequence of everyone participating closely in the exploitation of large game helps to explain the limited demographic potential for Middle Paleolithic populations.

Labor Allocation and Population Competition

Where did the modern pattern of divided labor first evolve, and how might it have contributed to the evolutionary success of Upper Paleolithic Homo [sapiens] sapiens? Upper Paleolithic humans were big game hunters, as were the Middle Paleolithic people before them, but Upper Paleolithic groups supplemented their diets in more versatile ways, particularly where the diversity of animal and plant species was naturally great. In the Jordan and Nile River valleys, a variety of small quick animals were added to the diets quite early on. Even fish, seeds and tubers, late additions to human diets elsewhere in the Old World, were exploited along the rivers and lakes of the Great Rift System that links Africa and Asia (Stewart, 1989; Wright, 1994; Weiss et al., 2004) during the Last Glacial Maximum 23,000–20,000 years ago.

The Upper Paleolithic also presents widespread evidence for the manufacture of elaborate clothing and shelters. Craft toolkits were, as one might expect from ethnographic experience, more elaborate and abundant in sites of the higher latitudes (e.g., Berke, 1984; Soffer et al., 1998; Owen, 2005), but they occur in sites throughout Eurasia from the Upper Paleolithic onward (Kuhn and Stiner, 2001). Micro-wear evidence from stone tools documents similar increases in the complexity of craftsmanship; edge damage on Upper Paleolithic stone tools from hide and particularly leather (both wet and dry) preparation is common (e.g., Vaughn, 1985; Donahue, 1988), even in the Initial Upper Paleolithic phase in southern Turkey (Martínez-Molina, 2005). The behavioral contrast in labor organization between the Middle and Upper Paleolithic therefore is suggested both in the realm of subsistence and the domain of technological support.

Here lies a critical point: the two dimensions of variability in recent forager behavior - technology and dietary breadth - must be considered simultaneously across cases and environments in order to appreciate a fundamental socioeconomic distinction between Middle and Upper Paleolithic populations. The technologies of recent foragers are most complex at high latitudes, and thus we can expect the strongest archaeological evidence for divided, collaborative labor in colder environments to be expressed in material culture. The diets and foraging activities of individuals are more varied in lower latitude environments (Kelly, 1995), where ecosystems also harbor greater natural biodiversity, and the division of labor is most vividly expressed by the great breadth of individual and group diets. Both of these dimensions of forager behavior testify to the inherent flexibility of modern human responses to environmental variation. Together, the two dimensions expose coarse but useful generalizations about how recent foragers tend to solve the problems of environmental risk and variable food supplies.

While these observations belabor the obvious from an ethnographic perspective, such adjustments to environmental variation are not typical of Middle Paleolithic populations. Diversification during the Upper Paleolithic may be emphasized more in subsistence or in technology from one region to another, but either (or both) were clearly within their capacity. This behavioral contrast in the technological and dietary dimensions of culture is significant for the niche evolution, environmental carrying capacity, and changes in the internal organization of Paleolithic societies. It also seems that Upper Paleolithic society differed from Middle Paleolithic in Eurasia due to wider range of economic and social roles overall.

We do not believe that stereotypical patterns of divided labor were an inevitable evolutionary development. Rather, the modern pattern of divided cooperative labor by age and gender could have been an historical accident, stemming in part from the tropical and sub-tropical environments where *Homo sapiens* first evolved. Cooperative economies organized around complementary subsistence roles are more likely to develop spontaneously and repeatedly in low latitude regions for at least three reasons: (1) all classes of food resource other than large game are more diverse and abundant in low latitude ecosystems, and some are available for a greater part of the year; (2) plant resources such as tubers may be especially abundant, and early examples of intensive plant processing first appear in archaeological records at low latitudes; (3) resources that children can collect for themselves are more diverse and abundant, giving children and their mothers greater options for economic independence. Under these conditions individuals have more options in their foraging agendas, and strategies are free to diverge into a greater range of roles.

The African Middle Stone Age is not as extensively documented as the Paleolithic record in Eurasia, but there are hints of a greater range of subsistence and technological roles in some areas, based on fish remains and bone harpoons (Yellen et al., 1995) and scattered reports of early grinding tools suitable for processing seeds or nuts (McBrearty and Brooks, 2000). The eastern Mediterranean Basin (a.k.a. the Levant), situated at the northern end of the rift, is host to what are arguably the earliest Upper Paleolithic culture complexes in Eurasia (Bar-Yosef, 2000). Some, though not all, of these early Upper Paleolithic assemblages also manifest early evidence for dietary expansion (Stiner, 2001; Stiner et al., 2002).

Many of the new foods added to human diets in the Upper Paleolithic associate with distinct foraging substrates, are costly to capture or process, and differ from large game hunting in the energetic currencies most relevant to their exploitation. Specifically, time spent searching and capturing prey is a central consideration in the case of large hoofed animals; the absolute volume acquired and access rights may be much more important in the case scattered patches of edible plants or small animals (Table 11.1; see also Stephens and Krebs, 1986: 7-9 on currency assumptions in foraging models). The benefits of niche separation within human groups are likely to increase as the diet broadens over the long run, due to less overlap or symmetry in the schedules and locations in which various foods can be obtained (reviewed by Pianka, 1988: 254). A population of diverse specialists (our UP population) might actually out-compete a population of generalists (MP population) in which all individuals hold more similar roles, even if average individual foraging efficiency is lower within the Upper Paleolithic population (Horan et al., 2005). This kind of within-population diversification would be especially advantageous in environments where a variety of key resources occur at disparate locations or times (MacArthur and Levins, 1964, 1967; Pianka, 1988: 254), or if distinct mechanical strategies are required to obtain them efficiently. Though we propose that the advantages of divided, cooperative labor first arose in the tropics or subtropics, such economic systems would have conferred different but equally valuable advantages in patchy and seasonally

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variable temperate environments. In cooler regions, individual roles in producing and maintaining high-quality clothing and shelter may substitute for diversifying foraging roles.

McBrearty and Brooks' (2000) important summary article documents precocious developments in technology and art on the African continent. Also very significant is the uneven distribution of these phenomena in time and space, as if the features of interest in Middle Stone Age cultures genuinely came and went many times. The same may be said for the archaeological record of the Near East (Bar-Yosef, 2000). No single continent of origin is necessary to this hypothesis about the origins of the modern division of labor, even if this is how it turned out. Instead the pattern was one of many and often isolated experiments across diverse subtropical habitats. Low latitude ecosystems provide consistently rich opportunities for dietary diversification, should natural selection favor this behavior for any reason. Problems of dating notwithstanding, the geography of early developments in "modern human behavior" - art, stone-tipped weapons, bone tools are often cited - includes much of Middle Stone Age Africa and adjacent areas of western Asia (e.g., Kuhn et al., 2001; Vanhaeren et al., 2006) and possibly also eastern Europe.

The spread of "collaborative economies" would have stemmed from their demographic consequences. As the modern humans entered new environments with novel food supplies and physical challenges, the basic (tropical) system would have continued to change without losing its diverse, collaborative character, because of the competitive advantage of greater efficiency (Winterhalder and Goland, 1993). In patchy and seasonally variable temperate environments, clothing and shelter technology became as or more important than diversifying foraging roles.

There is little reason to believe that this cultural transition marks the beginning of human "inventiveness". The value of innovations for labor collaboration was set by the unprecedented juxtaposition of two economically distinct populations. The demographic edge of Upper Paleolithic foragers over neighboring Middle Paleolithic populations was probably quite subtle, yet more than enough to make a difference over a few thousand years (Zubrow, 1989).

Most narratives of human evolutionary history are orthogenetic in that they portray change as a simple progression of physical or cultural forms. Yet the history of hominin diets after roughly 500,000 years ago is not marked by progressive increases in their basic aptitude as hunters of large animals. Rather, there seems to have been an evolutionary trade-off between tightly bound cooperation among group members in surrounding prey and killing them with simple weapons at close range, and an increasing incidence of solo or small-party hunting, wherein advantages were gained from the greater efficiency of high-investment weapons/systems. The rising importance of the latter system, even in combination with the first, effectively freed some individuals to engage at times in quite different and spatially remote foraging activities. This trade-off represents over the long term a shift in the value of individual forager's time and a relaxation of the requirement that individuals stay in nearly continuous proximity to one another. With these kinds of changes in hunting, we also see greater or more intensive exploitation of plants and the generation and maintenance of complex material culture in support of the food quest.

On the Problem of Neandertal Extinction

How might one behaviorally defined "population" have driven another to extinction or largely replaced it, if the differences in demographic potential were marginal? The Neandertals, the most recent of Middle Paleolithic hominins, thrived for more than 100,000 years and then went extinct soon after 30,000 years ago (Hublin et al., 1995; Mellars, 1996). How could they have persisted for such a long time and then suddenly become so fragile?

Competing populations need not be terribly different from one another in order for one to absorb or supplant the other. Competitive exclusion in its original conception is said to occur only if two populations come into competition and cannot achieve an evolutionary stable coexistence (Pianka, 1988: 221-222). If both populations were small at the outset and existed well below environmental carrying capacity, each could at first grow exponentially, limited mainly by their respective reproductive potentials. Later, as the habitat(s) fills-in, the growth rate of each population would decelerate. Populations are unlikely to have identical rates of increase, competitive abilities or carrying capacities, and a threshold will be reached when one population suddenly gains an incremental advantage. While one population stops growing, the other's rate of increase is still positive and eventually inhibits the first population. In this way, the second population will eventually exclude the first.

In the concept of a "rugged fitness landscape" (Wright, 1932; Palmer, 1991), within which high points represent adaptive configurations of relatively greater fitness and low points areas of reduced fitness, selection tends to drive populations toward the optimal peak that is closest to the population's starting point. This occurs even though the rugged fitness landscape includes many fitness peaks of varying heights, representing local sub-optima, separated by many "valleys". Historical contingency plays a critical part in this process: having ascended one fitness peak, it is very difficult for that population to shift to another, even if a distant peak provides greater maximum fitness. Radical peak-shifting is seldom rewarded under these circumstances, because crossing deep valleys necessarily involves a reduction in fitness. Only severe environmental or demographic perturbations may dislodge the subject population from the sub-optimal fitness peak it currently occupies, metaphorically clearing the way to a higher peak now visible on the horizon and accessible.

Neandertals, though long successful in Eurasia, were ascending a local fitness peak that may not have been the highest in the total fitness landscape. While they were alone in Eurasia, existing at low densities, there would have been no benefit

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to diversified subsistence. Indeed there may not have been room in much of their natural range for experimentation with lower-return resources. The low latitudes have, by contrast, probably always supported the densest hominin populations and also presented the most consistent incentives for dietary diversification due to their inherently higher biodiversity. Diversified economies in these regions could represent a high fitness peak relative to all others. Here, human populations would likely undergo repeated episodes of expansion, and possess certain social and economic pre-adaptations as part of their evolutionary legacies.

We suggest the demographic expansion of early Upper Paleolithic populations caused perturbations in the fitness landscape that had not existed previously in Eurasia. The more flexible foraging and technological systems of Upper Paleolithic populations provided greater micro-population stability_l allowed them to supplant indigenous Middle Paleolithic populations. It seems that Upper Paleolithic groups were also exceptionally good at holding on to any habitat gained, apparently by reducing the probability of population crashes and effectively hugging the ceiling of environmental carrying capacity. These qualities allowed Upper Paleolithic populations to expand rapidly through Eurasia after 45,000 years ago.

In this way of thinking, the group-level economic advantages of Upper Paleolithic populations was a byproduct of a genderbased division of labor and food sharing. The "inflexibility" of Middle Paleolithic culture was a product of the success and stability of that adaptation, rather than being a question of lower intelligence. In a few areas at least, late Neanderthals did develop or adopt some features of the "modern behavioral repertoire" (d'Errico et al., 1998, 2003). However, estimates of the rates of long-term demographic increase before 50,000 years ago are remarkably low, a conclusion that also is supported by the zooarchaeological evidence.

There seems to have been a lack of economic incentives for large-brained, mobile Middle Paleolithic hunters to squeeze more out of traditional food supplies, and little if any long-term selection for greater foraging efficiency. This implies that, like other organisms - but unlike recent humans - Middle Paleolithic hominins responded to population-resource imbalances almost exclusively through localized depopulation, rather than by increasing food yields by intensifying resource extraction or diet diversification (Stiner and Kulm, 2006). More difficult to explain than Middle Paleolithic conservatism is how Upper Paleolithic populations managed to exist at higher densities in the same range of environments. An important clue as to how higher population density could become a permanent condition lies in persistent diversification during the Upper Paleolithic period onward and a net lowering of humans position in regional food webs.

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References

- Adler, D.S., Bar-Oz, G., Belfer-Cohen, A., Bar-Yosef, O., 2006. Ahead of the game – Middle and Upper Paleolithic hunting behaviors in the southern Caucasus. Current Anthropology 47, 89–118.
- Anderson-Gerfaud, P., 1990. Aspects of behavior in the Middle Paleolithic: functional analysis of stone tools from southwest France. In: Mellars, P. (Ed.), The Emergence of Modern Humans: An Archaeological Perspective. University Press, Edinburgh, pp. 389–418.
- Audouze, F., 1987. The Paris Basin in Magdalenian times. In: Soffer,O. (Ed.), The Pleistocene Old World: Regional Perspectives.Plenum, New York, pp. 183–200.
- Bailey, R.C., 1991. The Behavioral Ecology of Efe Pygmy Men in the Ituri Forest, Zaire. Museum of Anthropology, University of Michigan, Ann Arbor, MI.
- Bailey, R.C., Aunger, A., 1989. Net hunters vs. archers: variations in women's subsistence strategies in the Ituri Forest. Human Ecology 17 (3), 273–297.
- Balikci, A., 1970. *The Netsilik Eskimo*. Natural History Press, Garden City, NY.
- Barton, R.N.E., Currant, A., Fernandez-Jalvo, Y., Finlayson, C., Goldberg, P., Macphail, R., Pettit, P., Stringer, C., 1999. Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard, and Ibex caves. Antiquity 73, 13–24.
- Bar-Yosef, O., 1981. The Epi-Palaeolithic complexes in the southern Levant. In: Cauvin, J., Sanlaville, P. (Eds.), Préhistoire du Levant. Éditions du C.N.R.S, Paris, pp. 389–408.
- Bar-Yosef, O., 2000. The Middle and early Upper Paleolithic in Southwest Asia and neighboring regions. In: Bar-Yosef, O., Pilbeam, D. (Eds.), The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean. Peabody Museum Bulletin 8. Peabody Museum Press, Harvard University, Cambridge, MA, pp. 107–156.
- Berger, T., Trinkaus, E., 1995. Patterns of trauma among the Neanderthals. Journal of Archeological Science 22, 841–852.
- Berke, H., 1984. The distributions of bones from large mammals at Petersfels. In: Berke, H., Hahn, J., Kind, C.-J. (Eds.), Upper Palaeolithic Settlement Patterns in Europe. Institut fur Urgeschichte der Universitat Tübingen, Verlag Archaeologica Venatoria, Tübingen, pp. 103–108
- Beyries, S., 1987. Variabilité de l'Industrie Lithique as Mousterien. Approche Functionelle sur queleues Gisments Fraçaises. International Series S328. British Archaeological Reports, Oxford.
- Binford, L.R., 1968. Post-Pleistocene adaptations. In: Binford, S.R., Binford, L.R. (Eds.), New Perspectives in Archaeology. Aldine, Chicago, IL, pp. 313–341.
- Binford, L.R., 1978. Nunamiut Ethnoarchaeology. Academic Press, New York.
- Binford, L.R., 1984. Faunal Remains from Klasies River Mouth. Academic Press, Orlando, FL.
- Binford, L.R., 2001. Constructing Frames of Reference. University of California Press, Berkeley, CA.

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- Bird, D.W., Bliege Bird, R., 2000. The ethnoarchaeology of juvenile foragers: shellfishing strategies among the Meriam children. Journal of Anthropological Archaeology 19, 461–476.
- Bliege Bird, R., 1999. Cooperation and conflict: the behavioral ecology of the sexual division of labor. Evolutionary Anthropology 8, 65–75.
- Bliege Bird, R., Bird, D., 2002. Constraints of knowing or constraints of growing? Fishing and collecting by the children of Mer. Human Nature 13, 239–267.
- Blurton Jones, N., Hawkes, K., O'Connell, J.F., 1989. Studying the costs of children in two foraging societies: implications for schedules of reproduction. In: Standon, V., Foley, R. (Eds.), Comparative Socieoecology of Mammals and Man. Blackwell, London, pp. 365–390.
- Blurton Jones, N., Hawkes, K., O'Connell, J.F., 1997. Why do Hadza children forage? In: Seigel, N., Weisfield, G.E., Weisfield, C.C. (Eds.), Uniting Psychology and Biology: Integrative Perspectives on Human Development. American Psychological Association, Washington, DC, pp. 279–313.
- Boone, J., 2002. Subsistence strategies and early human population history: an evolutionary ecological perspective. World Archaeology 34, 6–25.
- Briggs, J.L., 1970. *Never in Anger: Portrait of an Eskimo Family*. Harvard University Press, Cambridge, MA.
- Broughton, J., 1997. Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: ichthyofaunal evidence from the Emeryville Shellmound, California. Antiquity 71, 845–862.
- Brugal, J.-P., Desse, J. (Eds.), 2004. Petits Animaux et Sociétiés Humaines, du Complément Alimentaire aux Resources Utilitaires, XXIV^e rencontres internationales d'archéologie et d'histoire d'Antibes, 546 pages.
- Bunn, H.T., Harris, J., Isaac, G., Kaufulu, Z., Kroll, E., Schick, K., Toth, N., Behrensmeyer, A.K., 1980. FxJj50, an early Pleistocene site in northern Kenya. World Archaeology 12, 109–136.
- Churchill, S.E., 1993. Weapon technology, prey size selection and hunting methods in modern hunter-gatherers: implications for hunting in the Palaeolithic and Mesolithic. In: Peterkin, G.L., Bricker, H.M., Mellars, P. (Eds.), Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia. Archeological Papers of the American Anthropological Association No. 4, Washington, DC, pp. 11–24.
- d'Errico, F., Zilhão, J., Baffier, D., Julien, M., Pelegrin, J., 1998. Neanderthal acculturation in western Europe? A critical review of the evidence and its interpretation. Current Anthropology 39, S1–S44.
- d'Errico, F., Julien, M., Liolios, D., Vanhaeren, M., Baffier, D., 2003. Many awls in our argument. Bone tool manufacture and use in the Châtelperronian and Aurignacian levels of the Grotte du Renne at Arcy-sur-Cure. In: Zilhão, J., d'Errico, F. (Eds.), The Chronology of the Aurignacian and of the Transitional Technocomplexes. Dating, Stratigraphies, Cultural Implications. Trabalhos de Arqueologia 33. Instituto Português de Arqueologia, Lisbon, pp. 247–270.
- Donahue, R., 1988. Microwear analysis and site function of Paglicci Cave, level 4a. World Archaeology 19, 357–375.
- Elston, R.G., Zeanah, D.W., 2002. Thinking outside the box: a new perspective on diet breadth and sexual division of labor in the Pre-archaic Great Basin. World Archaeology 34 (1), 103–130.
- Endicott, K.L., 1999. Gender relations in hunter-gatherer societies. In: Lee, R.B., Daly, R. (Eds.), The Cambridge Encyclopedia of Hunter-Gatherers. Cambridge University Press, Cambridge, pp. 411–418.
- Flannery, K.V., 1969. Origins and ecological effects of early domestication in Iran and the Near East. In: Ucko, P.J., Dimbleby, G.W.

(Eds.), The Domestication and Exploitation of Plants and Animals. Aldine, Chicago, IL, pp. 73–100.

- Gaudzinski, S., 2005. Monospecific or species-dominated faunal assemblages during the Middle Paleolithic in Europe. In: Hovers, E., Kuhn, S. (Eds.), Transitions Before the Transition: Evolution and Stability in the Middle Paleolithic and Middle Stone Age. Springer, New York, pp. 137–149.
- Goren-Inbar, N., Sharon, G., Melamed, Y., Kislev, M., 2002. Nuts, nut cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. Proceedings of the National Academy of Sciences of the USA 99 (4), 2455–2460.
- Grayson, D.K., Delpech, F., 2003. Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France). Journal of Archaeological Science 30, 1633–1648.
- Halperin, R.H., 1980. Ecology and mode of production: seasonal variation and the division of labor by sex among hunter-gatherers. Journal of Anthropological Research 36, 379–399.
- Hawkes, K., 1996. Foraging differences between men and women: behavioral ecology of the sexual division of labor. In: Steele, J., Shennan, S. (Eds.), The Archaeology of Human Ancestry: Power, Sex, and Tradition. Routledge, London, pp. 283–305.
- Hawkes, K., Bliege Bird, R., 2002. Showing off, handicap signaling, and the evolution of men's work. Evolutionary Anthropology 11, 58–67.
- Hawkes, K., Hill, K., O'Connell, J., 1982. Why hunters gather: optimal foraging and the Ache of eastern Paraguay. American Ethnologist 9, 378–398.
- Henshilwood, C.S., Marean, C.W., 2003. The origin of modern human behavior: critique of the models and their test implications. Current Anthropology 44, 627–652.
- Henshilwood, C., d'Errico, F., Vanhaeren, M., van Niekerk, K., Jacobs, Z., 2004. Middle Stone Age shell beads from South Africa. Science 304 (5669), 404.
- Horan, R.D., Bulte, E., Shogren, J., 2005. How trade saved humanity from biological exclusion: an economic theory of Neanderthal extinction. Journal of Economic Behavior and Organization 58, 1–29.
- Hublin, J.-J., Barroso, C., Medina, P., Fontugne, M., Reyss, J., 1995. The Mousterian site of Zafarraya (Andalucia, Spain): dating and implications on the paleolithic peopling processes of Western Europe. Comptes rendus de l'Académie des sciences. Série 2, Sciences de la terre et des planets 321, 931–937.
- Hurtado, A.M., Hill, K., 1987. Early dry season subsistence ecology of Cuiva (Hiwi) foragers of Venezuela. Human Ecology 15, 163–187.
- Jenness, D., 1922. The Life of the Copper Eskimo. Reports of the Canadian Arctic Expedition 1913–1918, N. 12. F.A. Acland, Ottawa.
- Kaplan, H., Hill, K., Lancaster, J., Hurtado, A.M., 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evolutionary Anthropology 9, 156–185.
- Keeley, L.H., 1988. Hunter-gatherer economic complexity and population pressure. Journal of Anthropological Archaeology 7, 373–411.
- Kelly, R.L., 1995. *The Foraging Spectrum*. Smithsonian Institution Press, Washington, DC.
- Klein, R.G., 1999. *The Human Career: Human Biological and Cultural Origins*. (2nd edition). University of Chicago Press, Chicago, IL.
- Klein, R.G., Edgar, B., 2002. *The Dawn of Human Culture*. Wiley, New York.
- Kuhn, S.L., Stiner, M.C., 2001. The antiquity of hunter-gatherers. In: Panter-Brick, C., Layton, R.H., Rowley-Conwy, P.A. (Eds.), Hunter-Gatherers: Interdisciplinary Perspectives. Cambridge University Press, Cambridge, pp. 99–142.

•

Kuhn, S.L., Stiner, M.C., 2006. What's a mother to do? A hypothesis about the division of labor among Neanderthals and modern humans in Eurasia. Current Anthropology 47, 953–980.

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- Kuhn, S.L., Stiner, M.C., Reese, D.S., Güleç, E., 2001. Ornaments in the earliest Upper Paleolithic: new results from the Levant. Proceedings of the National Academy of Science 98 (13), 7641–7646.
- Landes, R., 1938. The Ojibwa Woman. Norton, New York.
- Laughlin, W., 1969. The demography of hunters: an Eskimo example. In: Lee, R.B., Devore, I. (Eds.), Man the Hunter. Aldine, Chicago, IL, pp. 241–243.
- Lemorini, C., 2000. Reconnaître de Tactiques d'Exploitation du Milieu au Palélithique Moyen. La Contribution de l'Analyse Fonctionelle. Étude Fonctionelle des Indsutries Lithiques au Grotta Breuil (Latium, Italie) et de La Colombette (Bonnieux, Valcluse, France). International Series 858. British Archaeological Reports, Oxford.
- Lieberman, D.E., Devlin, M., Pearson, O.M., 2001. Articular surface area responses to mechanical loading: effects of exercise, age and skeletal location. American Journal of Physical Anthropology 116, 266–277.
- Lupo, K.D., Schmitt, D.N., 1997. Experiments in bone boiling: nutritional returns and archaeological reflections. Anthropozoologica 25–26, 137–144.
- Macarthur, R.H., Levins, R., 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences of the USA 51, 1207–1210.
- Macarthur, R.H., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101, 377–385.
- Madella, M., Hovers, E., Jones, M.K., Goldberg, P., Goren, Y., 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): the evidence from Phytolith studies. Journal of Archaeological Science 29, 703–719.
- Marlowe, F.W., 2005. Hunter-gatherers and human evolution. Evolutionary Anthropology 14, 54–67.
- Martínez Molina, K., 2005. Análisis Functional de Industrias Líticas del Pliestoceno Superior. El Paleolítico Medio del Abric Romaní (Capellades, Barcelona) y del Paleolítico Superior de Üçağızlı (Hatay, Turquía) y del Molí del Salt (Vimbodí, Tarragona). Cambios en los Patrones Funcionales entre el Paleolítico medio y el Superior. Ph.D. Dissertation, Faculty of Letters, Universitat Rovira I Virgili.
- Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: development of a high-resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1–29.
- McBrearty, S., Brooks, A., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of Human Evolution 39, 453–563.
- Mellars, P., 1996. *The Neanderthal Legacy: An Archaeological Perspective* from Western Europe. Princeton University Press, Princeton, NJ.
- Nagaoka, L., 2002. The effects of resource depression on foraging efficiency, diet breadth, and patch use in southern New Zealand. Journal of Anthropological Archaeology 21, 419–442.
- Osgood, C., 1940. *Ingalik Material Culture*. Yale University Publications in Anthropology, No. 22. Yale University Press, New Haven, CT.
- Owen, L., 2005. Distorting the Past: Gender and Division of Labor in the European Upper Paleolithic. Kerns, Tübingen.
- Palmer, R., 1991. Optimization on rugged fitness landscapes. In: Perelson, E., Kaufman, S. (Eds.), Molecular Evolution on Rugged Fitness Landscapes. Addison, Redwood City, CA, pp. 3–25.

- Panter-Brick, C., 2002. Sexual division of labor: energetic and evolutionary scenarios. American Journal of Human Biology 14 (5), 627–640.
- Pennington, L., 1989. Bowes and Church's Food Values of Portions Commonly Used. Harper & Row, New York.
- Pennington, R., 2001. Hunter-gatherer demography. In: Panter-Brick, C., Layton, R.H., Rowley-Conwy, P.E. (Eds.), Hunter-Gatherers: Interdisciplinary Perspectives. Cambridge University Press, Cambridge, pp. 170–204.
- Pianka, E.R., 1988. *Evolutionary Ecology* (4th edition). Harper & Row, New York.
- Potts, R., 1984. Home bases and early hominids. Scientific American 72, 338–347.
- Richerson, P., Boyd, R., Bettinger, R., 2001. Was agriculture impossible during the Pleistocene but mandatory during the Holocene?A climate change hypothesis. American Antiquity 66, 387–412.
- Semino, O., Passarino, J., Oefner, P.J., Lin, A.A., Arbuzova, S., Beckman, LE., De Benedictis, G., Francalacci, P., Kouvatsi, A., Umborska, S., Marcikiae, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A.S., Cavalii-Sforza, L.L., Underhill, P.A., 2000. The genetic legacy of Paleolithic *Homo sapiens* in extant Europeans: a Y-chromosome perspective. Science 210, 1155–1159.
- Shea, J., 1997. Middle Paleolithic spear point technology. In: Knecht, H. (Ed.), Projectile Technology. Plenum, New York, pp. 79–106.
- Shennan, S., 2002. Genes, Memes and Human History. Darwinian Archaeology and Cultural Evolution. Thames & Hudson, London.
- Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. Soffer, O., 1994. Ancestral lifeways in Eurasia – the Middle and Upper
- Paleolithic records. In: Nitecki, M.H., Nitecki, D.V. (Eds.), Origins of Anatomically Modern Humans. Plenum, New York, pp. 101–119.
- Soffer, O., Adovasio, J.M., Hyland, D.C., Klima, B., Svoboda, J., 1998. Perishable technologies and the genesis of the Eastern Gravettian. Anthropologie 36 (1–2), 43–68.
- Speth, J.D., Clark, J.L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3, 1–42.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Stewart, K.M., 1989. Fishing Sites of North and East Africa in the Late Pleistocene and Holocene: Environmental Change and Human Adaptation. International Series 521. British Archaeological Reports, Oxford.
- Stiner, M.C., 1994. Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton, NJ.
- Stiner, M.C., 2001. Thirty years on the "Broad Spectrum Revolution" and Paleolithic demography. Proceedings of the National Academy of Sciences of the USA 98 (13), 6993–6996.
- Stiner, M.C., 2003. Zooarchaeological evidence for resource intensification in Algarve, southern Portugal. Promontoria 1 (1), 27–61.
- Stiner, M.C., 2005. *The Faunas of Hayonim Cave (Israel):* A 200,000-Year Record of Paleolithic Diet, Demography & Society. American School of Prehistoric Research Monographs. Peabody Museum Press, Harvard University, Cambridge, MA.
- Stiner, M., Kuhn, S., 2006. Changes in the "connectedness" and resilience of Paleolithic societies in Mediterranean ecosystems. Human Ecology 34, 693–712.
- Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small game use, the Broad Spectrum Revolution, and Paleolithic demography. Current Anthropology 41, 39–73.
- Stiner, M.C., Pehlevan, C., Sagir, M., Özer, I., 2002. Zooarchaeological studies at Üçag&inodot, zl&inodot, Cave: preliminary results on

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11. Paleolithic Diet and the Division of Labor

Paleolithic subsistence and shell ornaments. Araşterma Sonuçları Toplantısı, Ankara 17, 29–36.

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- Tchernov, E., 1992. Evolution of complexities, exploitatation of the biosphere and zooarchaeology. Archaeozoologica V (1), 9–42.
- Tchernov, E., 1998a. Are Late Pleistocene environmental factors, faunal changes and cultural transformations causally connected? The case of the southern Levant. Paléorient 23 (2), 209–228.
- Tchernov, E., 1998b. The faunal sequence of the southeast Asian Middle Paleolithic in relation to hominid dispersal events. In: Akazawa, T., Aoki, K., Bar-Yosef, O. (Eds.), Neanderthals and Modern Humans in West Asia. Plenum Press, New York, pp. 77–90.
- Trinkaus, E., 1983. Neandertal postcrania and the adaptive shift to modern humans. In: Trinkaus, E. (Ed.), The Mousterian Legacy. International Series 164, British Archaeological Reports, Oxford, pp. 165–200.
- Trinkaus, E., 1986. The Neandertals and modern human origins. Annual Review of Anthropology 15, 193–218.
- Vanhaeren, M., d'Errico, F., Stringer, C., James, S.L., Todd, J.A., Mienis, H.K., 2006. Middle Paleolithic Shell Beads in Israel and Algeria. Science 312, 1785–1788
- Vaughn, P.C., 1985. Use-Wear Analysis of Flakes Stone Tools. University of Arizona Press, Tucson, AZ.
- Waguespack, N.M., 2005. The organization of male and female labor in foraging societies: implications for early Paleoindian archaeology. American Anthropologist 107 (4), 666–676.
- Walker, R., Hill, K., Kaplan, H., McMillan, G., 2002. Age-dependency in hunting ability among the Ache of eastern Paraguay. Journal of Human Evolution 42, 639–657.
- Watanabe, H., 1969. Subsistence and ecology of northern food gatherers with special reference to the Ainu. In: Lee, R., Devore, I. (Eds.), Man the Hunter. Aldine, Chicago, IL, pp. 69–77.

- Weiss, E., Wetterstrom, W., Nadel, D. Bar-Yosef, O., 2004. The broad spectrum revisited: evidence from plant remains. Proceedings of the National Academy of Sciences of the USA 101 (26), 9551–9555.
- Weniger, G.-C., 1987. Magdalenian settlement pattern and subsistence in Central Europe: the southwestern and central German cases. In: Soffer, O. (Ed.), The Pleistocene Old World: Regional Perspectives. Plenum, New York, pp. 201–215.
- West, D., 1997. *Hunting Strategies in Central Europe During the Last Glacial Maximum.* International Series 672. British Archaeological Reports, Oxford.
- Wiessner, P., 2004. Owners of the future: calories, cash and selfsufficiency in the Nyae Nyae area between 1996 and 2003. Visual Anthropology Review 19 (1–2), 149–159.
- Winterhalder, B., Goland, C., 1993. On population, foraging efficiency, and plant domestication. Current Anthropology 34, 710–715.
- Wrangham, R., Jones, J.H., Layden, G., Pilbeam, D., Conklin-Brittain, N., 1999. The raw and the stolen: cooking and the ecology of human origins. Current Anthropology 40, 567–594.
- Wright, K., 1994. Ground-stone tools and hunter-gatherer subsistence in southwest Asia: implications for the transition to farming. American Antiquity 59, 238–263.
- Wright, S., 1932. The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proceedings of the 6th International Congress on Genetics 1, 356–366.
- Yellen, J.E., Brooks, A.S., Cornelissen, E., Klein, R.G., Mehlman, M., Stewart, K., 1995. A middle Stone Age worked bone industry from Katanda, upper Semliki River valley (Kivu), Zaire. Science 268, 553–556.
- Zubrow, E., 1989. The demographic modelling of Neandthal extinction. In: Mellars, P., Stringer, C.B. (Eds.), The Human Revolution.Princeton University Press, Princeton, NJ, pp. 212–231.

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Author Query:

[Au1]: Kindly confirm author initials and year for P.Weissner, 2004, personal communication.

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