

What's a Mother to Do?

The Division of Labor among Neandertals and Modern Humans in Eurasia

by Steven L. Kuhn and Mary C. Stiner

Recent hunter-gatherers display much uniformity in the division of labor along the lines of gender and age. The complementary economic roles for men and women 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 that earlier hominins pursued more narrowly focused economies, with women's activities more closely aligned with those of men with respect to schedule and ranging patterns than in recent forager systems. More broadly based economies emerged first in the early Upper Paleolithic in the eastern Mediterranean region and later in the rest of Eurasia. The behavioral changes associated with the Upper Paleolithic record signal a wider range of economic and technological roles in forager societies, and these changes may have provided the expanding populations of *Homo sapiens* with a demographic advantage over other hominins in Eurasia.

Anthropologists have long recognized that the division of labor by gender and age is a universal property of small-scale human societies. Since Isaac's (1978) landmark paper, paleoanthropologists have viewed the formalized division of economic roles and attendant patterns of food sharing as important milestones in human evolutionary history. Isaac and later Lovejoy (1981) argued that distinct economic roles for males and females first appeared in the late Pliocene. Even researchers who disagreed with Isaac's and Lovejoy's emphasis on the importance of hunting to early hominids seem to have implicitly accepted the notion that some sex or gender roles crystallized very early in human evolutionary history (e.g., Zihlman 1989; Zihlman and Tanner 1978).

Most researchers currently reject the idea that a gendered division of labor emerged in the Pliocene, at least not in its modern form (see Kuhn and Sarther 2000; Liebowitz 1986; McBrearty and Moniz 1991; Rose and Marshall 1996; O'Connell et al. 2002; Wrangham et al. 1999). The lasting contribution of Isaac's and Lovejoy's papers is that they shifted the focus of archaeological studies of human evolution away from simple technological or economic "landmarks" such as the beginnings of tool use or hunting or the mastery

of fire and toward more complex socioeconomic characteristics. In the intervening years, intensive studies of chimpanzees and other nonhuman primates have shown that many supposedly unique characteristics of humans—tool use and hunting of mammals, to name two—also occur among some nonhuman primates, particularly the greater apes (e.g., Stanford 1996; Whitten et al. 2001; Wrangham and Bergman-Riss 1990; Wynn and McGrew 1989). Some degree of niche separation and activity patterns between adult males and females is documented for a variety of large-mammal species (reviewed by Pianka 1988, among others), and some social mammals share food with other adults in their group. For instance, most of the canids share food but forage similarly irrespective of sex; chimpanzee males and females may forage differently but seldom deliberately provision others with food. Nonetheless, recent humans are remarkable for cooperative economies that combine pervasive sharing and complementary roles for individuals of different ages and sexes.

Although division of economic labor by sex and age is an especially salient feature of the recent human condition, we still do not know when it appeared or how it came about. Hypotheses about sex-related activity differentiation among Pliocene hominins certainly merit continued investigation. However, in contrast to Isaac and Lovejoy, we argue that the typical patterns of labor division emerged relatively late in human evolutionary history. With respect to Eurasia, the archaeological record of the Neandertals (the most recent of the "nonmodern" hominins) exhibits little evidence for the kinds of distinct economic roles typically fulfilled by women in recent hunter-gatherer groups. It appears that Neandertal

Steven L. Kuhn is Professor of Anthropology at the University of Arizona, P.O. Box 210030, Tucson, AZ 86731-0030, U.S.A. (skuhn@email.arizona.edu). **Mary C. Stiner** is Professor of Anthropology and Associate Curator of Zooarchaeology at the Arizona State Museum of the University of Arizona, P.O. Box 210030, Tucson, AZ 86731-0030, U.S.A. (mstiner@email.arizona.edu). This paper was submitted 25 VI 05 and accepted 20 III 06.

males, females, and juveniles alike participated in a narrow range of economic activities that centered on obtaining large terrestrial game. This apparent absence of regular economic differentiation in Middle Paleolithic cultures (including that of the Neandertals) is consistent with the distinctive features of human demography and anatomy of this period. Better evidence for foraging economies based on a range of complementary subsistence roles coincides with the emergence of the early Upper Paleolithic. Such cooperative economic systems may have given Upper Paleolithic humans a demographic advantage over Neandertals and their contemporaries, facilitating the rapid expansion of Upper Paleolithic culture throughout Eurasia. We argue that these sorts of cooperative economic systems are more likely to have evolved first in the tropics or subtropics. Though it was by no means a necessary outcome of the great diversity of animal and plant communities at low latitudes in Africa or Asia—any more than domestication was an inevitable result of the hunting of wild goats—the evolutionary “opportunities” for diet-breadth expansion and increased efficiency via cooperation would have recurred most often in the lower latitudes, where biotic diversity generally is greatest.

This paper is divided into three parts. The first part concerns observations about the division of labor by age and gender among historically and ethnographically documented foraging peoples. The second part reviews archaeological evidence for differentiated, complementary economic roles or the lack thereof before the appearance of modern humans in Eurasia. The third part considers where this unique, nearly universal human pattern might have evolved and how it might have contributed to the evolutionary success of *Homo sapiens*.

Ideas about the Division of Labor among Recent Hunter-Gatherers

Some anthropologists question the relevance of information about recent foragers for understanding Pleistocene hominin behavior. Neither Neandertals nor *H. erectus* were modern humans, it is said; they lacked modern humans' behavioral capacities, and thus we cannot assume that they exhibited the same behavioral regularities and patterns. Other critics point to geographic biases in the historic and ethnographic records of foragers or to the fact that the lifeways of all recent hunter-gatherers have been affected greatly by interaction with farming neighbors, colonial powers, or large-scale indigenous societies (Gardner 1991; Marlowe 2005; Schrire 1984; Spielman and Eder 1994; Wobst 1978; Woodburn 1988).

All of these are valid points, but they do not necessarily undermine the relevance of knowledge about recent foragers to the study of our hominin forebears (e.g., Marlowe 2005). Hunter-gatherers of the nineteenth and twentieth centuries were certainly not Pleistocene “relics,” and we cannot use them as direct analogues for Plio-Pleistocene hominids. Nor should we use narratives from ethnography or ethnoarchaeology to “fill in the gaps” in early archaeological records:

such practices do not teach us anything about the past. Generalizations about recent hunter-gatherers are most helpful when they reveal points of discordance between what we expect from historical experience and what seems to have gone on during the Pleistocene. In other words, models developed from data on recent hunter-gatherers are most informative precisely when they prove to be inadequate predictors of patterns encountered in the Paleolithic record. Where they fail to account for what we know about earlier hominins, modern human analogs show us more specifically how our ancestors were not like us and what we need to explain about human evolution.

The basic generalization from which we begin is the nearly axiomatic division of subsistence labor by gender and age documented in virtually all recent foraging peoples: put most simply, men hunt, women and children gather.¹ More precisely, males are normally responsible for obtaining large terrestrial and aquatic animals, whereas females and, in some cases, juveniles focus their efforts on vegetable foods and smaller animals in addition to helping process the big animals. This basic form of gendered division of labor is expressed both in ideology and in practice in nearly every ethnographically documented foraging group. There is but one well-known exception, the Agta (Estioko-Griffin and Griffin 1981), whose women regularly did most of the hunting, and there is still no widely accepted explanation for this unique situation.

The ethnographic record also shows us that the boundaries between economic roles are permeable and that individuals may pass from one role to another over the course of their lifetimes. Although tendencies toward division of labor by gender are quasi-universal among recent foragers, *individual* departures from this pattern are numerous, according to preference, context, and individual circumstances. On a given day, almost anyone in any foraging society might take advantage of opportunities to bag a big animal or to pick berries, albeit within the limits of their physical capacities. Among high-latitude hunter-gatherers, widowed women or daughters in families without sons could become successful and habitual hunters (e.g., Briggs 1970; Jenness 1922; Landes 1938). In tropical situations, individual women's decisions about whether to participate in group hunts may be related to the availability of better economic options (Bailey and Aunger 1989). Likewise, male hunters often (though not always) take vegetable foods or small game when a good opportunity pres-

1. This paper discusses differentiation of economic roles and activities according to gender as determined largely by sex and age and does not consider questions of political and social inequalities in “egalitarian” societies. Obviously, what people do and how different roles are valued in particular societies are closely linked to asymmetries in access to critical resources and social networks. However, while we feel on relatively safe ground with broad generalizations about male, female, and possible juvenile economic roles, it may be impossible to make similarly general statements about power relations between genders in hunter-gatherer societies (cf., e.g., Draper 1975 and Estioko-Griffin 1981 with Rosaldo and Lamphere 1974, 3, and Freidl 1995).

ents itself (Bailey 1991; Endicott 1999, 412, and references therein).

The roles of children are less well studied and apparently more variable. It takes many years for children to achieve the physical attributes and skills needed to fulfill their expected roles in adulthood (e.g., Bird and Bliege Bird 2000, 2003; Bliege Bird and Bird 2002; Kramer 2005); data from a few societies indicate that youths did not achieve full productive capacities until age 20 or so (Walker et al. 2002; Kaplan et al. 2000, 58–59). Nonetheless, older children in both tropical and subarctic environments are sometimes reported to have provided a significant part of their own dietary intake (e.g., Laughlin 1968, 241–42; Watanabe 1968, 76–77), even becoming temporary specialists of sorts. The variable economic roles of children seem to depend on the kinds of foraging opportunities available in a given habitat. Blurton Jones, Hawkes, and O'Connell (1989, 1997) attribute stark differences in the economic contributions of children among Hadza and !Kung foragers to the kinds of “child-friendly” foods available and the dangers faced by wandering children in their respective environments.

One might suggest that the widespread reports of gendered division of labor among recent and past foragers alike are the result of mapping modern Western social roles and values onto other societies—consciously or unconsciously. There may be some validity to this argument, especially when one is dealing with interpretations of archaeological cases (e.g., Fedigan 1986, 60–61; Gero 1995), but the universality of the reported patterns of divided labor implies that ethnographers were not totally blinded by their own prejudices and preconceptions. Moreover, because the academic payoff to finding exceptions to any rule is quite high, we can be confident that cases to the contrary have been reported.

That women sometimes become successful hunters and men become gatherers means that the universal tendency to divide subsistence labor by gender is not solely the result of innate physical or psychological differences between the sexes; much of it must be learned. There are a number of credible noncompeting explanations for the recurring pattern of division of labor among hunter-gatherers (Panter-Brick 2002; Shennan 2002, 195–96). First, men and women may have different foraging agendas related to their roles in child care and the certainty of the adults' genetic relationships to dependent offspring. As Hawkes and colleagues (Hawkes 1991, 1996; Hawkes and Bliege Bird 2002) have argued, food obtained and shared by male hunters may in some cases have more to do with prestige and social networking than with feeding their own children. Of course, this scenario already presupposes a gendered division of labor: males are free to broker meat into social rewards only where women are able to feed children through their own labor alone. Second, avoidance of the more dangerous subsistence pursuits by women and children protects the reproductive core of the population

from undue risk,² preferentially exposing the more “expendable” males. Obviously, the limited physical competence and endurance of children reduce their potential subsistence contributions (Bliege Bird and Bird 2002; Kramer 2005). A third explanation for gendered division of labor across recent foraging societies is that the demands of child care often restrict women of reproductive age to activities that can be interrupted with minimum cost and entail relatively limited mobility (Kelly 1995, 268–69). Any lack of opportunity to acquire and refine certain necessary skills would further limit the ease with which women may shift to hunting when demands of child care are less exigent.

There is a respectable body of data on variation in the importance of individuals' resource contributions, hunted and gathered, to group diet among foraging peoples of the recent period. Three general tendencies are important for this discussion. The most obvious of these is that large game and animal foods in general (terrestrial or aquatic) tend to be most important in the higher-latitude environments of the world (e.g., Binford 2001; Keeley 1988; Kelly 1995; Kuhn and Stiner 2001; Marlowe 2005). In some arctic and subarctic regions, there are comparatively few small animals to be had and no vegetable foods of dietary significance, so large game accounts for a very large proportion of all food consumed. Gathered vegetable foods and small game naturally tend to be more important to human diets in low latitudes. It is interesting, in addition, that the total range of variation is greatest in the tropics and subtropics (Hayden 1981a; Hiatt 1978; Kelly 1995; Lee 1968): meat is not simply replaced with plant foods as one approaches the equator, and some tropical groups may depend to a significant degree on the hunting of large animals.

The second tendency in resource use among forager societies concerns the kinds of vegetable foods eaten. Everyone eats fruits and greens when possible, but no foraging group has been able to base its diet on these kinds of plants. Foraging people who rely on plant foods for a major part of their caloric intake tend to concentrate their efforts on a distinct range of range of foods consisting of some combination of seeds, nuts, and tubers (Keeley 1995; Kuhn and Stiner 2001). These foods, while abundant and nutritious enough to serve as staples, tend to be time-consuming to collect, process, or cook. Grass seeds, for example, may provide substantial amounts of fat, carbohydrates, and protein, but the work needed to extract the maximum nutrition from them translates into relatively low net yields (Kelly 1995, 81–82). It is for this reason that the return rates for most staple plant foods, which are low per unit time spent but fairly high per unit raw weight obtained, differ so much from those for large game animals, whose value is high per unit time (table 1). There is, in essence,

2. It takes roughly 15–20 years for a female human to reach reproductive age, and normally she produces only one child at a time (this is especially true among foragers), with appreciable intervals between the births of subsequent children.

Table 1. Net Energy Yields of Various Food Classes Consumed by Recent Foragers by Yield per Hour (kJ/hr) and Yield by Unit Weight (kJ/kg)

	N cases	kJ/hr			kJ/kg	
		Mean	Min.	Max.	Mean	sd
Large game	4	63,398 ^a	36,000	75,115	6,980 ^b	1,383
Small mammals	14	16,034 ^a	1,672	56,317	6,980 ^b	1,383
Reptiles	3	15,850 ^a	17,556	12,435	4,489 ^b	715
Birds	3	4,472 ^a	961	8,255	—	—
Roots and tubers	14	6,120 ^a	418	26,133	2,926 ^c	1,680
Roots and tubers	9	10,412 ^a	3,695	23,333	2,926 ^c	1,680
Roots and tubers	13	1,882 ^d	1,045	2,300	3,136 ^d	2,338
Seeds and nuts	34	3,520 ^a	380	18,538	13,188 ^c	9,334
Seeds and nuts	9	6,508 ^c	1,203	24,933	13,188 ^c	9,334
Seeds and nuts	6	—	—	—	19,372 ^d	6,250
Foliage	—	—	—	—	1,250 ^c	819
Foliage	3	—	—	—	1,534 ^d	186
Fruits	—	—	—	—	2,403 ^c	1,463

^aData from Kelly (1995, table 3.3).

^bData from Hawkes, Hill, and O'Connell (1982), Hurtado and Hill (1987).

^cData from Pennington (1989).

^dData from Wiessner (2004 and personal communication); cases are from Nyae Nyae area minus those where elephant damage was severe for tubers.

^eData from Wright (1994, table 2).

a fundamental division or difference in the currencies governing foraging returns from hunting large animals and many gathered foods—meat from large game provides high returns per unit time invested, whereas nuts and seeds (and some corms and roots) provide reliable and rich returns from a given unit of land but at high cost with respect to time and energy. Certain tubers may provide much higher yields after cooking (Wrangham et al. 1999) than do nuts and seeds, but their distribution is limited to certain environments: they are less important ecologically in Eurasia than in Africa.

The third tendency concerns the roles filled by “woman the gatherer” in environments such as the Arctic, where the options for gathering or small-game hunting are quite limited. Among recent foragers who lived at high latitudes, women and even children assumed primary responsibility for a variety of nonsubsistence tasks, including collection of water and fuel, transport, and construction of housing, as well as the manufacture of tools and clothing (Halperin 1980; Waguespack 2003, 2005). The importance of these roles for group survival should not be undervalued. Activities such as the preparation of skins and manufacture of clothing and shelters are skill-intensive, physically demanding, and extraordinarily time-consuming (e.g., Osgood 1940). Good clothing and shelter are as vital for survival as plentiful food, and in fact Arctic hunters could not function without highly effective skin clothing (Balicki 1970, 104). Just as Inuit women sometimes became hunters, families with few or no female members made sure that their sons were trained in sewing (Briggs 1970).

To summarize, the fact that partitioned cooperative labor is so widespread among recent foragers suggests a basic un-

derlying explanation arising from the economic agendas and reproductive roles of males and females. The widely discussed generalizations about “man the hunter” and “woman the gatherer” represent a useful baseline model of recent *H. sapiens* for comparison with the behavioral record of earlier humans. One can assert this without requiring any essential or direct connection between biological sex or age and economic role; it is clear that these roles are subject to negotiation and social sanctions and that rules were often bent. Yet the basic, nearly universal rules of divided, cooperative labor seem to have worked well in many times and places. In addition, high-latitude societies of the recent period help us anticipate alternative female roles where most food comes from hunting large animals. These alternative roles have distinctive technological signatures that should be preserved in the archaeological record.

Archaeological Evidence for Gendered Division of Labor before Modern Humans in Eurasia

We will compare the Neandertals and modern *H. sapiens*, two human variants regarded by many investigators to be quasi-contemporary but behaviorally distinct (e.g., Klein 1999; Mellars 1996). A long history of research on Neandertals and their habit of depositing large amounts of debris in sites create richer possibilities for comparison with recent human groups than is true for earlier hominins. In addition, Neandertals established permanent populations from northern Europe to the southern Mediterranean Basin, allowing us to consider how subsistence and technology varied across a range of environmental circumstances and latitudes. The richness of this archaeological record is necessary for identifying the presence or absence of classic human patterns in the Middle Paleolithic period.

Neandertals lived in western and central Eurasia between roughly 250,000 and 30,000 years ago. They are an endless source of fascination for anthropologists because of their combination of familiar and unfamiliar characteristics. Although their bodies were quite robust, their brains were as large on average as those of modern humans when adjusted for body mass. The preserved elements of their toolkits, so-called Middle Paleolithic or Mousterian industries, were comparatively simple and their modes of aesthetic expression nonexistent or unpreserved. Yet Neandertals buried their dead, a gesture that seems essentially human to many observers.

One of the most striking economic characteristics of the Neandertals was their devotion to the pursuit of large terrestrial game animals. From the ecological viewpoint of dietary breadth, Neandertals maintained exceptionally narrow foraging regimens (Stiner 2001, 2002). Questions about whether Neandertals were mighty hunters or obligate scavengers, once prominent in the archaeological literature, now are largely dead issues. In fact, Neandertals seem to have been

habitual predators of large and medium-sized hoofed animals such as gazelle, deer, wild horses, boar, bison, and wild cattle (cf. Burke 2000; Chase 1986; Hoffecker, Baryshnikov, and Potapova 1991; Gaudzinski 1995; Griggo 2005; Jaubert et al. 1990; Marean and Assefa 1999; Speth and Tchernov 1998, 2001; Stiner 1994; Tchernov 1989; Thieme 1997). Large terrestrial herbivores account for the majority of identifiable bone specimens in virtually every known Middle Paleolithic zooarchaeological collection attributed to human actions. Moreover, because these game animals were large, they typically accounted for more than 95% of the potential animal foods procured by weight (fig. 1; Stiner 2005). This exceptional dependence on large game holds true for the Middle Paleolithic regardless of latitude: from southern Israel or northern Germany, terrestrial game dominates Middle Paleolithic faunas by total game weight and by number of bone specimens. Although few, studies of stable isotopes from Neandertal skeletal remains also suggest a diet heavily oriented toward meat (Bocherens and Drucker 2003; Bocherens et al. 1999, 2005; Fizet et al. 1995; Richards et al. 2000, 2001).

This is not to say that Neandertals and their contemporaries studiously ignored resources other than large game. Durable parts of shellfish and small animals are present in many Middle Paleolithic sites, especially in the Mediterranean Basin (Stiner et al. 1999; Speth and Tchernov 2002). It is important to recognize, however, that such remains are almost always limited to easily collected species such as tortoises, marine mollusks, ostrich eggs, and large lizards, depending on the area. The exploitation of immobile or slow-moving small animals makes sense in terms of optimal-foraging models: the ease of capture and low handling costs make up for their small size, bringing net yields close to those of medium-sized to large game. Some of the small prey species had limited potential for population growth and recovery from predation, meaning that they could not have provided substantial amounts of food for many people for very long (Stiner, Munro, and Surovell 2000). The apparently minor contribution of small game to Neandertal diets cannot be dismissed as the product of preservation bias. The bones of small mammals, tortoises, and the shells of mollusks tend to be quite durable, and tests for differential preservation in recent excavations indicate no substantive biases against small-game remains in a number of key sites (e.g., Stiner 1994, 2005). Recovery techniques can affect data from older excavations, but, if so, these same biases should apply to the Upper Paleolithic. In fact the remains of small mammals and very fragile bird bones are much more common in later Upper Paleolithic faunas of the same regions that were recovered using the same range of techniques.

Evidence for the use of vegetable foods in the Middle Paleolithic is even more limited than that for small animals. We do not expect many plant remains to be preserved over such vast time spans, and few are. A few Middle Paleolithic sites in the Mediterranean Basin (Barton et al. 1999; Bar-Yosef et al. 1992, 530; Lev et al. 2005; Madella et al. 2002) have yielded

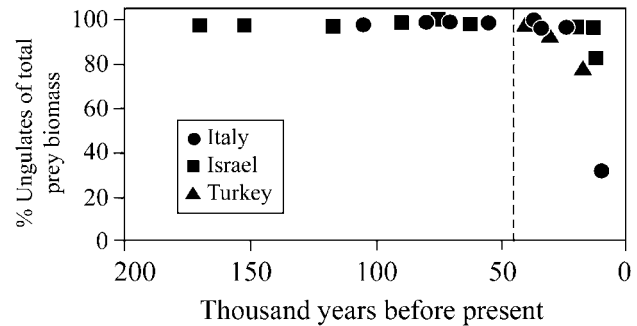


Figure 1. Percentage of total prey biomass represented by large ungulates consumed by Paleolithic foragers over time in Mediterranean faunal assemblages from Israel, Italy, and Turkey. The importance of large game begins to drop after about 45,000 years ago (broken line) and greatly accelerates after about 15,000 years ago.

burned seeds and possible hammerstones for cracking hard shells of nuts or acorns. These cases are rare, however, and involve very small amounts of material. Heavy dependence on plant foods among historic foragers generally entails an emphasis on seeds, nuts, or other resources that require intensive processing. In these contexts, grinding or crushing as well as extensive cooking are vital for extracting maximum nutrition from seeds, and thus the requisite items of material culture are sure indicators of subsistence intensification in more recent periods. Unlike macrobotanical remains, grinding or milling stones are durable classes of artifacts, easily recognized in the archaeological record and in the ethnographic present. Yet, except for hammerstones, which have many potential uses, artifacts dedicated to grinding or crushing food simply are not represented in the Neandertal toolkit (Kuhn and Stiner 2001). Vegetable foods may well have been part of Middle Paleolithic diets in Eurasia, but these were more like salads, snacks, and desserts than energy-rich staples. (Grinding stones are known from the contemporaneous Middle Stone Age in Africa, a point we will return to later.)

Recently, some researchers have discussed the possible role of tubers and other geophytes in human diet and evolution (Wrangham et al. 1999). Although these arguments have broad relevance in Africa, tubers are not likely to have been staples in most of Eurasia. Large underground storage organs are common among plant taxa in arid sub-Saharan Africa, but the high-yield edible plant foods of temperate and Mediterranean Eurasia tend to be seeds and nuts that, while potentially nutritious, require more effort to collect and process and thus afford low net yields (see table 1; Kelly 1995, 81–82).

It should be clear from this brief review that the Eurasian Middle Paleolithic record provides few direct indications of the full spectrum of subsistence roles typically filled by women and children in recent foraging societies. Obviously, absence of evidence is not evidence of absence, but the relevance of this old saw declines with the mounting number of cases of

absence. The archaeological literature contains high-quality reports on faunal assemblages from dozens of Middle Paleolithic sites across several regions, and none has yielded good evidence for heavy reliance on small game or intensive exploitation of vegetable foods.

Of course, many of the Neandertals occupied relatively high-latitude environments during cold phases of the Upper Pleistocene epoch. They also lived at a time when Eurasia hosted extraordinarily rich and diverse communities of large mammals. In game-rich high-latitude settings, evidence from recent foragers leads us to expect a dietary bias toward large game or a heavy dependence on fish. Ethnographic experience would also lead us to predict that in such contexts females would have taken on the role of technology specialists. Here again, the ethnographic record fails us as a predictor of Middle Paleolithic behavior. The Eurasian Middle Paleolithic is known for its low level of technological elaboration. Toolkits were limited to simple stone and wooden implements. We simply do not find the kinds of complex, costly, high-investment artifacts typically made by craftspeople in recent northern foraging groups, at least with durable components composed of stone, bone, antler, or ivory.

Direct evidence for clothing is elusive in the Paleolithic record as a rule. European Neandertals almost certainly wore skin garments of some kind and possibly constructed artificial shelters as well. However, the types of artifacts commonly used to make tailored, weather-resistant clothing and well-insulated artificial shelters—bone needles and awls, for example—did not appear until the early Upper Paleolithic. In addition, edge damage on stone tools thought to indicate working of dry hide (leather), while present, is never especially common in assemblages from Middle Paleolithic/Neandertal sites (e.g., Anderson-Gerfaud 1990; Beyries 1987; Lemorini 2000). A recent study of microscopic patterns of damage on artifacts from the late Middle Paleolithic site of Abric Romaní in Spain (Martinez Molina 2005, 343–44) for example, reveals that traces left by working of hides are very rare in comparison with damage produced by butchery activities, even though hide working tends to produce recognizable edge damage more quickly under experimental conditions. Further, the indications of hide working are confined to damage from contact with fresh hides.

No matter how one chooses to interpret the ethnographic record, it is impossible to argue that Neandertal females and juveniles were fulfilling the same roles—or even an equally diverse suite of economic roles—as females and juveniles in recent hunter-gatherer groups. This contrast is apparent both in the realm of subsistence and in the related domain of technological support. It is clear that the socioeconomic dimensions of Neandertal life differed significantly from anything we know from historic foraging groups.

So what were those Middle Paleolithic women and children up to? Three hypotheses present themselves:

1. Women and children were doing comparatively little apart from having babies and growing up.

2. Women and children were collecting small-package resources (small game and vegetable foods) but consuming them mostly in the field rather than carrying them to the places (base camps) that archaeologists usually excavate.

3. Women, children, and men all participated actively and consistently in the acquisition of large animals.

The first scenario, attractive though it might be, is unlikely on energetic and human morphological grounds. The marked skeletal and muscular robusticity of the Neandertals is generally interpreted as evidence for high levels of activity among both males and females. Moreover, recent experimental work (Lieberman and Pearson 2001; Lieberman, Devlin, and Pearson 2001) suggests that the overall skeletal robusticity that characterizes Neandertals and other archaic *Homo* populations is likely the result of high activity levels during childhood development. Neandertal children were doing a lot of something, even if it is not clear just what.

The second hypothesis is that women and juveniles were essentially economically independent of males. This would imply a rather different kind of social organization from what obtains among recent human groups, though a similar model has been proposed to explain discordant evidence for early Holocene subsistence in the American Great Basin (Zeanah 2004; Elston and Zeanah 2002). This hypothesis also predicts a class of archaeological evidence—field consumption stations for gathered resources—that currently is not documented for the Middle Paleolithic but is present in the Holocene archaeological record of the Great Basin. Archaeological recovery or recognition bias cannot account for the absence of sites dominated by small game and vegetable foods in the Middle Paleolithic. Detailed regional surveys have been conducted in many areas of Eurasia. The results of isotopic studies of Neandertal skeletal material conducted to date point neither to a significant plant food contribution nor to significant inter-individual differences in diet (Bocherens et al. 1999, 2005; Fizet et al. 1995; Richards et al. 2000). Admittedly, however, the human fossil sample is currently too small to permit detection of possible differences between males and females.

We would like to consider the third alternative, namely, that the archaeological record is fairly representative of Middle Paleolithic diets and that females and juveniles participated in the hunting of large terrestrial game more extensively and more directly than has been documented among recent foragers. This is not to deny the importance of large-game hunting among many recent foragers. Rather, it is the narrowness of the large-game focus during the Middle Paleolithic that attracts our attention. By “direct” participation in hunting we mean cooperative integration of at least two options: (1) close physical contact with large prey and (2) assistance to hunters by beating the bushes or otherwise reducing prey escape routes with warm bodies. There is little hope of finding straightforward evidence of this phenomenon, but some indirect evidence does exist.

One of the most important potential consequences of a subsistence system in which females and juveniles were so

closely tied to large-game hunting concerns demography. Some of the social carnivores that rely on large game, such as Cape hunting dogs and wolves, have comparatively large litters and high reproductive rates (Ewer 1973), but this is not the case for humans. Further, the hunting of large animals is a rough and dangerous business, all the more so if equipped with Middle Paleolithic weapons systems, which emphasized the use of thrusting spears at close range (Churchill 1993; Shea 1997). Evidence for healed fractures is common on Neandertal upper limbs and skulls, attesting to their rough-and-tumble livelihood (Berger and Trinkaus 1995). It is unlikely that females and juveniles routinely put themselves in the positions of highest risk during a hunting operation—we need not imagine women and children in hand-to-hand combat with giant Pleistocene herbivores. Rather, their serving as beaters or game drivers, for example, could have contributed significantly to the groups' hunting success and arguably was essential in light of the weapons systems of the time. Even this practice carried risks, albeit lower risks than those taken on by the hunters who actually dispatched the animals. Any increased mortality among young people and women, the reproductive core of the population, would have dampened the demographic potential of Neandertal groups.

Although large game can yield high average return rates per unit effort, it is somewhat unpredictable as a staple resource. Modern hunters armed with bows and arrows or even guns come home empty-handed as often as not. For adult metabolisms, this high day-to-day variance is not a particular problem, and the high quality of meat (and fat) as food and the high net yields from hunting compensate for the unpredictability of large game. Irregular supplies of food, particularly complete protein and certain fats, are, however, more problematic for growing children and pregnant or lactating women (Bliege Bird 1999; Hawkes 1991, 1996; Kaplan et al. 2000; Wrangham et al. 1999). A consistent if modest supply of high-quality food is important for proper development. An irregular supply of food, even with a diet of high average quality, would place greater periodic nutritional stress on juveniles during development, again limiting reproductive potential.

More generally, a heavy dependence on large game for the bulk of one's food energy implies an ecological position very high in the trophic pyramid, and among mammals top carnivores are able to sustain only relatively low population densities. Upper Paleolithic hunters were also top carnivores, but their options for supplementing the diet were a good deal broader (see below) than those of the Neandertals. The demographic consequences of this difference between Middle and Upper Paleolithic diets would have been compounded by the high estimated caloric needs of Neandertals, as indicated by their massive frames (Sorensen and Leonard 2001), and the fact that most Neandertals lived in relatively cold environments, where calories would have been burned even faster.

In sum, the hypothesis of less sharply differentiated subsistence roles among men, women, and children in economies

that focused principally on large game animals would imply that Neandertals existed at very low population densities. Independently, a number of researchers have come to the conclusion that early human populations, including Neandertals, were small and had rather limited potentials for long-term growth or local stability compared with recent modern humans (e.g., Hovers and Belfer-Cohen 2006; Lahr and Foley 2003). The long-term population trajectory for Pleistocene humans suggests an annual rate of increase several orders of magnitude lower than that of any known natural population (Pennington 2001; Richerson, Boyd, and Bettinger 2001). Clearly, these early populations had the potential to grow over the short term, and as predators of large mammals they also enjoyed high dispersal capabilities. Long-term growth rates were low apparently because early human populations seldom attained large sizes and were subject to frequent and catastrophic crashes (Boone 2002; Caramelli et al. 2003; Richerson, Boyd, and Bettinger 2001; Semino et al. 2000; Shennan 2002, 118–19). This inference is entirely consistent with a narrow dependence on high-stakes resources, particularly large game. Neandertals may have been “living fast,” with very high caloric intake mainly from large mammals. This would have been a fragile system: in flush times, Neandertals would have lived high on the hog (or the red deer), but they may have lacked the kind of diversified resource base and labor network for spreading subsistence risk needed to buffer them from major population losses in lean times. In this regard, Middle Paleolithic subsistence poses a significant contrast to the adaptations of recent hunter-gatherers and those of the Upper Paleolithic.

The Evolution of the Gendered Division of Labor and Its Contribution to the Evolutionary Success of *H. sapiens*

If Neandertals, the hominin taxon that immediately preceded Upper Paleolithic humans in Eurasia, did not practice typical forms of gendered division of economic labor, the question remains when and how this pattern appeared in other Pleistocene human populations. Both the subsistence and the technological evidence in Eurasia indicate that the “when” is the earliest Upper Paleolithic, coincident with the dispersal of anatomically modern humans throughout Eurasia. The questions of where and how are far more difficult to answer.

Work in several study areas around the Mediterranean Basin shows that a wider variety of small-animal resources were incorporated into human diets with the Upper Paleolithic (fig. 2; Stiner 2001). While reptile and shellfish exploitation is clearly evidenced early in the Middle Paleolithic, the Upper Paleolithic period saw the addition of substantial numbers of birds, quick small mammals (mainly rabbits and hares [Stiner 2001]), and eventually fish to human diets. With the late Upper Paleolithic, 20,000 years ago, there is also evidence for collection and intensive processing of wild seeds, fish, or both

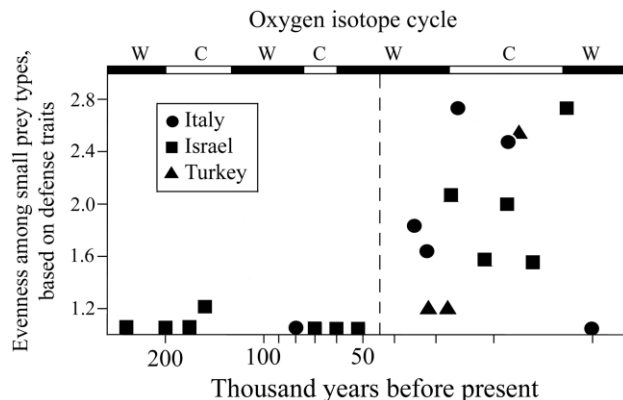


Figure 2. Evenness in the representation of three small-game categories in Paleolithic faunas, based on prey defense mechanisms (slow game, quick-running terrestrial mammals, and quick-flying birds) (3 = most even, 1 = least even). Evenness here reflects a continuum in dietary breadth: narrow diets place disproportionate emphasis on one or very few highly ranked resources (i.e., return rate is high for effort expended); broad diets involve more even emphasis on a combination of high-return and lower-ranked resources because the availability of preferred types has declined. The range of small game exploited increases dramatically in many cases after about 45,000 BP (broken line). Time is expressed on a logged scale, as are oxygen isotope climate cycles; C, cold stage, W, warm stage.

in semiarid areas such as the Levant (Wright 1994) and the Nile Valley (Peters 1991; Stewart 1989; Van Neer 1986). The situation merely intensified after 12,000 years ago, culminating in some regions with the so-called wetland revolution (e.g., Coles 1992; Enghoff 1991). Isotopic evidence from cooler areas of Europe also attests to increasing dietary breadth as the Upper Paleolithic wore on (Richards et al. 2001), when hominins appear to have existed at slightly lower trophic positions than did the Neandertals before them.

In addition to dietary shifts, the Upper Paleolithic archaeological record presents widespread evidence for the manufacture of elaborate clothing and shelters. What we find is not preserved skin garments but rather the implements typically associated with sewing—bone awls and eyed needles, sometimes in great numbers (e.g., Berke 1984). These implements became a regular part of human toolkits rather suddenly in the early Upper Paleolithic. Such technologies were, as one might expect, more elaborate and abundant in sites of the higher latitudes, but they are found throughout Eurasia (reviewed by Kuhn and Stiner 2001). The range of manufacture-intensive items in Upper Paleolithic sites includes a wide variety of bone, antler, and ivory artifacts, only a fraction of which represent components of weapons (cf. Hayden 1981b; Knecht 1997), and even cordage and basketry (Soffer et al. 1998). Other direct evidence for elaborate manufacturing behavior is found in patterns of microscopic damage to the edges of stone tools. In marked contrast to the condition of

Middle Paleolithic artifacts, edge damage from working skins, particularly dry hide (leather), is common in Upper Paleolithic assemblages. At Üçağızlı Cave, a site in the southern Mediterranean Basin, wear from processing both wet and dry hides is present on the majority of Upper Paleolithic stone artifacts examined (Martinez Molina 2005, 424–25; see also Donahue 1988; Vaughn 1985). Technological and subsistence data suggest that a wider range of subsistence and social roles were in place with the beginning of the early Upper Paleolithic in Eurasia. Obviously, we cannot be certain about who was filling these roles: we do not know the sex of the people making the hide tents and clothing or collecting the small game. The key point is that diverse roles were there to be filled in the early Upper Paleolithic but apparently not in the Middle Paleolithic.

Why did this trend in Eurasia begin only with the appearance of Upper Paleolithic cultures? The first anatomically modern humans of western Asia, for example, possessed essentially the same Middle Paleolithic-type material culture as the Neandertals, who actually succeeded them in the region (Bar-Yosef 2000; Shea 2006a). It is only later—after 50,000 years ago—that major technological and dietary changes are manifest in Eurasia. One response to this question is to look for some essential property of modern humans as the explanation for differences between them and modern humans. One could argue, for example, that rapidly evolved cognitive differences stand behind the changes (e.g., Klein 1999, 2001; Klein and Edgar 2002). Certainly, the persistence of economies based on complementary economic roles and food sharing implies the ability to both negotiate roles and penalize those who deviate from expected norms (Kelly 1995, 161–81). But we are unsure what makes that transition possible, and citing a sudden, fundamental neurological shift would be stretching the point in this case.

As an alternative we adopt an explicitly biogeographic perspective on interpopulation competition. The modern pattern of division of labor by age and gender could have been a historical accident relating in part to the array of environments in which *H. sapiens* first evolved. Current genetic evidence indicates that this occurred in sub-Saharan Africa as early as 200,000 years ago (e.g., Cann 2001; Cann, Stoneking, and Wilson 1987; Ingman et al. 2000; Templeton 2002; White et al. 2003). This ancestral population subsequently dispersed into the rest of the world, eliminating or absorbing endemic hominin populations. The mechanism for the dispersal of *H. sapiens* and the degree of interbreeding with local indigenous populations remain disputed. However, nearly everyone agrees that there was a major dispersal of people (and thus their genes) from southern Africa sometime after 100,000 years ago, setting the stage for the current global distribution of *H. sapiens*. The origin of the Upper Paleolithic is not easily traced to Africa, however; the earliest indications of this culture complex are documented in the Levant (Bar-Yosef 2000).

Cooperative economies organized around complementary subsistence roles are in fact more likely to develop in tropical

and subtropical areas, irrespective of continent. There are three reasons for this. First, food resources other than large game—small animals, plant foods, and insects—are more diverse and abundant in low-latitude ecosystems, and they often are available for a greater part of the year than in temperate and colder ecosystems. Human diets need not automatically diversify in these situations, but the potential exists for it when the abundance of preferred (highly ranked) resources declines for any reason. Areas of intersection between several major biogeographic zones such as occur around the eastern Mediterranean Basin can enhance this latitudinal effect (e.g., Blondel and Aronson 1999). Second, plant resources such as tubers are more abundant in tropical and subtropical ecosystems, especially in semiarid ones. Though most types of tubers must be cooked in order to render them digestible (Wrangham et al. 1999), these resources generally afford greater net returns than seeds and nuts (Keeley 1988, 1995; Kelly 1995). Third, resources that children can potentially procure for themselves are more diverse and abundant in tropical and subtropical systems, giving children—and therefore mothers—greater options for economic independence. In other words, the semiarid tropical environments of Africa and Asia were places in which early systems of cooperation and division of labor by age and gender were far more likely to arise. For a combination of ecological, demographic, and historical reasons, diversified economies were a good deal less likely to develop among native populations in temperate Eurasia, regardless of their basic behavioral capacities.

Is there any evidence that diversified economies based on cooperation and division of labor evolved first in the lower latitudes? Because of a shorter history of research, the African record corresponding to the origins of modern humans (the Middle Stone Age, or MSA) is not as extensively documented as the Paleolithic record in Eurasia. Nonetheless, there are a number of clues that a greater range of subsistence and technological roles could have existed in the MSA. For example, both fish skeletal remains and bone harpoons (Yellen et al. 1995) indicate that fishing may have appeared in the MSA as much as 40,000 years earlier than in temperate Eurasia. There are also scattered but consistent reports of grinding stones in early MSA assemblages (McBrearty and Brooks 2000; McBrearty and Tryon 2005), suggesting intensive processing of vegetable foods in at least some localities by a fairly early date. Data from tropical East Asia are far fewer. The eastern Mediterranean Basin, a subtemperate region with extraordinary biological diversity (see Blondel and Aronson 1999), is host to both what are arguably the earliest Upper Paleolithic culture complexes in Eurasia (Bar-Yosef 2000) and the earliest clear evidence of dietary expansion in Eurasia.

While provocative, these scattered archaeological observations do not help us to understand how a phenomenon such as partitioned labor and social roles became a universal property of the Upper Paleolithic and later cultures in nearly every environment (cold or warm) it came to occupy. We propose that the success of “collaborative economies” in the

context of the global expansion of *H. sapiens* stems from their demographic consequences. A diversified, cooperative subsistence economy would have provided several distinct advantages to dispersing groups of *H. sapiens*. Most important, by ensuring even slightly more regular food supplies and thereby buffering the reproductive core of populations from excessive risk, this socioeconomic configuration would have given modern humans a demographic edge over indigenous hominins in Eurasia, allowing the invading populations to spread at the expense of local groups.³ Adding a diversity of gatherable prey and plants to the diet also effectively put humans at a slightly lower trophic level, meaning that larger populations could be sustained per unit land available (see also O’Connell n.d.).

The competitive advantage enjoyed by moderns came not just from new weapons and devices but from the ways in which their economic lives were organized around the buffering advantages of cooperation and complementary subsistence roles for men, women, and children. The demographic consequences of increasing diversity in economic roles and diets were probably subtle at the start, but, given the time spans involved, they were enough to make a difference. As Upper Paleolithic humans entered new environments with novel resources and challenges, the basic tropical system would have continued to change while seldom losing its diversity because of the competitive demographic advantage that went with it. The ability to adjust complementary roles to the opportunities and limitations of diverse environments eventually produced the vast range of foraging economies known in historic times. The competitive value of complementary, diverse roles in the new areas colonized by *H. sapiens* was determined by the novel juxtaposition with competing resident populations.

How might one behaviorally defined “population” have driven another to extinction or largely replaced it if the differences in demographic potential were marginal? Competitive exclusion in its original conception (reviewed by Pianka 1988) is proposed to occur only if two populations come into competition and cannot achieve evolutionary stable coexistence. If both populations were small at the outset (below environmental carrying capacity), each could have grown exponentially, limited mainly by the rates determined by their reproductive potentials. As the habitat(s) filled in, however, the growth rate of each population would have been progressively reduced. Because the populations would have been unlikely to have identical rates of increase, competitive abilities, and carrying capacities, a critical point would have been reached when one population suddenly gained an incremental

3. We remain agnostic about the level of taxonomic distinction between Neandertals and *H. sapiens* and about the degree to which they might have contributed to the modern human genome. People today everywhere look a lot more like the earliest *H. sapiens* than like Neandertals. Whether the earlier hominins were driven to extinction or absorbed into a much larger gene pool is not directly relevant to the current argument.

advantage. Theoretical models and experimental data indicate that, as an ecological vacuum is filled, one population's rate of increase drops to zero while the other's rate of increase is still positive. The second population increases still further and in so doing intensifies its competitive inhibition of the first, reducing the actual rate of increase of the first population to a negative value. The first population is now declining while the second is still increasing, and, according to Pianka and others (e.g., MacArthur 1972), exclusion of the first population is only a matter of time.

What, then, are the ecological consequences of the human tendency to divide labor? Perhaps there was a two-tiered effect: The proverbial jack-of-all-trades is master of none, so individuals tend to specialize somewhat according to age, gender, and innate abilities, but the population's total competitive ability in a saturated environment is enhanced through a collective tendency to diversify and to maintain heterogeneous strategy sets. A population of diverse specialists (our hypothetical Upper Paleolithic population) might actually out-compete a population of generalists (Middle Paleolithic population) in which all individuals held more similar roles, even if average individual foraging efficiency was lower in the former (Horan, Bulte, and Shogren 2005). This kind of within-population diversification may become especially advantageous (Pianka 1988, 254; MacArthur and Levins 1964, 1967) where key resources are separated in terms of location and timing of availability or where different mechanical strategies are required to obtain them efficiently. Though the advantages of divided, cooperative labor first arose in the tropics or subtropics, such economic systems would have conferred different advantages in spatially patchy and seasonally variable temperate environments, where roles such clothing and shelter technology became as important in some areas as diversified foraging roles.

Conclusion

Most narratives of human evolutionary history are decidedly orthogenetic. They portray the history of our species as a simple progression of physical or cultural forms. Yet skeletal and archaeological data frequently show us that evolutionary trajectories are anything but linear. The same applies to the current discussion. For example, the emergence of the genus *Homo* some 2.5 million years ago was accompanied by increasing consumption of meat from large animals (scavenged or hunted). However, the history of hominin diets after roughly 500,000 years ago is not marked by a simple progressive increase in the aptitude of hominins as hunters of large animals (Stiner 2002). We have argued that, if anything, the dispersal of *H. sapiens* was facilitated by a broadening of diets, in which large-mammal hunting was increasingly supplemented with lower-ranked animal foods and eventually vegetable foods. Moreover, many changes in hunting practices represented shifts in the way labor was devoted to this activity.

There was an evolutionary trade-off between cooperation among most group members in surrounding prey and killing them with simple weapons at close range and the increasing incidence of solo or small-party hunting wherein advantages were gained from the greater efficiency of high-investment weapons systems. The increasing importance of the latter system, even in combination with the first, more often freed other individuals to engage in quite different and spatially remote foraging activities. This trade-off over the long term represents a shift in the value of the individual forager's time and a relaxation of the requirement that individuals always stay in proximity to one another during the food quest.

By the same token, there was nothing inevitable about the origins and spread of forager economic patterns based on gendered division of labor, even if this was the historical trajectory in most of the world. This particular development may have been a by-product of the habitats in which *H. sapiens* happened to have evolved, although just how and when it appeared in certain low-latitude environments remains to be fully understood. Moreover, the observation that the first skeletally modern humans in the eastern Mediterranean used similar technologies to conduct the same range of activities as the Neandertals that replaced them in the region (Shea 1989) shows either that marked division of labor and complementary economic roles were not typical of the earliest *H. sapiens* groups or that these traits did not always provide a distinct advantage. While the shifting geographic distributions of skeletally distinct Middle Paleolithic hominins may have followed climate-driven changes in environment, the shifting distributions of Upper Paleolithic populations defy such an explanation; in fact, the geographic expansion of the Upper Paleolithic appears nearly independent of oscillations in Pleistocene climate and environments (Tchernov 1998).

The concept of "fitness landscapes" may be useful in understanding the origins and eventual success of gendered division of labor among human foragers and the fact that the way of life of the Neandertals, relatively successful for more than 100,000 years, was so fragile when confronted with a distinct competing population. The term was originally coined by Wright (1932) to refer to a topographic construct describing the influence of a range of different factors on the fitness of a population of organisms. High points on the landscape represent adaptive configurations of relatively greater fitness, whereas topographic lows represent areas of reduced fitness.

In a simple fitness landscape, all factors converge to create one Mount Fuji-like peak, a single behavioral and/or physical phenotype that provides a near-optimal adaptive solution to a wide range of environmental problems. Because organisms that can maintain higher levels of fitness will be evolutionarily successful, selection tends to drive populations toward the single peak from any starting point on the fitness landscape. A more interesting and probably more widely applicable con-

struct is the rugged or broken fitness landscape (e.g., Palmer 1991). Rugged fitness landscapes are characterized by many fitness peaks of varying heights (representing local suboptima) separated by “valleys” representing adaptive states of lower fitness. Selection will still drive populations toward adaptive configurations associated with higher levels of fitness, but on a rugged landscape the populations will tend to climb the peak closest to their starting position, which may not be the highest peak on the landscape. This is where historical contingency comes in. Once a population has begun to ascend a particular fitness peak, it is very difficult for it to shift to another, even if the second peak represents greater maximum fitness. This is because shifting between peaks necessarily involves an immediate reduction in fitness, something evolutionary processes seldom promote or reward. At the same time, severe environmental or demographic perturbations may serve to dislodge a population from its current suboptimal fitness peak, providing at least the opportunity for survivors to begin climbing an even higher peak that now happens to be accessible.

Tropical or subtropical latitudes have probably always supported the densest hominid populations, at the same time presenting the greatest potentials for dietary diversification because of their inherently higher biodiversity of all sorts. In these environments, diversified economies may represent a high fitness peak relative to all others. Dietary diversification is simply more likely to emerge *repeatedly* in low-latitude habitats, and thus human populations in these areas are more likely to undergo repeated episodes of expansion (for related early discussions of this concept, see Binford 1968; Flannery 1969). Human groups expanding from regions characterized by higher plant and animal diversity would have possessed certain social and economic preadaptations as part of their evolutionary legacies.

In contrast, the terrestrial subsistence opportunities typical of northern Eurasia were unlikely to lead to similar patterns. Without dispute, Neandertals were successful for long periods doing whatever it was they did. They were ascending a local fitness peak, though perhaps not the highest in the total fitness landscape. They were “living fast,” with very high caloric intake from high-yield but risky subsistence resources. So long as they were alone in Eurasia, existing at perpetually low population densities, there would have been no benefit to diversified subsistence. Indeed, there may not have been room in much of their biogeographic range for local experimentation with other economic strategies that gave lower overall returns, even if some of these strategies ultimately could have supported greater sustained population growth over the long term. The demographic expansion of early Upper Paleolithic populations resulted in perturbations in the fitness landscape that had not existed previously, putting the heretofore successful Neandertal socioeconomic patterns at a competitive disadvantage.

Acknowledgments

We thank David Pilbeam, Luke Premo, Ofer Bar-Yosef, Polly Wiessner, and three anonymous CA reviewers for their many insightful comments, criticisms, and suggestions for improving the penultimate version of this manuscript. This paper is dedicated to the fond memory of Amilcare Bietti, who first helped us to get acquainted with Neandertals and with whom we worked for many years.

Comments

Guy Bar-Oz and Mina Weinstein-Evron

Zinman Institute of Archaeology, University of Haifa, Haifa 31905, Israel (guybar@research.haifa). 10 VII 06

Understanding Pleistocene hominin behavior, particularly the transition from the Middle Paleolithic to the Upper Paleolithic in Eurasia, remains one of the most intriguing and compelling issues in prehistory and paleoanthropology. Several hypotheses have recently been suggested to explain the apparent increasing sociocultural and cognitive fitness of modern humans over Neandertals (e.g., Gamble 1999; Klein 2000; Hoffecker 2002; Shea 2003; Hovers and Kuhn 2006). In spite of the plethora of archaeological research involving biological and environmental studies, the nature of the processes that underlie the emergence of modern behavior is not yet fully understood. A major obstacle derives from the occurrence of two hominin types in the Middle Paleolithic of the Levant—Levantine Neandertals and anatomically modern *Homo sapiens*—and from the fact that the temporal, biological, and cultural relationships between the two remain unclear. Kuhn and Stiner present a new and challenging hypothesis on modern human origins and the demise of the Neandertals. They suggest that the roots of Neandertal extinction may well be found in a clear gender- and age-based division of labor accompanying the onset of the Upper Paleolithic in Eurasia and that it was the ensuing shift from a narrow reliance on large game to a marked increase in the exploitation of small game that ultimately provided the expanded population of *H. sapiens* with a demographic advantage over other hominins in Eurasia. The paper provides important food for thought and is likely to prompt further pertinent research.

The rich and ever-growing database from Israel permits rigorous testing of the suggested hypothesis. Furthermore, the time scale relevant to the discussion is amply represented in the Israeli record. Since the Levantine corridor is a main crossroads from Africa to Eurasia and the beginning of the change discussed is arguably best documented in the archaeological record of the region, the Israeli data can serve to highlight the cultural and social changes pertinent to the processes that Kuhn and Stiner hypothesize. Although the relationship between Nean-

dertals and modern humans is not established, their possible contemporaneity may eventually allow the suggested models to be extended to the study of demographic and population dynamics related to earlier transitions. Thus, the southern Levant is one of the main geographic area that one is likely to zoom in on when seeking to decipher the suggested cultural evolution processes by exploring variations and developments in foraging strategies, social behavior, and landscape use. We have a few questions relevant to the discussion.

Can this hypothesis be tested with the available archaeological data? We agree that plant remains and ground stone implements may hold the key to understanding the social division of labor, but plant remains are rarely preserved (but see Nadel et al. 2004; Weiss et al. 2004) and the evidence for ground stone implements is meager.

Does the abundance of small-game remains in the record provide an unequivocal basis for identifying gender behavioral differences? The abundance of small-game remains might also result from demographic pulses (Stiner et al. 1999; Stiner, Munro, and Surovell 2000), intensification of resource processing (Stiner and Munro 2002; Munro 2004), or technological innovations and developments in hunting technologies (Lupo and Schmitt 2005). Hunting variation may obscure important intra- and intersite variability in prehistoric foraging efforts. Other archaeozoological analyses have demonstrated that Neandertals and modern humans employed virtually identical large-ungulate-hunting tactics and food procurement subsistence strategies (e.g., Kaufman 2002; Adler et al. 2006 and references therein; Bar-Oz and Adler 2005).

How general is this phenomenon? In order to examine the Middle Paleolithic Upper Paleolithic transition we need to control for biogeographic and environmental variation and temporal fluctuations. Although all the sites discussed here are in the Mediterranean region, they represent different subregions and habitats. Therefore we first need to establish the local pattern within each region separately. To extract relevant information regarding specific sites or areas, a detailed representation of the data may prove useful. For example, in figures 1 and 2 the sites from which the data were obtained are not specified. Also, it is not clear whether the case studies presented in the two figures are the same and whether the taxonomic abundance values presented are statistically significant. Changes in taxonomic diversity seem to have appeared later than 45,000 BP, and therefore one may wonder whether there were delays in the influence of the various cultural, technological, and social factors at play.

While these and other questions remain to be addressed, Kuhn and Stiner have staked out a new research agenda for the future. When supported by additional data, the division of labor may indeed prove to be one of the major factors that, together with other cultural, behavioral, and cognitive developments, worked to enhance modern human competitive advantage over Neandertals and their contemporaries. Taken together, the synergistic effect of these factors naturally amounts to more than the sum of its parts.

Jean-Pierre Bocquet-Appel

UPR 2147, CNRS, 44, rue de l'Amiral Mouchez, Paris 75014, France (bocquet-appel@ivry.cnrs.fr). 31 V 06

The ethological inference that can be drawn from sexual dimorphism in the great apes is disappointing. With the same dimorphism, chimpanzees produce an aggressive, hierarchical, and male-dominated society (Manson and Wrangham 1991) while bonobos produce a hedonistic society with females slightly dominant (de Waal 1997; Stanford 1999). From the archaeological data, however, Kuhn and Stiner infer a key sociological difference between Neandertals and anatomically modern humans: the probable lack of any sexual division of labour in the former and its invention by the latter. They consider its effects on hunting productivity and ultimately on demography the determining factor in the disappearance of the Neandertals and their replacement by anatomically modern humans. Their persuasive article demands an effort to delve further into Neanderthal demography, which remains imprecise for lack of data.

With the isolation of small bands of *Homo erectus* from the rest of their metapopulation on the European peninsula, these bands, as noted by Kuhn and Stiner, were subject to frequent and catastrophic crashes that have been detected in the age distribution of the archaic humans of Atapuerca HS (Bocquet-Appel and Arsuaga 1999). Nevertheless, to counteract demographic and environmental stochasticity there had to be a flow of genetic and cultural information between bands (Bocquet-Appel 1986), as is attested by the relative phenotypic and cultural homogeneity of Neandertals over long distances. The Neanderthal metapopulation, on the order of perhaps 10,000–20,000 individuals but subdivided into small groups, was caught, according to Kuhn and Stiner, in a demographic trap—a system of steady-state equilibrium that may have relied, for example, on techniques for hunting large ungulates by direct contact combined with collectively organized concentration or isolation of animals in which no division of labour occurred. Furthermore, the invasion of Neanderthal Eurasia by modern humans occurred not over a continuous territory but rather, judging by the distribution of Aurignacian sites across Europe, in successive waves across five or six well-defined regions (Bocquet-Appel et al. 2005; Bocquet-Appel and Demars 2000a 2000b) separated by relatively large geographical distances that would have supported herds of several million ungulates. Lack of connection between these regions would certainly have helped to accelerate the takeover of resources, given the number of invaders and the length of time that would have been required in a single but continuous zone of continental size. To further the discussion, I feel that two issues deserve to be addressed in more depth: how Neandertals used their spare time and their seeming inability to make factual history.

While it is well known that there is a relationship between population size and division of labour and that division of

labour could not have existed below a certain population level (Boserup 1965), what has been omitted is the initial division at the origin of this relationship, the sexual division of labour. This is commonly thought of as a natural fact that has existed from time immemorial as an extension of reproductive functions and differences in physical strength, as suggested by the sexual dimorphism of living and fossil primates. By leaving aside the issue of cognitive capabilities (if these can be assimilated with mere cerebral volume, which is identical in the two competing metapopulations), Kuhn and Stiner have taken a further step into the etiology of an aspect of demographic models that helps to increase the intensification of production systems—including the division of labour—according to John Stuart Mill's law of diminishing returns. This law is a systemic response to population growth (Boserup 1965; Levine 1965). However, the question remains what, apart from hunting (which would certainly not have taken up all their time), individual owners of a 1,500-cm³ brain could do the rest of the time.

Sewall Wright's fitness landscape is determined by the physical forces of genetics. The convergence of the system has a strong inertial effect and can be diverted from its initial course only gradually or by a catastrophic interruption of the convergence mechanism, as indicated by Kuhn and Stiner. Would this inertia in a genetic model, lasting over an evolutionary time scale, also have applied to social relationships among archaic humans? Would these social relationships have been only a means, selected over the long term, of regulating individual relationships between undifferentiated beings *à la* Emile Durkheim, incapable of adaptation/innovation over the short duration of a generation's experience—in other words, incapable of producing factual history? But then, how can this be reconciled with the notion of Neanderthals as the authors of so-called transition industries and apparently capable of adopting technological innovations (see, e.g., Bailey and Hublin 2006) arising from a sexual division of labour among their competitors and perhaps, therefore, amongst themselves?

Erella Hovers

Institute of Archaeology, The Hebrew University of Jerusalem, Mt. Scopus, Jerusalem 91905, Israel
(hovers@mscc.huji.ac.il). 28 VI 06

In discussing the Middle-to-Upper-Paleolithic transition, paleoanthropologists have shifted from a tautological worldview in which the mere occurrence of *Homo sapiens* was perceived as an explanation for the species's evolutionary success to theory-based approaches seeking to explain the behavioral characteristics that underlie that success. Kuhn and Stiner's paper is a stimulating addition to this evolving research tradition with a particularly appealing emphasis on the role of historical contingency in recent human evolution. The concept of "rugged fitness landscapes," admittedly not always

referred to as such, has been pivotal in discussions of human evolution and has underlain many studies of the Middle and Upper Paleolithic records (e.g., Boyd and Richerson 1992; Finlayson 2004; Hovers 1997; Kuhn and Hovers 2006; O'Connell 2006). Here Kuhn and Stiner identify the emergence of the sexual division of labor as a uniquely modern human behavior that contributed to the demographic stability of *H. sapiens* populations while at the same time disrupting the suboptimal equilibrium in which Neandertals had survived for so long. It thus increased the ability of modern populations to out-compete the Neandertals.

Whereas details of initial conditions, evolutionary pathways, phenotypes, and timing are historically contingent, fundamental "ecological, functional, and directional aspects of the history of life are replicable and predictable" (Vermeij 2006, 1804). Kuhn and Stiner's premise that economic diversification and the ensuing selection for a sexual division of labor were more likely to have emerged among primates living in the tropics falls into the category of such predictable trajectories and is certainly plausible. Indeed, sexual division of labor is seen in chimpanzee populations, among which female hunting is almost unknown whereas males tend to invest less time and be less efficient in tool-assisted vegetal food extraction (Boesch and Boesch 1984, 1989; Boesch and Boesch-Achermann 2000; Stanford 1996, 1999).

The main challenges to the hypothesis probably emerge from the paleoanthropological record rather than from any theoretical perspectives and concern sexual division of labor as the driving force of the scenario. Kuhn and Stiner present a compelling argument for the effectiveness of the sexual division of labor in the context of diverse dietary niches and build on it an arguably plausible scenario for understanding Neandertal-modern interaction and explaining the success of modern humans in western Eurasia. Under the theoretical premises outlined by Vermeij (2006) we need not expect homogeneous conditions—or homogeneous behaviors—to underlie the successful colonization of modern humans in each geographic locale (see Hovers and Belfer-Cohen 2006). This reduces the explanatory power of Kuhn and Steiner's hypothesis. At least some of the regions where moderns replaced local populations were warm and ecologically diverse and offered a broad dietary niche. If sexual division of labor was a response to such conditions, it was likely to have risen independently in these places.

Tracing Kuhn and Stiner's scenario backward in time, it is interesting that division of labor does not appear to have emerged in sub-tropical Africa even before the emergence of modern humans, as resource diversity, the postulated trigger for its emergence, would have been in place. Perhaps the various pre-*H. sapiens* African hominins were not cognitively able to devise extractive strategies that relied on social allocation of labor and resources. This reasoning, however, will put the weight of the argument on vaguely defined (and in fact vaguely recognized archaeologically) cognitive rather than social, behavioral or technological innovations. Endorsing

such a claim brings us back to a Middle-to-Upper Paleolithic transition as it was understood several decades ago, namely, a descriptive, non-explanatory scheme. Another possibility is that technological knowledge did not catch up with the emerging social alignments and the pre-sapiens hominins in Africa could not produce the type of lasting physical evidence of the behavior that we search for in the archaeological record. But then the same could be said of the Neandertals. Both points are archaeologically moot.

Assuming that a sexual division of labor was not part of a behavioral package of the earliest populations dispersing from Africa, it might have emerged in a colder environment as a response to a different environmental trigger. Kuhn and Stiner emphasize the sexual division of labor as a mechanism of perking up life in the tropics, but this behavior could have evolved as a necessity of life in a cold climate. Neandertals were faced with the dilemma of enhancing extractive gains (by women and older children pulling their weight through participation in hunts) as opposed to minimizing the survival risk to their offspring due to the harsh climate (e.g., Fitzhugh 2001; Ugan, Bright, and Rogers 2003). High thermo-regulatory costs would have promoted the use of high-level (i.e., meat-rich) diets (Aiello 2003) but would also have necessitated enhanced parental investment in Neandertal neonates and infants. As is common in the mammalian world, females would have been responsible for this investment and almost by default would have been prevented from participation in highly mobile and risky endeavors such as big-game hunting. "Grandmothering" (in the sense of Hawkes et al. 1998) would have been a partial substitute for maternal care only at a relatively late ontogenetic age of the offspring.

It is certainly true that the Eurasian Middle Paleolithic record does not show much by way of the technological equipment one might expect to occur in societies with a division of labor. But in fact such tools are not really prolific in the early stages of the Eurasian Upper Paleolithic. Their rather sporadic occurrence on the Eurasian scene in the span when moderns displaced Neandertals is not consistent with their interpretation as part of a behavioral repertoire that provided the colonizing moderns with an adaptive edge over Neandertals.

So what is a paleoanthropologist to do? For the time being, perhaps, we should bide our time before endorsing the sexual division of labor as a telltale sign of behavioral modernity.

Katharine MacDonald and Wil Roebroeks

Faculty of Archaeology, Leiden University, P.O. Box 9515, 2300 RA Leiden, The Netherlands (k.macdonald@arch.leidenuniv.nl). 27 VI 06

Kuhn and Stiner attempt to reconstruct the evolutionary history of a division of labour in humans on the basis of ethnographic evidence for hunter-gatherers and the archaeological record for subsistence and technology. In addition, they

present an explanation for a number of differences in the Middle and Upper Palaeolithic record based on inferred differences in the environment and demography of Neandertals and anatomically modern humans. As an alternative to prevailing explanations focusing on cognitive differences, this line of argument is well worth pursuing. We would like to suggest two aspects of the archaeological and fossil evidence that should be taken into account in future work and a relevant interpretive framework.

Kuhn and Stiner rightly state that we have come a long way since the debate over the question whether Neandertals were mighty hunters or obligate scavengers. However, we should be careful not to replace this with a new black-and-white characterization, that of narrow versus very broad foraging regimens for Neanderthals versus modern humans. Isotope studies suggest that while some Upper Palaeolithic modern humans had different, broader diets, other modern humans and Neandertals in Europe ate similar ranges of foods (Richards n.d.). Many Upper Palaeolithic groups seem to have neglected aquatic resources as far as their archaeology goes, and not all Upper Palaeolithic humans built archaeologically visible dwellings. On the basis of the archaeological record, some Upper Palaeolithic humans behaved in many domains in a "Neandertal way." Factors that caused variation within the Upper Paleolithic may to some degree have caused the differences between the Middle and the Upper Palaeolithic record, and charting these factors may be a very productive line of future research (MacDonald, Roebroeks, and Verpoorte n.d.).

Secondly, Kuhn and Stiner fail to address a significant body of data relevant to male-female interaction in the deep past—the skeletal fossil record. For instance, Aiello and Key (2002) have drawn attention to the impact of changing hominin body size on the energetic costs of reproduction for females. Increasing female energy requirements have implications for social organization and foraging behaviour (Aiello and Key 2002; Key and Aiello 2000). These researchers suggest that *H. erectus* females could have met the increased energy costs in a number of ways, including shortening interbirth intervals and persuading other people to cooperate in provisioning dependent children. Large body size in Neandertals compared with modern humans implies even higher female reproductive energy cost. Using Aiello and Key's approach and estimates of body mass from Ruff et al. (1997), we can estimate that Neandertal females would have faced daily energy costs during gestation and lactation of about 2,750–3,020 kcal. This is about 20% higher than for *H. erectus* females and 10% higher than for middle Upper Palaeolithic humans. These differences in energy requirements are an important entry point for reconstructing Neandertal social organization and may suggest that Neandertals and Upper Palaeolithic modern humans would have behaved differently even under the same environmental conditions.

Finally, while Stiner and Kuhn comment on the various alternative explanations for the division of labour in hunter-

gatherer societies, they do not fully explore the potential of these models for addressing changes in social organization in the past. Models from evolutionary ecology have been fruitfully applied to the understanding of variability in human behaviour under different ecological conditions, including foraging strategies, food sharing, male-female division of labour, and mating strategies (Winterhalder and Smith 2000). In particular, a number of writers have suggested that models of conflict and cooperation in male and female reproductive strategies can be used to explain sex differences in foraging and food sharing and their variation in different hunter-gatherer groups (see, e.g., Bird 1999). These models provide the opportunity to explore the way changes in ecological circumstances (e.g., resource structure or energy requirements in males and females) would alter the costs and benefits for men and women of focusing on particular food resources, cooperating or sharing resources with particular people, or spending time on other tasks (see, e.g., Key and Aiello 2000). If it generated predictions testable in the archaeological record, for example, for diet breadth, this approach could be useful for explaining not only the differences between the Middle and Upper Palaeolithic records in Europe but also the variation in the Upper Palaeolithic record outlined above. Integrating these various lines of evidence with a framework that can explain spatio-temporal variability in the archaeological record may offer more insight into the issues addressed by Kuhn and Stiner and provide a convincing alternative explanation of differences in the archaeological record.

Kenneth Martínez

Àrea de Prehistòria, Universitat Rovira i Virgili, Plaça Imperial Tàrraco, 1, 43005 Tarragona, Spain
(kenneth@prehistoria.urv.net). 19 VI 06

It is gratifying to see one's work used by colleagues to explore new interpretive paths, particularly when these paths consider the archaeological record of the Lower and Middle Paleolithic to be traces of human societies which, like those of any other age, must be studied from an anthropological and a historical perspective. My commentary will focus on the second section, which reviews the archaeological evidence on the way age and gender affect the role that each member plays in the economy of the group.

In studies of lithic technology it is essential to bear in mind that production and consumption are two interdependent parameters in equilibrium. The spatial and temporal organization of lithic production and the morphological, technical, and metric characteristics of the objects depend directly on when and how the implements were used and what for. These latter aspects can be interpreted by use-wear analyses. As a function of the homogeneity in the use of artifacts, these analyses also enable the determination of the general character of lithic production. Thus, the number of phases in the production process, the degree to which they are specialized, the

simplification of the work, the specialization of production areas and the standardization of the tools (morphometric, material, or functional) are often presented as evidence of economic specialization and therefore as a reflection of greater technical and social complexity (Risch 2002). On this basis, I shall discuss the conclusions that, in my opinion, can be drawn from the functional analysis cited in the article (Martínez 2005). The lithic production of the Romaní shelter is characterized by its versatility, a single tool type being used for butchering (79.4%), scraping fresh hides (19.2%), and whittling green wood ($N = 1$). Thus tasks directly involved in providing food are clearly dominant. In addition to this type of implement, there are retouched objects, mainly denticulates, representing less than 10% of the assemblage. This retouch cannot be regarded as a technical specialization for a specific use, because it is used for the same purposes as the natural edges of flakes. Nevertheless, percentage-wise, the retouches are used to a greater extent for scraping fresh hides. Thus a minimal investment in technology may increase the versatility of flakes by making their edges are more resistant and capable of coping with more demanding tasks. Therefore, it can be concluded that during the Middle Paleolithic at the Abric Romaní there was neither economic specialization nor complex organization of production. The Neanderthal groups spent most of their time capturing prey and processing the carcasses. Manufacturing was restricted to occasional wood-working and the preservation of hides. The lack of diversity in activities, at least in lithic-tool use, indicates that group members had no need to specialize, and this in turn explains the absence of specialized tools. The limited development of productive activities means that Neanderthal groups were under no pressure to optimize resources. This suggests that the Neanderthal world was sparsely populated, because historically intergroup contact and competition have always led to economic growth. It is precisely this that could have happened during the transition to the Upper Paleolithic, when shifting human populations led to contact between groups that gave rise to competition that was resolved by social and technological innovations. Therefore, I consider it fundamental to explain the the increased production at the beginning of the Upper Paleolithic. In groups from the Middle Paleolithic there was probably a basic division of tasks and cooperation among members; in fact, intragroup solidarity with ill, handicapped, or old members has been demonstrated. In my opinion, then, the difference between the two periods lies in the intensification and optimization of the productive possibilities within the group that were prompted by intergroup competition (Johnson and Earle 1987). Increasing production and improving the finished products required specialized tools such as the tools of the Upper Paleolithic, and this in turn would have led to the specialization of group members (according to age or gender) so that their mastery of the increasingly complex productive processes would guarantee the best results. Therefore, in my opinion, the fact that this economic and social intensification within the group led to dividing up

and supplementing the activities carried out by its members is the consequence and not the cause of the transformations in the Upper Paleolithic.

John J. Shea

Anthropology Department, Stony Brook University, Stony Brook, NY 11794-4364, U.S.A. (john.shea@sunysb.edu). 31 V 06

Kuhn and Stiner present an interesting exploration of the role that gender- and age-based division of labor may have played in the dispersal of *Homo sapiens* into western Eurasia after 40,000–50,000 years ago. Though varying from context to context, such gender/age-based divisions of labor are universal features of preindustrial human adaptations. They have relatively clear correlates in material culture, hide-scraping tools, mortar stones for plant processing, and in-bulk collection of small game, most of which also become common features in the archaeological record of western Eurasia after 40,000–50,000 years ago. Kuhn and Stiner make as strong a case as is possible that the absence of evidence for these behaviors in contexts associated with Neandertals prior to 40,000 years ago is neither a function of sampling error nor a result of taphonomic bias. They conclude that Neandertals' narrow focus on large terrestrial prey supported small, stable populations but ones with limited potential for growth. Early *H. sapiens* also maintained small populations but increased their potential for growth after 50,000 years ago by focusing on smaller prey species. This is a reasonable hypothesis, and the evidence they have marshaled supports it. They have presented an interesting model—one with considerable explanatory power, grounded as it is in the theoretical framework of human behavioral ecology, and one that can be tested by future research.

In reconstructing prehistoric subsistence strategies, we archaeologists have to base our models on the empirical facts, not speculations about the possible-but-not-preserved. Yet, we also have to remain fully cognizant that there are significant “known unknowns” about Neandertal subsistence that reflect preservation biases in the archaeological record. Neandertals originated around 200,000–300,000 years ago and ranged from the shores of the Atlantic to the mountains of western Asia until their extinction ca. 30,000 years ago. Yet most of what we know about Neandertal subsistence strategies comes from sites clustered around the Mediterranean Basin (mainly Italy and Israel), Franco-Cantabria, Germany, Crimea, and, lately, the Caucasus Mountains. Most of these sites date to the marine oxygen-isotope stages 4–3 (ca. 75,000–35,000 years ago). We are missing a lot, both chronologically and, more important, geographically. Nearly all ethnographic foragers and many of the larger nonhuman predators living in the Arctic and the taiga of Eurasia and North America derived a significant portion of their nutrition from fish, marine mammals, and migratory birds. The places where such animals would have congregated and thus have been available to Neandertals with the

greatest postencounter returns would have been rivers and streams, lakes, estuaries, and coastal habitats. Many of these landscapes, if they were not scoured away by glacial runoff, now lie offshore under hundreds of meters of water. Isotopic studies of Neandertal fossils have not revealed evidence for significant consumption of marine/aquatic resources, but the bone samples thus far examined are few and derived from relatively “young” sites located far inland from the former coastline (Bocherens and Drucker 2003). Obviously, these considerations do not refute Kuhn and Stiner's hypothesis, but they do suggest that we need to be careful about extrapolating the contrasts discussed in this paper to all Neandertal and all early *H. sapiens* populations throughout their considerable chronological and geographic ranges. Both Neandertals and *H. sapiens* were large-brained, social, and technologically adept species whose persistence through the wide swings of the Pleistocene climatic pendulum suggests that they were capable of significant behavioral variation.

Gender/age-based division of labor and broad-spectrum subsistence strategies now join several other uniquely derived and culturally universal behaviors of *H. sapiens*, namely, exosomatic symbol use (Henshilwood and Marean 2003) and the use of projectile weaponry (Shea 2006b), in a remarkably parallel geographic and chronological distribution. All seem to have appeared (or likely to have appeared) in Africa before 50,000 years ago and thence afterwards in Eurasia along with expanding *H. sapiens* populations. This correlation may not be coincidental. Exosomatic symbols and projectile weapons are powerful instruments of social organization in all human societies. The appearance of consistent evidence for exosomatic symbols (especially personal adornments) and projectile weaponry may be related to the shift from societies in which gender and age roles were largely determined by physiology to ones in which they had to be actively constructed, negotiated, disputed, and enforced.

It is increasingly clear that the period ca. 50,000 years ago marked a watershed in the ways *H. sapiens* populations integrated social, technological, and subsistence strategies. This paper has successfully identified gender- and age-based division of labor as a possible factor in what Binford (1989) terms a “transition to cultural adaptations.” The remarkable expansion of *H. sapiens*'s geographic range after 50,000 years ago suggests that these cultural adaptations are the underpinnings of our current global ecological dominion.

Olga Soffer

Department of Anthropology, University of Illinois, Urbana, IL 61801, U.S.A. (o-soffer@uiuc.edu). 23 VII 06

While I agree with Kuhn and Stiner that modern human lifeways differed from Neanderthals' not in capacities but in the habitual exercise of capacities and that these performances had social causes, their selective use of the archaeological record seems to me to undermine their arguments. Their

evidence for a broad-spectrum diet as a hallmark of “modernity” is regional rather than universal. Archaeozoological and bone chemistry studies show that significant changes in diet breadths in Eurasia appeared closer to the Last Glacial Maximum (Drucker and Boherens 2004; Richards et al. 2001), at least 20,000 years before other signs of behavioral “modernity.” Archaeological studies reveal little difference in the prey harvested by Middle and early Upper Paleolithic groups (e.g., Adler et al. 2006; Davies and Underdown 2006) and point to problems in interpreting increases in dietary breadth as signals of population growth rather than of changing climates (e.g., Finlayson 2004; Musil 2003). Middle Paleolithic sites with a broad spectrum of resources are not as rare as Kuhn and Stiner suggest (see, e.g., Rabinovich and Hovers 2004; Burchak-Abranovich 1980; Liubin 1998; Tsepkin 1980). Edge-wear and residue analyses show fowling at Starosele (Hardy 1999; Hardy and Kay 1999). In fact, the dietary importance of such *r*-selected resources as turtle may go as far back as Bed I at Olduvai (West 1994).

While subsistence and maintenance tasks are gendered among ethnographically known hunter-gatherers (Soffer, Adovasio, and Hyland 2002), using these observations to gender prehistoric tools is problematic. Given that ripped clothing in arctic temperatures spells mortal danger and northern hunters are equipped with needles and thread, the recovery of needles at Upper Paleolithic sites does not automatically signal a division of labor by gender. Nor do I understand why Kuhn and Stiner see hideworking at Upper Paleolithic sites as likely female labor while dismissing evidence for the scraping of hides at Middle Paleolithic sites as more of the same.

While grinding stones may appear in the eastern Mediterranean only at Upper Paleolithic sites, Chernysh (1965, 1982, 1987) has recovered some from Middle Paleolithic layers at Molodova I and V and reported use-wear evidence linking them with plant processing. They have also been recovered in small numbers at other Middle Paleolithic sites along the Dniestr as well as at the coterminous sites of Ripiceni Izvor (Paunescu 1965, 1987, 1989). Although these inventories have been noted in passing (e.g., Hoffecker 2002; Klein 1999) they have not, with the exception of Rogachev's (1973) article, been problematized. Madella et al. (2002) have used phytolith evidence to argue for the use of plants at Amud. Thus it may well be that the broadening of the Neanderthals' diet to include not only fish and bird (Finlayson 2004) but wild plant resources occurred late in their tenure in Eurasia. In fact, Kuhn (1995) and Stiner (1994) themselves have posited that significant changes in subsistence practices occurred somewhere around 50,000 years ago.

Conflating biology with behavior clearly creates problems here. The Near Eastern record, for example, shows archaics and moderns not only present at the same time but apparently living similar lives. The conflation sends Kuhn and Stiner searching for evidence for modern behavior in sub-Saharan Africa, but the evidence they report is problematic (see, e.g., Klein 1999, 2000), sparse, and, in any case, some 70,000 years

younger than the claimed anatomic modernity (see, e.g., White et al. 2003).

Kuhn and Stiner direct their gaze to Africa also because they ultimately privilege particular habitats with generative powers for social change. Thus what they present as a contingent historical development is still tied to seeing human actions as simply reactions to the natural environment. This approach raises the question why, if the sexual division of labor was not a one-time invention, it was successful at this place and time and not before. Why is this hominid expansion out of Africa due to the division of labor and earlier ones not? Furthermore, what happened to this contingent historical development in the Near East when moderns expanded there some 100,000 years ago?

I am in broad agreement with Kuhn and Stiner's conclusions that what lies behind the differences between the Middle and Upper Paleolithic records is a change in the organization of life and that it involved the gendered division of labor and concomitant institutionalized food sharing. I have argued that what our ancestors invented was interdependence and its perpetuation through invented social categories, kinship, and descent ideologies (Soffer 1994, 2000). Just who the inventors were, however, remains in contention. For Kuhn and Stiner it was the early anatomically moderns in Africa. For me the record suggests far more complex scenarios. While I welcome their challenging ideas and applaud their focus on the big questions, I think that the answers they have come up with can be improved by considering the global rather than a selective local record.

Nicole M. Waguespack

Department of Anthropology, University of Wyoming,
Laramie, WY 82071-3431, U.S.A. (nmwagues@uwyo.edu).
30 VI 06

While archaeologists have spent a vast amount of time and effort attempting to identify male versus female artifacts, activity areas, and task roles in the archaeological record, the more fundamental question why we *expect* hominins to have a gender-specific division of labor remains unanswered. To borrow an analogy from Kuhn and Stiner's arguments, the division of labor in the prehistoric “fitness landscape” does indeed contain a Mt. Fuji, and the view of human behavior (both past and present) from atop such a peak has broad implications. Kuhn and Stiner offer one intriguing view of modern human behavioral origins from such a perspective.

Arguing that a fundamental difference existed in the division of labor from the hunting-based economies of the Middle Paleolithic to the more technologically complex and resource-diverse economies of the Upper Paleolithic both provides a possible answer to the question why ethnographically known hunters and gatherers ubiquitously express basic consistencies in male and female task participation and provokes a new suite of questions regarding the costs and benefits of labor differ-

entiation. It must be considered how and why a presumably herbivorous (or omnivorous) pre-Neandertal hominin made the transition to large-game hunting while maintaining an equal-opportunity labor strategy and why technological developments which reduced hunting risk and variance did not eventually promote greater female participation in hunting as opposed to reducing it.

Numerous arguments have postulated a fundamental shift in labor organization at the onset of animal/plant domestication and/or as a result of increased human population densities (e.g., Keeley 1995; Keen 2006; Owens and Hayden 1997). Kuhn and Stiner's arguments posit a much earlier, perhaps more dramatic shift with modern human occupation of subtropical environments. While such environments do provide a diversity of resources which can be procured according to demographically advantageous labor strategies (i.e., with women and children selectively targeting small game and plants and men hunting large game), it could also be argued that such biodiverse environments offer resource opportunities equally accessible to all segments of a foraging population. Ethnographically, it is generally high-latitude and/or low-diversity environments in which divisions of labor by age and sex are most pronounced and reliance on big-game hunting is greatest. I agree that the narrow diet breadth of Neandertals coupled with a nondivisive labor strategy could have placed them at a real demographic disadvantage when confronted with a more competitive modern human labor strategy. However, the reproductive advantage of a cooperative yet segregated labor pool are potentially greatest in low-diversity/high-latitude environments in which the acquisition of risky prey items is a necessity. If such is the case, it raises the question how Neandertals developed a successful hunting-based subsistence economy in Ice Age Eurasia and why modern humans first segregated their labor pools in lower latitudes.

If a cooperative economy provides a relatively more stable source of calories and a less risk-prone procurement regime (at least for some) collectively results in greater demographic potential, why are there no ethnographic examples in which the primary division of labor falls along lines other than sex? As reviewed by Kuhn and Stiner and others, there are reproductive reasons for men's and women's relative likelihood of engaging in risky procurement endeavors with a high degree of variance in return rates (e.g., hunting). That the vast majority of female foragers do not actively hunt medium-sized and large game makes sense from a general reproductive perspective. But in the larger scheme of things, as prehistoric weapon systems allowed hunters to capture prey at increasingly greater distances with increasing accuracy, thus reducing the risk of injury, one could argue for an increasingly active role of women as hunters. The demographic advantages of a division of labor could still have been achieved through divisions such as those based on skill, age, or sociopolitical distinctions.

Kuhn and Stiner's arguments seem to require that female and subadult collection of plant and small-game resources be

so advantageous as to become a necessary part of the behavioral repertoire. In certain situations, such as the Pleistocene colonization of the Americas, where animal resources may have been plentiful relative to human needs and plants/small game were only minimally utilized, the sexual division of labor appears to have supported a more "Neandertal-like" subsistence strategy rather than promoting the use of a diverse suite of food resources (Waguespack 2005). While these and many other issues require resolution, they are the product of the unique and intriguing perspective offered by Kuhn and Stiner, who have managed to scale the Mt. Fuji of prehistoric behavior and provide a theoretically encompassing description of the view.

Reply

We thank our colleagues for their insightful and stimulating comments, pointing out weaknesses in our arguments and indicating ways in which the ideas we presented might be extended or redirected. Some common themes arise from the comments, although we are struck most by their overall diversity.

Our paper deals in generalizations about time periods, hominids, and cultural units. While we believe that these generalizations are valid, there is also much to be gained by investigating the specifics of Neandertal and modern human ecology in different regions and by sampling as many paleoenvironments as possible. We concur with Bar-Oz and Weinstein, Hovers, Shea, and others that it will be important to focus on empirical studies of possible changes in hominin socioecology in specific habitats and ecozones. Reliable data on Middle and Upper Paleolithic lifeways are indeed more geographically limited than the known biographic range of these Pleistocene peoples, and this problem stands in the way of knowing the true limits of hominin adaptations. Distinguishing "absence of evidence" from "evidence of absence" is particularly difficult and will remain so for some time to come. The Paleolithic records of Central Asia, the Arabian Peninsula, South or Southeastern Asia, and the Mediterranean peninsulas should each present unique and often extreme conditions to which hominids had to respond.

It already is clear, nonetheless, that dietary change at the Middle-Upper Paleolithic transition varied in character or timing across Eurasia. There are some broadly comparable developments in this process when examined from an ecological perspective. The variety therein does not necessarily undermine the existence of trends, just as trends do not exclude the possibility of variation or even the existence of rare exceptions. In high latitudes, as we noted, the contribution of plant foods and small animals to post-Middle Paleolithic diets was often much lower and the broadening of diets delayed compared with what happened at lower latitudes. Po-

tential blind spots in well-studied regions due to marine transgression or shifts in continental hydrology (as Shea notes) must also exist, since we know from other locations that marine and lacustrine resources were in play. It is important in these circumstances to look to complementary economic activities for evidence of expanded economic roles such as production of shelter, clothing, and artifacts. Along with Shea, Hovers, and many other archaeologists, we will continue to pursue additional data through fieldwork and collections studies. This paper is fundamentally an attempt to focus the discussion and develop useful criteria based on data and behavioral ecological principles. Nothing is gained by waiting until “all of the data are in” to take steps toward defining the problem.

MacDonald and Roebroeks are concerned that we did not consider body mass and metabolic needs of males versus females between periods. This is a very interesting topic, and some excellent, provocative work has been done on it by Aiello and colleagues, among others. Perhaps we were remiss in not citing this work, but it neither supports nor undermines our arguments directly. First, as far as we are aware, assessments of energy requirements tend to yield highly relative, gross, and oft-revised estimates of daily caloric needs. Second, proposing that Neandertal females needed lots of energy and fat does not explain what foods they consumed or how (or from whom or where) they got them. Likewise, the convincing argument that Neandertals would have required at least some clothing to survive the worst conditions they faced (Aiello and Wheeler 2003) does not specify who made the clothing and how much effort they put into making it. Third, studies of hominin bioenergetics identify the direction and force of evolutionary pressures on extinct taxa. They do not tell us how or whether the organisms in question responded to them. Neandertal females may have supported low levels of fertility and poor infant viability because of constraining factors other than metabolism-mass relations. We agree with Hovers that there must be connections among body size, energetics and reproductive ecology, and labor allocation and that these connections could both promote a diet rich in meat (and especially fat) and necessitate enhanced parental investment. It is entirely possible that we have underestimated the importance of parental care in the allocation of labor. In this regard our paper might be viewed as a first attempt at a “model of circumstance” for features of Neandertal reproductive ecology.

Some of the comments seem misdirected, among them MacDonald and Roebroek's first and third points and the similar response from Soffer. What we consider a universal or obligate characteristic of *Homo sapiens* is not broad-spectrum subsistence but the inherent flexibility with which to adopt it when needed. That some Upper Paleolithic modern humans had “Neandertal-like” diets (their term, not ours) is not a point of contention. In addition, there is no reason to think of human forager groups, even ones with very broad diets, as assemblages of ecological generalists. They are better characterized as a group of cooperating, sharing specialists. We look forward to the eventual publication of the papers

cited by MacDonald and Roebroeks, but it is fair to say that we have been making the same point for the past five years (e.g., Kuhn and Stiner 2001; Stiner 2002). It is true that we “did not fully explore” the evolutionary ecological literature on alternative models of circumstance and mechanism for the evolution of cooperation. That would best be left for another paper (or several).

We do not dismiss, as Soffer says, Middle Paleolithic female labor, including hide preparation. We suggest, on the basis of the paucity of dry hide working, for example, in the camp work routines of many Upper Paleolithic sites, that it generally was not as labor-intensive. Some version of divided labor probably also obtained during the Middle Paleolithic. We do argue that the labor of females (and children) was very important to subsistence activities outside the stereotypical hunter-gatherer pattern. The differences between the Middle and Upper Paleolithic patterns of labor allocation by gender and age likely resided in the nature of schedules and land use, or the scale of integrated diversity.

Bar-Oz and Weinstein pose several questions relating in some way to test implications and geographic scales of study. The Levantine paleoanthropological record is among the best documented and continuous in the Old World and thus very attractive for evolutionary studies. But clinal variation across regions and large tracts of time has also been critical for our thinking. Any question about the generality of a phenomenon in human evolution requires consideration of the spatial and temporal scales at which it should be studied. It has been most productive to examine variation across geographic clines far larger than the boundaries of most countries. Casting the net more widely in the form of clinal comparisons helps to get around this problem. Otherwise local studies tend to suffer from the trap of locally unique explanations.

We agree with Bar-Oz and Weinstein and Soffer that there is no simple connection between small-game use and gender. The increasing diversity of small prey types—which vary much more than large prey in capture requirements, substrates, and other characteristics—only means that there was diversification in the ways of getting complete protein for a greater range of personnel. Unfortunately, information on staple plant use (seeds, nuts, tubers) and on grease rendering from bone in the form of durable grinding and pounding equipment lags behind in archaeological studies (but see, e.g., Weniger 1987; Wright 1994). While evidence for ground stone implements is rare prior to the Last Glacial Maximum, these kinds of implements have been found even in some recently excavated early Upper Paleolithic sites in the Levant (e.g., Üçağızlı Cave). The cases Soffer notes are not unique: there are occasional reports of early grinding stones from other regions (de Beaune 1989). However, their function is uncertain, and they may well have been used as anvils or for processing pigments. Our point was not that such artifacts did not exist but that as far as archaeologists know they were never regular components of Middle Paleolithic food-processing toolkits.

Soffer's observation that we have privileged certain records

in our comparisons is correct. That doing so should undermine our arguments is a point that applies to all paleoanthropological claims, and therefore debate in these circumstances must turn to the question of how sampling choices are justified. We have relied on data sets for which good stratigraphic and taphonomic control and reasonable dating, not to mention consistent reporting, are available. Soffer admits that this is not the case for the majority of exceptions she notes about groundstone technology in the Middle Paleolithic, for example, and we agree with her. Still, she is right to note that milling and groundstone technology studies are not yet fully “problematized,” and we hope that our paper will help to stimulate more of this kind of research.

As Shea notes, the isotopic record of Neandertal diet is also regionally and chronologically biased. Because of the effects of burial time and temperature on the diagenesis of organics in skeletal tissues, some of the biases favoring high-latitude populations may never be overcome. The isotope record is nevertheless certain to hold surprises. We note, however, that the recently studied Neandertal from St.-Césaire is supposed to be associated with high-biomass rather than steppic environmental conditions (Bocherens et al. 2005). We are less convinced by assertions that much of the potential record of possible use of marine and freshwater resources by Neandertals has been erased by geological forces. This is certainly true of some coastlines but, because of topographic differences, among other factors, not all of them. Many of the known Middle Paleolithic sites are associated with bodies of water, and there are several examples of limited shellfish exploitation by Neandertals. In any case, finding evidence for Middle Paleolithic fishing would not necessarily alter the basic parameters of our argument, though we are prepared to step back to the drawing board as more information on aquatic exploitation becomes available.

Soffer echoes the findings of several zooarchaeologists that large-game hunting has not been a great help for distinguishing Middle Paleolithic from Upper Paleolithic economies (Stiner 2002). These conclusions generally do not take into account processing or new tradeoffs in technological investments, hunting-party sizes, time, and risk. Having contributed data in support of these findings, we now prefer to ask what changes in means of access—social as well as mechanical—could have come about with labor and social diversification.

Hovers notes that craft tools are not so common in the earliest Upper Paleolithic—that they become more abundant later in the period. This is true, but it is important to emphasize that craft tools (mostly of bone) are not *absent* in the early Upper Paleolithic even though it is less extensively documented than the Middle Paleolithic. Similar tools are absent from the rich records of the Middle Paleolithic and earlier periods in the same regions.

Martínez poses the fundamental question whether changes in the social relations of production across the Middle–Upper Paleolithic boundary are a cause or a consequence of the “transformations” represented by the Eurasian Upper Pale-

olithic. We argue the former (or a result of feedback processes), the latter. This is not an issue to be resolved in a paragraph or two, stemming as it does from basic differences in the theoretical perspectives from which we work. However, the opposition between the viewpoints may not be as stark as it seems. We can suggest that the changes in the organization of technology that he observes are consequences of social transformations brought on by different relations between subsets of human societies.

As a researcher investigating social and economic organization outside the Paleolithic context, Waguespack brings a somewhat different perspective to the discussion. Her point that changes in technology such as improved weaponry for killing at a distance could relax boundaries between stereotypical subsistence roles is a good one. In fact, we know only that novel roles in subsistence and technology seem to have opened up during the Upper Paleolithic. As we said, we do not know just who was filling those roles (a point also raised by Soffer). Ethnographic evidence suggests that we should expect to find a great deal of variation around the “normal state” of age- and gender-based roles in the past (see also Owen 2005). Perhaps the success of *H. sapiens* was due more to this inherent flexibility than to the “normal” condition. Waguespack proposes that the best evidence for intensification and diversifying roles is to be found among high-latitude hunter-gatherers. We agree with respect to technological support of the food quest but not for several other potential dimensions of economic diversity.

Bocquet-Appel raises two very challenging questions for which we have no definitive answers. Both questions ultimately lead back to the relationship between cultural and biological evolution, an important frontier in anthropological research. Much important work has been done on the differences between cultural and genetic transmission (e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981), but we still know little about differences in the dynamics of cultural and biological change over very long time spans.

One point made by Bocquet-Appel in his first question, referring to the phenotypic and cultural homogeneity of Neandertals, deserves some clarification. We are not prepared to assess morphological homogeneity among Neandertals, but we do believe that the cultural uniformity of the Middle Paleolithic has been exaggerated somewhat. The impression that Neandertal material culture is monotonous derives in part from a research bias toward certain regions (western Europe, the Levant) and the historic application of homogenizing artifact typologies. Neandertals may well have engaged in a comparatively limited range of activities compared with recent hunter-gatherers, and they certainly produced a limited range of basic artifact forms, but they produced those artifacts by a remarkable diversity of technical methods (e.g., Boëda 1991; Delagnes and Meignen 2006). With this caveat, it might be possible to maintain genetic/anatomical homogeneity and low levels of cultural diversity under conditions of population instability. If residual Neandertal populations retreated to refugia during the harshest glacial phases, the contact between

population subsets (groups) formerly separated might have been enough to inhibit genetic divergence. Meanwhile, certain forms of “bias-transmission” (Boyd and Richerson 2005) could have maintained behavioral distinctions among subgroups, especially if the behaviors in question were more or less neutral (e.g., methods of flake production).

Bocquet-Appel also raises the question whether the concept of rugged fitness landscapes can be applied to cultural evolution, with its greater potential for rapid and profound change. In principle, major innovations could allow cultural organisms to jump more directly from one fitness peak to another. It is clear too that Neandertals were capable of inventing new ways of doing things. Hafting and use of mastics both seem to have developed during the Middle Paleolithic, in addition to diverse core preparation techniques, and some late Neandertal populations produced so-called transitional industries (although the evidence and explanations remain hotly contested). However, because few novel behaviors are perfect from the outset, the adoption (spread) of innovations could still have involved significant losses of fitness. Moreover, stochastic loss of cultural information in small, unstable populations could in some cases have inhibited the spread and persistence of even the most advantageous innovations (Hovers and Belfer-Cohen 2005). Hovers raises the related possibility of technical knowledge’s “not catching up,” which is arguably related to the relative persistence of cultural institutions that may conserve and transmit knowledge across generations.

Hypotheses about decreased birth intervals and different durations of prenatal development have not held up well for the Late Pleistocene or remain very controversial. In addition, mortality data from Pleistocene burial populations are uneven and difficult to evaluate, to say the least. Though it is only speculation at this point, we suspect that early demographic pulses during the Late Pleistocene did not involve significant increases in human birth rates but instead came from reductions in child mortality due to behavioral insulation and new, socially mediated mechanisms for distributing risk. Whatever the reason, however, the archaeological evidence indicates that many Upper Paleolithic human populations existed closer to environmental carrying capacity than Middle Paleolithic and earlier hominin populations. This greater demographic stability would have enhanced the possibilities for conserving the long-term corporate memory (i.e., greater stability of cultural institutions) that is fundamental to maintaining alliance and cooperative networks.

Our main goal in writing this paper was to stimulate discussion of a subject and present some ways of approaching its core anomalies. We used available knowledge about variation in recent hunter-gatherer societies and a series of deep archaeological records for which we have comparable detailed information. Of course, the larger questions should ultimately be explored in as many other dimensions as possible. We would hope that others will join in the process, as the nature of the questions asked is too vast to be attacked from all sides at once or with our limited ranges of expertise. We do not

believe that this paper represents the last word on Neandertal socio-economics and division of labor. We fervently hope that it does not. If it does nothing more than promote greater focus on evidence for plant food and small-game exploitation and technological activities other than flaking stone, then it will have had its desired effect. Having rendered social and economic changes during the later Pleistocene with a broad brush, filling in from the areas we know best, we look forward to many surprises as more details become available.

—Steven L. Kuhn and Mary C. Stiner

References Cited

- Adler, D. S., G. Bar-Oz, A. Belfer-Cohen, and O. Bar-Yosef. 2006. Ahead of the game: Middle and Upper Palaeolithic hunting behaviors in the southern Caucasus. *Current Anthropology* 47:89–118. [GB, MW, OS]
- Aiello, L. C. 2003. Neandertal thermo-regulation and the glacial climate. In *Neanderthals and modern humans in Europe during the Last Glaciation*, ed. T. H. van Andel and W. Davies, 147–56. Cambridge: MacDonald Institute for Archaeological Research. [EH]
- Aiello, L. C., and C. Key. 2002. The energetic consequences of being a *Homo erectus* female. *American Journal of Human Biology* 14:551–65. [KM, WR]
- Aiello, L. C., and P. Wheeler. 2003. “Neanderthal thermoregulation and the glacial climate,” in *Neanderthals and modern humans in the European landscape of the Last Glaciation*, ed. T. H. van Andel and W. Davies, 147–66. Cambridge: McDonald Institute for Archaeological Research.
- Anderson-Gerfaud, P. 1990. Aspects of behavior in the Middle Paleolithic: Functional analysis of stone tools from southwest France. In *The emergence of modern humans: An archaeological perspective*, ed. P. Mellars, 389–418. Edinburgh: Edinburgh University Press.
- Bailey, R. C. 1991. *The behavioral ecology of Efe Pygmy men in the Ituri Forest, Zaire*. Ann Arbor: Museum of Anthropology, University of Michigan.
- Bailey, R. C., and R. Auinger. 1989. Net hunters vs. archers: Variations in women’s subsistence strategies in the Ituri Forest. *Human Ecology* 17:273–97.
- Bailey, S. E., and J. J. Hublin. 2006. Dental remains from the Grotte du Renne at Arcy-sur-Cure (Yonne). *Journal of Human Evolution* 50:485–508. [JPB]
- Balikci, A. 1970. *The Netsilik Eskimo*. Garden City, NY: Natural History Press.
- Barton, R. N. E., A. Currant, Y. Fernandez-Jalvo, C. Finlayson, P. Goldberg, R. MacPhail, P. Pettit, and C. Stringer. 1999. Gibraltar Neanderthals and results of recent excavations in Gorham’s, Vanguard, and Ibex caves. *Antiquity* 73:13–24.
- Bar-Oz, G., and D. S. Adler. 2005. Taphonomic history of the Middle and Upper Palaeolithic faunal assemblage from Ortvale Klde, Georgian Republic. *Journal of Taphonomy* 3: 185–211. [GB, MW]

- Bar-Yosef, O. 2000. The Middle and early Upper Paleolithic in Southwest Asia and neighboring regions. In *The geography of Neandertals and modern humans in Europe and the Greater Mediterranean*, ed. O. Bar-Yosef and D. Pilbeam, 107–56. Peabody Museum Bulletin 8.
- Bar-Yosef, O., B. Vandermeersch, B. Arensburg, A. Belfer-Cohen, P. Goldberg, H. Laville, L. Meignen, Y. Rak, J. Speth, E. Tchernov, A.-M. Tillier, and S. Weiner. 1992. The excavations in Kebara Cave, Mt. Carmel. *Current Anthropology* 33:497–550.
- Berger, T., and E. Trinkaus. 1995. Patterns of trauma among the Neanderthals. *Journal of Archaeological Science* 22: 841–52.
- Berke, H. 1984. The distributions of bones from large mammals at Petersfels. In *Upper Palaeolithic settlement patterns in Europe*, ed. H. Berke, J. Hahn, and C.-J. Kind, 103–8. Tübingen: Verlag Archaeologica Venatoria.
- Beyries, S. 1987. *Variabilité de l'industrie lithique au Moustérien: Approche fonctionnelle sur quelques gisements français*. British Archaeological Reports International Series S328.
- Binford, L. R. 1968. Post-Pleistocene adaptations. In *New perspectives in archaeology*, ed. S. R. Binford and L. R. Binford, 313–41. Chicago: Aldine.
- . 1989. Isolating the transition to cultural adaptations: An organizational approach, in *The emergence of modern humans: Biocultural adaptations in the Later Pleistocene*, ed. E. Trinkaus, 18–41. New York: Cambridge University Press. [JJS]
- . 2001. *Constructing frames of reference*. Berkeley: University of California Press.
- Bird, R. 1999. Cooperation and conflict: The behavioural ecology of the sexual division of labour. *Evolutionary Anthropology* 8:65–75. [KM, WR]
- Bird, D. W., and R. Bliege Bird. 2000. The ethnoarchaeology of juvenile foragers: Shellfishing strategies among the Meriam children. *Journal of Anthropological Archaeology* 19: 461–76.
- . 2003. Mardu children's hunting strategies in the Western Desert, Australia. In *Hunter-gatherer children*, ed. B. Hewlett. Senri: Senri Ethnological Studies.
- Bliege Bird, R., 1999. Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology* 8:65–75.
- Bliege Bird, R., and D. Bird. 2002. Constraints of knowing or constraints of growing? Fishing and collecting by the children of Mer. *Human Nature* 13:239–67.
- Blondel, J., and J. Aronson. 1999. *Biology and wildlife of the Mediterranean region*. Oxford: Oxford University Press.
- Blurton Jones, N., K. Hawkes, and J. O'Connell. 1989. Studying the costs of children in two foraging societies: Implications for schedules of reproduction. In *Comparative socioecology of mammals and man*, ed. V. Standon and R. Foley, 365–90. London: Blackwell.
- . 1997. Why do Hadza children forage? In *Uniting psychology and biology: Integrative perspectives on human development*, ed. N. Seigel, G. E. Weisfield, and C. C. Weisfield, 279–313. Washington, D.C.: American Psychological Association.
- Bocherens, H., D. Billiou, A. Marotti, M. Patou-Mathis, M. Otte, D. Bonjean, and M. Toussaint. 1999. Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of Last Interglacial Neanderthal and mammal bones in Scladina Cave (Belgium). *Journal of Archaeological Science* 26:599–607.
- Bocherens, H., and D. E. Drucker. 2003. Reconstructing Neanderthal diet from 120,000 to 30,000 BP using carbon and nitrogen stable isotopic abundances. In *Le rôle de l'environnement dans le comportements des chasseurs-cuillieus préhistoriques*, ed. M. Patou-Mathis and H. Bocherens, 1–8. British Archaeological Reports International Series 1105.
- Bocherens, H., D. G. Drucker, D. Billiou, M. Patou-Mathis, and B. Vandermeersch. 2005. Isotopic evidence for diet and subsistence pattern of the Saint-Césaire I Neanderthal: Review and use of a multi-source mixing model. *Journal of Human Evolution* 49:71–87.
- Bocquet-Appel, J. P. 1986. Small populations: Demography and paleoanthropological inferences. *Journal of Human Evolution* 14:683–91. [JPB]
- Bocquet-Appel, J. P., and J. L. Arsuaga. 1999. Age distributions of hominid samples at Atapuerca (SH) and Krapina indicate accumulation by catastrophe. *Journal of Archaeological Science* 26:327–38. [JPB]
- Bocquet-Appel, J. P., and P. Y. Demars. 2000a. Populational kinetics in Upper Palaeolithic in Western Europe. *Journal of Archaeological Science* 27:551–70. [JPB]
- . 2002b. Neanderthal contraction and modern human colonization of Europe. *Antiquity* 74:544–52. [JPB]
- Bocquet-Appel, J. P., P. Y. Demars, L. Noiret, and D. Dobrowsky. 2005. Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data. *Journal of Archaeological Science* 32:1656–68. [JPB]
- Boëda, E. 1991. Approche à la variabilité des systèmes de production lithique des industries du Paléolithique inférieur et moyen: Chronique d'une variabilité attendue. *Techniques et Culture* 17–18:37–79.
- Boone, J. 2002. Subsistence strategies and early human population history: An evolutionary ecological perspective. *World Archaeology* 34:6–25.
- Boesch, C., and H. Boesch. 1984. Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution* 13:415–40. [EH]
- . 1989. Hunting behavior of wild chimpanzees in the Taï National Park. *American Journal of Physical Anthropology* 78:547–73. [EH]
- Boesch, C., and H. Boesch-Achermann. 2000. *The chimpanzees of the Taï Forest*. Oxford: Oxford University Press. [EH]
- Boserup, E. 1965. *The conditions of agricultural growth: The*

- economics of agrarian change under population pressure*. Chicago: Aldine. [JPB]
- Boyd, R., and P. J. Richerson. 1985. *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- . 1992. How microevolutionary processes give rise to history. In *History and evolution*, ed. M. H. Nitecki and D. V. Nitecki, 179–210. Albany: State University of New York Press. [EH]
- . 2005. *The origin and evolution of cultures*. Oxford: Oxford University Press.
- Briggs, J. L. 1970. *Never in anger: Portrait of an Eskimo family*. Cambridge: Harvard University Press.
- Burchak-Abramovich, N. I. 1980. Remains of birds from the cave of Kudaro (in Russian). In *The Kudaro Paleolithic cave sites in southern Osetia*, ed. I. K. Ivanova and A. G. Chernyakhovskij, 98–110. Moscow: Nauka. [OS]
- Burke, A. 2000. The view from Starosele: Faunal exploitation at the Middle Palaeolithic site in western Crimea. *International Journal of Osteoarchaeology* 10:325–35.
- Cann, R. L. 2001. Genetic clues to dispersal in human populations: Retracing the past from the present. *Science* 291: 1742–48.
- Cann, R. L., M. Stoneking, and A. C. Wilson. 1987. Mitochondrial DNA and human evolution. *Nature* 325:31–35.
- Caramelli, D., C. Lalueza Fox, C. Vernesi, M. Lari, A. Casoli, F. Mallegni, B. Chiarelli, I. Dupanloup, J. Bertrampetit, G. Barbujani, and G. Bertorelle. 2003. Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans. *Proceedings of the National Academy of Sciences, U.S.A.* 100:6593–97.
- Cavalli-Sforza, L. L., and M. W. Feldman. 1981. *Cultural transmission and evolution: A quantitative approach*. Princeton: Princeton University Press.
- Chase, P. G. 1986. *The hunters of Combe Grenal: Approaches to Middle Paleolithic subsistence in Europe*. British Archaeological Reports International Series 286.
- Chernysh, A. P. 1965. *Lower and Middle Paleolithic of the Dniestr region* (in Russian). *Trudy Komissii po Izucheniyu Chetvertichnogo Perioda* 25. [OS]
- . 1982. Paleolithic multilayer Molodova I site (in Russian). In *Molodova I: Unique Mousterian settlement in the middle Dniestr region*, ed. G. I. Goretsky and I. K. Ivanova, 6–102. Moscow: Nauka. [OS]
- . 1987. The standard multilayered site Molodova V: Archaeology. In *The multilayered Paleolithic site Molodova V*, ed. I. K. Ivanova and S. M. Tseitlin, 7–93. Moscow: Nauka. [OS]
- 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 *Hunting and animal exploitation in the later Palaeolithic and Mesolithic of Eurasia*, ed. G. L. Peterkin, H. M. Bricker, and P. A. Mellars, 11–24. *Archeological Papers of the American Anthropological Association* 4.
- Coles, B., ed. 1992. *The wetland revolution in prehistory*. Exeter: Prehistoric Society.
- Davies, R., and S. Underdown. 2006. The Neanderthals: A social synthesis. *Cambridge Archaeological Journal* 16: 145–64. [OS]
- de Beaune, S. A. 1989. Essai d'une classification typologique des galets et plaquettes utilisés au Paléolithique. *Gallia Pré-histoire* 31:27–64.
- Delagnes, A., and L. Meignen. 2006. Diversity of lithic production systems during the Middle Paleolithic in France: Are there any chronological trends? In *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, ed. E. Hovers and S. Kuhn, 85–107. New York: Springer.
- de Waal, F. 1997. *Bonobo: The forgotten ape*. Berkeley: University of California Press. [JPB]
- Donahue, R. 1988. Microwear analysis and site function of Paglicci Cave, Level 4a. *World Archaeology* 19:357–75.
- Draper, P. 1975. !Kung women: Contrasts in sexual egalitarianism in foraging and sedentary contexts. In *Toward an anthropology of women*, ed. R. Reiter, 77–109. New York: Monthly Review Press.
- Drucker, D., and H. Bocherens. 2004. Carbon and nitrogen stable isotopes as tracers of change in diet breadth during Middle and Upper Paleolithic in Europe. *International Journal of Osteoarchaeology* 14:162–77. [OS]
- Elston, R. G., and D. W. Zeanah. 2002. Thinking outside the box: A new perspective on diet breadth and sexual division of labor in the Prearchaic Great Basin. *World Archaeology* 34:103–30.
- Endicott, K. L. 1999. Gender relations in hunter-gatherer societies. In *The Cambridge encyclopedia of hunter-gatherers*, ed. R. B. Lee and R. Daly, 411–18. Cambridge: Cambridge University Press.
- Enghoff, I. B. 1991. Mesolithic eel-fishing at Bjørnsholm, Denmark, spiced with exotic species. *Journal of Danish Archaeology* 10:105–18.
- Estioko-Griffin, A., and P. Griffin. 1981. Woman the hunter: The Agta. In *Woman the gatherer*, ed. F. Dahlberg, 121–51. New Haven: Yale University Press.
- Ewer, R. F. 1973. *The carnivores*. London: Weidenfeld and Nicholson.
- Fedigan, L. M. 1986. The changing role of women in models of human evolution. *Annual Review of Anthropology* 15: 25–66.
- Finlayson, C. 2004. *Neanderthals and modern humans: An ecological and evolutionary perspective*. Cambridge: Cambridge University Press. [EH]
- Fitzhugh, B. 2001. Risk and invention in human technological evolution. *Journal of Anthropological Archaeology* 20:125–67. [EM]
- Fizet, M., A. Mariotti, H. Bocherens, B. Lange-Badre, B. Vandermeersch, J. Borel, and G. Bellon. 1995. Effect of diet, physiology, and climate on carbon and nitrogen stable isotopes of collagen in a late Pleistocene anthropic paleo-

- ecosystem (France, Charente, Marillac). *Journal of Archaeological Science* 22:67–79.
- Flannery, K. V. 1969. Origins and ecological effects of early domestication in Iran and the Near East. In *The domestication and exploitation of plants and animals*, ed. P. J. Ucko and G. W. Dimbleby, 73–100. Chicago: Aldine.
- Freidl, E. 1995. Society and sex roles. In *Annual editions: Anthropology*, ed. E. Angeloni, 136–41. Guilford, CT: Dushkin Publishing.
- Gamble, C. 1999. *The Palaeolithic societies of Europe*. Cambridge: Cambridge University Press. [GB, MW]
- Gardner, P. 1991. Foragers' pursuit of individual autonomy. *Current Anthropology* 32:543–72.
- Gaudzinski, S. 1995. Wallertheim revisited: A reanalysis of the fauna from the Middle Palaeolithic site of Wallertheim (Rheinhausen/Germany). *Journal of Archaeological Science* 22:51–66.
- Gero, J. 1995. Railroading epistemology: Paleoindians and women. In *Interpreting archaeology*, ed. I. Hodder, M. Shanks, A. Alexandri, V. Buchli, J. Carman, J. Last, and G. Lucas, 175–80. New York: Routledge.
- Griggo, C. 2005. Mousterian fauna from Dederiyeh Cave and comparisons with fauna from Umm el Tlel and Douara Cave. *Paléorient* 30:149–62.
- 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: 379–99.
- Hardy, B. L. 1999. Microscopic residue analysis of stone tools from the Middle Paleolithic site of Starosele. In *The Middle Paleolithic of Western Crimea*, vol. 2, ed. V. P. Chabai and K. Monigal, 179–96. Études et Recherches Archéologiques de l'Université de Liège 87. [OS]
- Hardy, B. L. and M. Kay. 1999. Stone tool function at Starosele: Combining residue and use-wear evidence. In *The Middle Paleolithic of Western Crimea*, vol. 2, ed. V. P. Chabai and K. Monigal, 197–210. Études et Recherches Archéologiques de l'Université de Liège 87. [OS]
- Hawkes, K. 1991. Showing off: Tests of another hypothesis about men's foraging goals. *Ethnology and Sociobiology* 11: 29–54.
- . 1996. Foraging differences between men and women: Behavioral ecology of the sexual division of labor. In *The archaeology of human ancestry: Power, sex, and tradition*, ed. J. Steele, and S. Shennan, 283–305. London: Routledge.
- Hawkes, K., and R. Bliege Bird. 2002. Showing off, handicap signaling, and the evolution of men's work. *Evolutionary Anthropology* 11:58–67.
- Hawkes, K., K. Hill, and J. O'Connell. 1982. Why hunters gather: Optimal foraging and the Ache of eastern Paraguay. *American Ethnologist* 9:378–98.
- Hawkes, K., J. J. O'Connell, N. G. Blurton Jones, H. Alvarez, and E. L. Charnov. 1998. Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences, U.S.A.* 95:1336–39. [EH]
- Hayden, B. 1981a. Subsistence and ecological adaptations of modern hunter/gatherers. In *Omnivorous primates: Gathering and hunting in human evolution*, ed. R. Harding and G. Teleki, 344–421. New York: Columbia University Press.
- . 1981b. Research and development in the Stone Age: Technological transitions among hunter-gatherers. *Current Anthropology* 22:519–48.
- Henshilwood, C. S., and C. W. Marean. 2003. The origin of modern human behavior. *Current Anthropology* 44:627–51. [JJS]
- Hiatt, B. 1978. Woman the gatherer. In *Woman's role in aboriginal society*, ed. F. Gale, pp. 4–15. Canberra: Australian Institute of Aboriginal Studies.
- Hoffecker, J. F. 2002. *Desolate landscapes: Ice-Age settlement in Eastern Europe*. New Brunswick: Rutgers University Press. [GB, MW]
- Hoffecker, J. F., G. Baryshnikov, and O. Potapova. 1991. Vertebrate remains from the Mousterian site of Il'skaya I (northern Caucasus, USSR): New analysis and interpretation. *Journal of Archaeological Science* 18:113–47.
- Horan, R. D., E. Bulte, and J. Shogren. 2005. How trade saved humanity from biological exclusion: An economic theory of Neanderthal extinction. *Journal of Economic Behavior and Organization* 58:1–29.
- Hovers, E. 1997. Variability of lithic assemblages and settlement patterns in the Levantine Middle Paleolithic: Implications for the development of human behavior. Ph.D. diss., The Hebrew University. [EH]
- Hovers, E., and A. Belfer-Cohen. 2006. "Now you see it, now you don't"—modern human behavior in the Middle Paleolithic. In *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, ed. E. Hovers and S. Kuhn, 295–304. New York: Springer.
- Hovers, E., and S. Kuhn, eds. 2006. *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*. New York: Springer. [GB, MW]
- Hurtado, A. M., and K. Hill. 1987. Early dry season subsistence ecology of Cuiva (Hiwi) foragers of Venezuela. *Human Ecology* 15:163–87.
- Ingman, M., H. Kaessman, H. Pääbo, and U. Gyllensten. 2000. Mitochondrial genome variation and the origin of modern humans. *Nature* 408:703–13.
- Isaac, G. 1978. The food sharing behavior of proto-human hominids. *Scientific American* 238:99–108.
- Jaubert, J., M. Lorblanchet, H. Laville, R. Slott-Moller, A. Turq, and J-P. Brugal. 1990. *Les chasseurs d'aurochs de la Borde*. Editions de la Maison des Sciences de l'Homme, Documents d'Archéologie Française, 27.
- Jenness, D. 1922. *The life of the Copper Eskimo*. Reports of the Canadian Arctic Expedition 1913–1918, no. 12.
- Johnson, A. W., and T. Earle. 1987. *Evolution of human societies*. Stanford: Stanford University Press. [KM]
- Kaplan, H., K. Hill, J. Lancaster, and A. M. Hurtado. 2000. A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology* 9:156–85.

- Kaufman, D. 2002. Re-evaluating subsistence skill of Levantine Middle and Upper Palaeolithic hunters: A comparison of the faunal assemblages. *Oxford Journal of Archaeology* 21:217–29. [GB, MW]
- Keeley, L. H. 1988. Hunter-gatherer economic complexity and “population pressure.” *Journal of Anthropological Archaeology* 7:373–411.
- . 1995. Protoagricultural practices among hunter-gatherers: A cross-cultural survey. In *Last hunters, first farmers*, ed. T. D. Price and A. B. Gebauer, 243–72. Santa Fe: School of American Research.
- Keen, I. 2006. Constraints on the development of enduring inequalities in Late Holocene Australia. *Current Anthropology* 47:7–38. [NMW]
- Kelly, R. L. 1995. *The foraging spectrum*. Washington, D.C.: Smithsonian Institution Press.
- Key, C., and L. C. Aiello. 2000. A prisoner's dilemma model of the evolution of paternal care. *Folia Primatologica* 71: 77–92. [KM, WR]
- Klein, R. G. 1999. *The human career: Human biological and cultural origins*. 2d ed. Chicago: University of Chicago Press.
- . 2000. Archaeology and the evolution of human behavior. *Evolutionary Anthropology* 17:17–36. [GB, MW]
- . 2001. Southern Africa and modern human origins. *Journal of Anthropological Research* 57:1–16.
- Klein R. G., and B. Edgar. 2002. *The dawn of human culture*. New York: Wiley.
- Knecht, H. 1997. *Projectile technology*. New York and London: Plenum Press.
- Kramer, K. L. 2005. Children's help and the pace of reproduction: Cooperative breeding in humans. *Evolutionary Anthropology* 14:224–37.
- Kuhn, S. L. 1995. *Mousterian lithic technology: An ecological perspective*. Princeton: Princeton University Press. [OS]
- Kuhn, S. L., and E. Hovers. 2006. General introduction. In *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, ed. E. Hovers and S. L. Kuhn, 1–13. New York: Springer. [EH]
- Kuhn, S., and K. Sarther. 2000. Food, lies, and paleoanthropology: Social theory and the evolution of sharing in humans. In *Social theory in archaeology*, ed. M. Schiffer, 79–96. Salt Lake City: University of Utah Press.
- Kuhn, S. L., and M. C. Stiner. 2001. The antiquity of hunter-gatherers. In *Hunter-gatherers: Interdisciplinary perspectives*, ed. C. Panter-Brick, R. H. Layton, and P. A. Rowley-Conwy, 99–142. Cambridge: Cambridge University Press.
- Lahr, M. M., and R. A. Foley. 2003. Demography, dispersal, and human evolution in the last glacial period. In *Neanderthals and modern humans in the European landscape during the last glaciation*, ed. T. H. van Andel and W. Davies, 241–56. Cambridge: McDonald Institute for Archaeological Research.
- Landes, R. 1938. *The Ojibwa woman*. New York: Norton.
- Laughlin, W. 1969. The demography of hunters: An Eskimo example. In *Man the hunter*, ed. R. B. Lee and I. DeVore, 241–43. Chicago: Aldine.
- Lee, R. B. 1968. What hunters do for a living, or How to make out on scarce resources. In *Man the hunter*, ed. R. B. Lee and I. DeVore, 30–48. Chicago: Aldine.
- Lemorini, C. 2000. *Reconnaître de tactiques d'exploitation du milieu au Paléolithique moyen: La contribution de l'analyse fonctionnelle—Étude fonctionnelle des industries lithiques au Grotta Breuil (Latium, Italie) et de La Colombette (Bonnieux, Valcluse, France)*. British Archaeological Reports International Series 858.
- Lev, E., M. E. Kislev, and O. Bar-Yosef. 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. *Journal of Archaeological Science* 32:475–84.
- Levine, A. L. 1965. Economic science and population theory. *Population Studies* 19(2):139–54. [JPB]
- Lieberman, D. E., M. Devlin, and O. M. Pearson. 2001. Articular surface area responses to mechanical loading: Effects of exercise, age, and skeletal location. *American Journal of Physical Anthropology* 116:266–77.
- Lieberman, D. E., and O. M. Pearson. 2001. Trade-off between modeling and remodeling responses to loading in the mammalian limb. *Bulletin of the Museum of Comparative Zoology* 156:269–82.
- Liebowitz, L. 1986. Origins of the sexual division of labor. In *Woman's nature: Rationalization of inequality*, ed. M. Lowe and R. Hubbard, 123–47. New York: Pergamon Press.
- Liubin, V. P. 1998. *The Acheulian epoch in the Caucasus* (in Russian). Institute for the Material Culture History Archaeological Studies 47. [OS]
- Lovejoy, C. O. 1981. The origin of man. *Science* 211:341–50.
- Lupo, K. D., and D. N. Schmitt. 2005. Small prey hunting technology and zooarchaeological measures of taxonomic diversity and abundance: Ethnoarchaeological evidence from Central African forest foragers. *Journal of Anthropological Archaeology* 24:335–53. [GB, MW]
- MacArthur, R. H. 1972. *Geographical ecology: Patterns in the distribution of species*. New York: Harper and Row.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences, U.S.A.* 51:1207–10.
- . 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377–85.
- MacDonald, K., W. Roebroeks, and A. Verpoorte. n.d. An energetics perspective on the Neandertal record. In *The evolution of hominid diets: Integrating approaches to the study of Palaeolithic subsistence*, ed. J. J. Hublin and M. P. Richards. New York: Springer. In press. [KM, WR]
- McBrearty, S., and A. Brooks. 2000. The revolution that wasn't: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39:453–563.
- McBrearty, S., and M. Moniz. 1991. Prostitutes or providers? Hunting, tool use, and sex roles in earliest *Homo*. In *Ar-*

- chaeology of gender: Proceedings of the Twenty-second Annual Conference of the Archaeological Association of University of Calgary*, 71–83. Calgary: University of Calgary.
- McBrearty, S., and C. Tryon. 2005. From Acheulean to Middle Stone Age in the Kapthurin Formation, Kenya. In *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, ed. E. Hovers and S. Kuhn, 257–78. New York: Springer.
- Madella, M., M. K. Jones, P. Goldberg, Y. Goren, and E. Hovers. 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): The evidence from phytolith studies. *Journal of Archaeological Science* 29:703–19. [OS]
- Manson, J. H., and R. W. Wrangham. 1991. Intergroup aggression in chimpanzees and humans. *Current Anthropology* 32:369–90. [JPB]
- Marean, C. W., and Z. Assefa. 1999. Zooarcheological evidence for the faunal exploitation behavior of Neandertals and early modern humans. *Evolutionary Anthropology* 8: 22–37.
- Marlowe, F. W. 2005. Hunter-gatherers and human evolution. *Evolutionary Anthropology* 14:54–67.
- Martínez Molina, K. 2005. Análisis funcional de industrias líticas del Pleistoceno superior, el Paleolítico medio del Abric Romaní (Capellades, Barcelona) y del Paleolítico superior de Üçağızlı (Hatay, Turquía) y del Molí del Salt (Vimodó, Tarragona): Cambios en los patrones funcionales entre el Paleolítico medio y el superior. Ph.D. diss. Universitat Rovira i Virgili.
- Mellars, P. 1996. *The Neanderthal legacy*. Princeton: Princeton University Press.
- Mertens, S. 1996. The Middle Paleolithic in Romania. *Current Anthropology* 37:515–21. [OS]
- Munro, N. D. 2004. Zooarchaeological measures of hunting pressure and occupation intensity in the Natufian: Implications for agricultural origins. *Current Anthropology* 45: S5–S33. [GB, MW]
- Musil, R. 2003. The Middle and Upper Palaeolithic game suite in Central and Southeastern Europe. In *Neanderthals and modern humans in the European landscape during the last glaciation*, ed. T. H. van Andel and W. Davies, 167–89. Cambridge: McDonald Institute for Archaeological Research. [OS]
- Nadel, D., E. Weiss, O. Simchoni, A. Tsatskin, A. Danin, and M. Kislev. 2004. Stone Age hut in Israel yields world's oldest evidence of bedding. *Proceedings of the National Academy of Sciences, U.S.A.* 101:6281–86. [GB, MW]
- O'Connell, J. 2006. How did modern humans displace Neanderthals? Insights from hunter-gatherer ethnography and archaeology. In *When Neanderthals and modern humans met*, ed. N. Conard. Tübingen: Kerns Verlag.
- O'Connell, J. F., K. Hawkes, K. D. Lupo, and N. G. Blurton-Jones. 2002. Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43:831–72.
- Osgood, C. 1940. *Ingalik material culture*. Yale University Publications in Anthropology 22.
- Owen, L. 2005. *Distorting the past: Gender and division of labor in the European Upper Paleolithic*. Tübingen: Kerns Verlag.
- Owens, D., and B. Hayden. 1997. Prehistoric rites of passage: A comparative study of transegalitarian hunter-gatherers. *Journal of Anthropological Archaeology* 16:121–61. [NMW]
- Palmer, R. 1991. Optimization on rugged fitness landscapes. In *Molecular evolution on rugged fitness landscapes*, ed. E. Perelson and S. Kaufman, 3–25. Redwood City, CA: Addison.
- Panther-Brick, C. 2002. Sexual division of labor: Energetic and evolutionary scenarios. *American Journal of Human Biology* 14:627–40.
- Paunescu, A. 1965. Sur la succession des habitats paléolithiques et postpaléolithiques de Ripiceni-Izvor. *Dacia, n.s.*, 9:5–32. [OS]
- . 1988. La passage du Paléolithique moyen au Paléolithique supérieur entre les Carpates et le Prut. In *L'homme de Néanderthal*, vol. 8, *La mutation*, ed. J. K. Kozłowski, 133–47. Études et Recherches Archéologiques de l'Université de Liège 31. [OS]
- . 1989. Le Paléolithique et le Mésolithique de Roumanie (un bref aperçu). *L'Anthropologie* 93:123–58. [OS]
- Pennington, L. 1989. *Bowes and Church's Food values of portions commonly used*. New York: Harper and Row.
- . 2001. Hunter-gatherer demography. In *Hunter-gatherers: Interdisciplinary perspectives*, ed. C. Panther-Brick, R. H. Layton, and P. A. Rowley-Conwy, 170–204. Cambridge: Cambridge University Press.
- Peters, J. 1991. Mesolithic fishing along the central Sudanese Nile and lower Atbara. *Sahara* 4:33–40.
- Pianka, E. R. 1988. *Evolutionary ecology*. 4th ed. New York: Harper and Row.
- Rabinovich, R., and E. Hovers. 2004. Faunal analysis from Amud Cave: Preliminary results and interpretations. *International Journal of Osteoarchaeology* 14:287–306. [OS]
- Richards, M. P. n.d. Isotopic evidence for European Upper Palaeolithic human diets. In *The evolution of hominid diets: Integrating approaches to the study of Palaeolithic subsistence*, ed. J.-J. Hublin and M. P. Richards. New York: Springer. In press. [KM]
- Richards, M. P., P. B. Pettitt, M. C. Stiner, and E. Trinkaus. 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. *Proceedings of the National Academy of Sciences, U.S.A.* 98:6528–32.
- Richards, M., P. Pettitt, E. Trinkaus, F. Smith, M. Paunovic, and I. Karavanić. 2000. Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proceedings of the National Academy of Sciences, U.S.A.* 97: 7663–66.
- Richerson, P., R. Boyd, and R. Bettinger. 2001. Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *American Anthropology* 66:387–412.
- Risch, R. 2002. Análisis funcional y producción social: Relación entre método arqueológico y teoría económica. In

- Análisis funcional: Su aplicación al estudio de sociedades prehistóricas*, ed. I. Clemente, R. Risch, and J. F. Gibaja, 19–30. British Archaeological Report–International Series 1073. [KM]
- Rogachev, A. N. 1973. About complex gathering as a subsistence practice during the Paleolithic epoch on the Russian Plain (in Russian). In *Anthropological reconstruction and the problems of paleoethnography*, ed. G. V. Lebedinskaya and M. G. Rabinovich, 127–42. Moscow: Nauka. [OS]
- Rosaldo, M., and L. Lamphere, eds. 1974. *Woman, culture, and society*. Stanford: Stanford University Press.
- Rose, L., and F. Marshall. 1996. Meat eating, hominid sociality, and home bases revisited. *Current Anthropology* 37:307–38.
- Ruff, C. B., E. Trinkaus, et al. 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387:173–76. [KM, WR]
- Schrire, C. 1984. Wild surmises on savage thoughts. In *Past and present in hunter-gatherer studies*, ed. C. Schrire, 1–25. New York: Academic Press.
- Semino, O., J. Passarino, P. J. Oefner, A. A. Lin, S. Arbuzova, L. E. Beckman, G. de Benedictis, P. Francalacci, A. Kouvatsi, S. Umborska, M. Marcikiae, A. Mika, B. Mika, D. Primorac, A. S. Santachiara-Benerecetti, L. L. Cavalli-Sforza, and P. A. Underhill. 2000. The genetic legacy of Paleolithic *Homo sapiens* in extant Europeans: A Y-chromosome perspective. *Science* 210:1155–59.
- Shea, J. 1989. A functional study of the lithic industries associated with hominid fossils in the Kebara and Qafzeh Caves. In *The human revolution: Behavioral and biological perspectives on the origin of modern humans*, ed. P. Mellars and C. Stringer, 611–25. Princeton: Princeton University Press.
- . 1997. Middle Paleolithic spear point technology. In *Projectile technology*, ed. H. Knecht, 79–106. New York: Plenum.
- . 2003. Neandertals, competition, and the origin of modern human behavior in the Levant. *Evolutionary Anthropology* 12:173–87. [GB, MW]
- . 2006a. The Middle Paleolithic of the Levant: Recursion and convergence. In *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, ed. E. Hovers and S. Kuhn, 189–212. New York: Springer.
- . 2006b. The origins of lithic projectile point technology: Evidence from Africa, the Levant, and Europe. *Journal of Archaeological Science* 33:823–46. [JJS]
- Shennan, S. 2002. *Genes, memes, and human history: Darwinian archaeology and cultural evolution*. London: Thames and Hudson.
- Soffer, O. 1994. Ancestral lifeways in Eurasia: The Middle and Upper Paleolithic records. In *Origins of anatomically modern humans*, ed. M. H. Netecki and D. V. Netecki, 101–19. New York: Plenum Press. [OS]
- . 2000. The last Neandertals. In *Early humans at the gates of Europe*, ed. D. Lordkipanidze, O. Bar-Yosef, and M. Otte, 139–46. Études et Recherches Archéologiques de l'Université de Liège. [OS]
- Soffer, O., J. M. Adovasio, and D. C. Hyland. 2002. Perishable technologies and invisible people: Nets, baskets, and “Venus” wear ca. 26,000 B. P. In *Enduring records*, ed. B. A. Purdy, 233–45. Oxford: Oxbow Press. [OS]
- Soffer, O., J. M. Adovasio, D. C. Hyland, B. Klima, and J. Svoboda. 1998. Perishable technologies and the genesis of the Eastern Gravettian. *Anthropologie* 36(1–2):43–68.
- Sorensen, M., and W. R. Leonard. 2001. Neandertal energetics and foraging efficiency. *Journal of Human Evolution* 40: 483–95.
- Speth, J. D., and E. Tchernov. 1998. The role of hunting and scavenging in Neandertal procurement strategies: New evidence from Kebara Cave (Israel). In *Neandertals and modern humans in western Asia*, ed. T. Akazawa, K. Aoki, and O. Bar-Yosef, 223–39. New York: Plenum Press.
- . 2001. Neandertal hunting and meat-processing in the Near East: Evidence from Kebara Cave (Israel). In *Meat-eating and human evolution*, ed. C. Stanford and H. Bunn, 52–72. Oxford: Oxford University Press.
- . 2002. Middle Paleolithic tortoise use at Kebara Cave (Israel). *Journal of Archaeological Science* 29:471–83.
- Spielman, K., and J. Eder. 1994. Hunters and farmers, then and now. *Annual Review of Anthropology* 23:303–23.
- Stanford, C. 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. *American Anthropologist* 98:96–113.
- . 1999. *The hunting apes: Meat-eating and the origins of human behavior*. Princeton: Princeton University Press. [EH, JPB]
- Stewart, K. M. 1989. *Fishing sites of North and East Africa in the Late Pleistocene and Holocene: Environmental change and human adaptation*. British Archaeological Reports International Series 521.
- Stiner, M. C. 1994. *Honor among thieves: A zooarchaeological study of Neandertal ecology*. Princeton: Princeton University Press.
- . 2001. Thirty years of the “Broad Spectrum Revolution” and Paleolithic demography. *Proceedings of the National Academy of Sciences, U.S.A.* 98:6993–96.
- . 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* 10(1):1–63.
- . 2005. *The faunas of Hayonim Cave (Israel): A 200,000-year record of Paleolithic diet, demography, and society*. Cambridge: Peabody Museum Press, Harvard University.
- Stiner, M. C., and N. D. Munro. 2002. Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. *Journal of Archaeological Method and Theory* 9:181–214. [GB, MW]
- Stiner, M. C., N. D. Munro, and T. A. Surovell. 2000. The tortoise and the hare: Small-game use, the broad spectrum

- revolution, and Paleolithic demography. *Current Anthropology* 41:39–73.
- Stiner, M. C., N. D. Munro, T. A. Surovell, E. Tchernov, and O. Bar-Yosef. 1999. Paleolithic population growth pulses evidenced by small animal exploitation. *Science* 283:190–94.
- Tchernov, E. 1989. The Middle Paleolithic mammalian sequence and its bearing on the origin of *Homo sapiens* in the southern Levant. In *Investigations in South Levantine prehistory (Préhistoire du Sud-Levant)*, ed. O. Bar Yosef and B. Vandermeersch, 25–38. British Archaeological Reports International Series 497.
- . 1998. Are Late Pleistocene environmental factors, faunal changes, and cultural transformations causally connected? The case of the southern Levant. *Paléorient* 23: 209–28.
- Templeton, A. R. 1992. Human origins and the analysis of mitochondrial DNA sequences. *Science* 255:737.
- Thieme, H. 1997. Lower Palaeolithic hunting spears from Germany. *Nature* 385:807–10.
- Tsepkin, E. A. 1980. Remains of fish from the Kudaro I cave (in Russian). In *The Kudaro Paleolithic cave sites in southern Osetia*, ed. I. K. Ivanova and A. G. Chernyakhovskij, 90–97. Moscow: Nauka. [OS]
- Ugan, A., J. Bright, and A. Rogers. 2003. When is technology worth the trouble? *Journal of Archaeological Science* 30: 1315–29. [EH]
- Van Neer, W. 1986. Some notes on the fish remains from Wadi Kubbania (Upper Egypt, late Paleolithic). In *Fish and archaeology: Studies in osteometry, taphonomy, seasonality, and fishing methods*, ed. D. C. Brinkhuizen and A. T. Clason, 103–13. British Archaeological Reports International Series 294.
- Vaughn, P. C. 1985. *Use-wear analysis of flaked stone tools*. Tucson: University of Arizona Press.
- Vermeij, G. J. 2006. Historical contingency and the purported uniqueness of evolutionary innovations. *Proceedings of the National Academy of Sciences, U.S.A.* 103:1804–9. [EH]
- Waguespack, N. M. 2003. Clovis hunting and the organization of subsistence labor. Ph.D. diss., University of Arizona.
- . 2005. The organization of male and female labor in foraging societies: Implications for early Paleoindian archaeology. *American Anthropologist* 107:666–76.
- Walker, R., K. Hill, H. Kaplan, and G. McMillan. 2002. Age-dependency in hunting ability among the Ache of eastern Paraguay. *Journal of Human Evolution* 42:639–57.
- Watanabe, H. 1969. Subsistence and ecology of northern food gatherers with special reference to the Ainu. In *Man the hunter*, ed. R. Lee and I. DeVore, 69–77. Chicago: Aldine.
- Weiss, E., W. Watterstrom, D. Nadel, and O. Bar-Yosef. 2004. The broad spectrum revisited: Evidence from plant remains. *Proceedings of National Academy of Sciences, U.S.A.* 101:9551–55. [GB, MW]
- Weniger, G.-C. 1987. Magdalenian settlement pattern and subsistence in Central Europe: The southwestern and central German cases. In *The Pleistocene Old World: Regional perspectives*, ed. O. Soffer, 201–15. New York: Plenum Press
- West, J. A. 1995. A taphonomic investigation of aquatic reptiles at Lake Turkana, Kenya: Significance for early hominid ecology at Olduvai Gorge, Tanzania. Ph.D. diss., University of Illinois, Urbana-Champaign.
- White, T., B. Asfaw, D. Degusta, H. Gilbert, G. Richards, G. Suwa, and F. C. Howell. 2003. Pleistocene *Homo sapiens* from Middle Awash, Ethiopia. *Nature* 423:742–51.
- Whitten, A., J. Goodall, W. C. McGrew, T. Nichida, V. Reynolds, Y. Sugiyama, C. E. G. Tutin, R. W. Wrangham, and C. Boesch. 2001. Charting cultural variation in chimpanzees. *Behavior* 138:1481–1516.
- Wiessner, P. 2004. Owners of the future: Calories, cash, and self-sufficiency in the Nyae Nyae area between 1996 and 2003. *Visual Anthropology Review* 19:149–59.
- Winterhalder, B., and E. A. Smith. 2000. Analyzing adaptive strategies: Human behavioural ecology at twenty-five. *Evolutionary Anthropology* 9:51–72. [KM, WR]
- Wobst, H. M. 1978. The archaeo-ethnology of hunter-gatherers, or The tyranny of the ethnographic record in archaeology. *American Antiquity* 43:303–9.
- Woodburn, J. 1988. African hunter-gatherer social organization: Is it best understood as a product of encapsulation? In *Hunters and gatherers*, vol. 1, *History, evolution, and social change*, ed. T. Ingold, D. Riches, and J. Woodburn, 31–64. Oxford: Berg.
- Wrangham, R., and E. V. Z. Bergman-Riss. 1990. Rates of predation by Gombe chimpanzees, 1972–1975. *Primates* 31: 157–70.
- Wrangham, R., J. H. Jones, G. Layden, D. Pilbeam, and N. Conklin-Brittain. 1999. The raw and the stolen: Cooking and the ecology of human origins. *Current Anthropology* 40:567–94.
- Wright, K. 1994. Ground-stone tools and hunter-gatherer subsistence in southwest Asia: Implications for the transition to farming. *American Antiquity* 59:238–63.
- Wright, S. 1932. The roles of mutation, inbreeding, crossbreeding, and selection in evolution. *Proceedings of the 6th International Congress on Genetics*, vol. 1, 356–66.
- Wynn, T., and W. McGrew. 1989. An ape's view of the Oldowan. *Man* 24:383–98.
- Yellen, J. E., A. S. Brooks, E. Cornelissen, R. G. Klein, M. Mehlman, and K. Stewart. 1995. A Middle Stone Age worked bone industry from Katanda, upper Semliki River valley (Kivu), Zaire. *Science* 268:553–56.
- Zeanah, D. W. 2004. Sexual division of labor and central place foraging: A model for the Carson Desert of western Nevada. *Journal of Anthropological Archaeology* 23:1–23.
- Zihlman, A. 1989. Woman the gatherer: The role of women in early hominid evolution. In *Gender and anthropology*, ed. S. Morgan, 21–40. Washington, D.C.: American Anthropological Association.
- Zihlman, A. L., and N. Tanner. 1978. Gathering and the hominid adaptation. In *Female hierarchies*, ed. L. Tiger and H. Fowler, 163–94. Chicago: Beresford Book Service.