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# 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

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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 *Homo sapiens* with a demographic advantage over other hominins in Eurasia.

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### Introduction

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

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in recent hunter-gatherer groups. It appears that Neandertal 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 ethnoar-

chaeology 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.<sup>1</sup> 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 much 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

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.

presents 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, 241–242; 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 offsprings. 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 population

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

<sup>a</sup>Data from Kelly (1995, table 3.3).

<sup>b</sup>Data from Hawks, Hill, and O'Connell (1982, Hurtado and Hill (1987).

<sup>c</sup>Data from Pennington (1989).

<sup>d</sup>Data from Wright (1994, table 2).

<sup>e</sup>Data from Wiessner (2004 and Wiessner, personal communication; cases are from Nyae Nyae area minus those where elephant damage was severe for tubers.

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 underlying 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 seemed 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 unrepresented. 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 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, large lizards, depending on the area. The exploitation of immobile or slow-moving small animals makes sense in terms of optional-foraging models: the ease of capture and low handling costs make up for their small size, bringing net yields close to those of medium 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

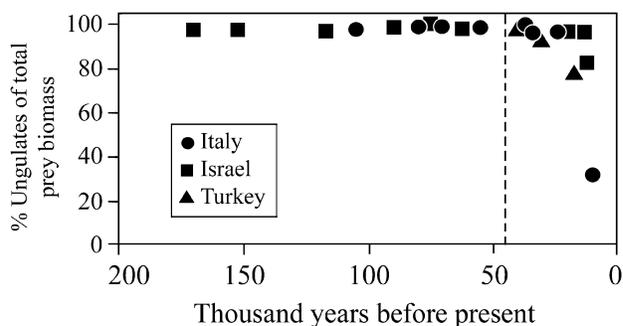


Fig. 1. Percentage of total prey biomass represented by large ungulates consumed by Paleolithic foragers over time in Mediterranean faunal assemblages from Israel, Italy, and Turkey. The importance of large game begins to drop after about 45,000 years ago (*broken line*), and greatly accelerates after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

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, as well as 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 sub-

sistence 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 2005; 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 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

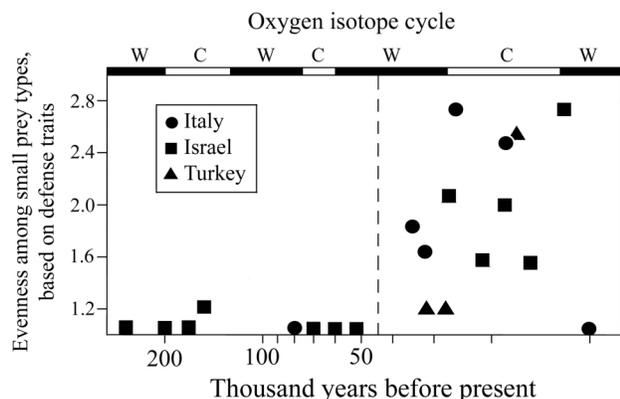


Fig. 2. Evenness in the representation of three small-game categories in Paleolithic faunas, based on prey defense mechanisms (slow game, quick-running terrestrial mammals, and quick-flying birds) ( $3 =$  most even,  $1 =$  least even). Evenness here reflects a continuum in dietary breadth: narrow diets 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). Symbols are for assemblages from Italy (circle), Israel (square), and Turkey (triangle). Time is expressed on a logged scale, as are oxygen isotope climate cycles; C, cold stage, W, warm stage.

collection and intensive processing of wild seeds, fish or both, 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 be-

havior 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 2005). 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 subtropical 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.<sup>3</sup> 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 abil-

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

ities, and carrying capacities, a critical point would have been reached when one population suddenly gained an incremental 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 ap-

plicable construct 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 more likely to undergo repeated episodes of expansion (for a 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.

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