2

A Lithic Perspective on Ecological Dynamics in the Upper Pleistocene of Western Eurasia

C. Michael Barton and Julien Riel-Salvatore

Neanderthals and their social and biological relationships to us have long been a subject of fascination spanning the scientific and lay communities. The hominins generally classified as Neanderthal are found in western Eurasia, from the Near East to Spain, and extend temporally from sometime in the late Middle Pleistocene through Oxygen Isotope Stage (OIS) 3 of the Upper Pleistocene (Finlayson et al. 2006; Harvati 2007; Klein 2003). Within this temporal and geographic range, Neanderthals almost certainly lived as mobile hunter-gatherers, with small family-based social groups occupying territories of variable sizes and moving between residential camps, which they occupied for variable lengths of time in order to acquire, process, and consume the resources they needed to survive and reproduce. Such a lifestyle leaves little in the way of material residues and most of what is left rapidly decomposes to invisibility from the standpoint of current archaeological data recovery methods. Even the bones of animals consumed and hominins who died are preserved only in exceptional circumstances. Stone artifacts are the only behavioral residues of Neanderthal behavior that remain in any abundance, scattered across the landscape—and these are largely discarded trash (Barton 1991; Frison 1968). There are probably more known Neanderthal sites than of any other premodern human. However, of the hundreds of thousands or millions of camps at which these Pleistocene hominins carried out their daily activities over the course of 100

to 200 kya and across some 2 million km², archaeologists know of only a few hundred (Klein 2003; Serangeli and Bolus 2008)—and most of these are in rockshelters and caves that probably were visited only rarely by these hunter-gatherers but that offer the exceptional conditions of preservation needed in order to find more than lithics (Laville, Rigaud, and Sackett 1980). Moreover, there is a general tendency for Paleolithic archaeologists to focus on one or a few deeply stratified sites, requiring many seasons of painstaking excavations. Such sites, while offering a long, diachronic view, provide but tiny windows on past human ecological behaviors, the kind of information that is needed to understand the drivers of human evolutionary dynamics.

In this chapter, we summarize continental-scale data on human ecology and land-use that builds on over a decade of prior work identifying robust proxy measures of Upper Pleistocene human land-use and mobility strategies, supported both by archaeological analysis and agent-based models. We begin with an overview of the theoretical framework for using Paleolithic lithic assemblages to study past human ecology. Subsequently, we present a synthesis of human land-use and ecology, in response to environmental change during the Upper Pleistocene. We conclude with a discussion of implications of this biogeographical change for human evolution.

MIDDLE-RANGE LITHIC THEORY

While a number of complex classification schemes have been devised to characterize the diversity of lithic artifacts found in the archaeological record, in fact much of the macroscopic variability noted by archaeologists results from a few fundamental characteristics of workable stone and the techniques needed to make it useable: stone is heavy, stone was necessary for all Paleolithic hunter/gatherers, stone tools have short use lives, and stone technology is messy.

Stone Is Heavy

Most lithics are made from rocks that are composed primarily of silicon dioxide (SiO_2). With a density of 2.2 g/cm³ a 20-cm-diameter piece of flint weighs 9.2 kg. The equal volume of water weighs 4.2 kg; a small child weighs around 7 kg. Modern dietary recommendations suggest that 9.2 kg of protein would meet the nutritional requirements of an average woman for 200 days and an average man for 164 days (Otten et al. 2006). In other words, for a mobile prehistoric forager on foot, stone for making tools had a much

higher energy cost to transport than many things of more direct importance to human survival. Given the high cost/return ratio of toolstone, foragers should have tried to minimize the amount of stone they needed to carry on a regular basis so that they could carry other items with higher and more direct energy payoffs.

Stone Was Necessary

If stone had such an apparently low direct return relative to the cost needed to transport it, why then do we find it associated with all past humans so ubiquitously? In fact, until very recently, stone was a critical resource for human survival (Kuhn 1992; McCall 2012). People began to make recognizable flaked-stone artifacts over two—possibly three—million years ago and may have used stone for much longer (Harmand et al. 2015; cf. McPherron et al. 2010; Kimbel et al. 1996; Semaw et al. 1997); by at least a million years ago we do not find traces of humans without also finding stone artifacts. Stone tools had become an essential component of being human (cf. Nowell and Davidson 2010). They were the fundamental technology needed to process resources and to make other technological items upon which humans increasingly came to depend for their survival. This meant that, in spite of its high transportation costs, to be without usable stone could be as fatal as to be without food—and in fact could result in a lack of food. Humans had to stockpile usable stone at places they visited regularly and/or carry it with them on their increasingly lengthy foraging trips (Kuhn 1992). The constant need for useable stone along with its high transport costs put humans under strong and continuous selection pressure to devise ways to get increasing usability out of decreasing mass.

Stone Tools Are Short-Lived

Many years ago, a student on a field project sported a t-shirt with the phrase "Love is fleeting, stone tools are forever." While a catchy turn of phrase (for archaeologists at least), it is a misleading portrayal of stone tools. Stone far outlasts the most enduring affection, but stone tools commonly have a use-life much shorter than even the most casual flirtation. As observed in many replicative and ethnoarchaeological studies, stone tool edges dull rapidly, retouch is not particularly effective at rejuvenating a worn edge, and retouch rapidly reduces the size of the tool to the point that it becomes unusable (Andrefsky 2009; Barton 1990; Dibble 1987; Frison 1968; Gould et al. 1971; White and Thomas 1972). The short use-life of lithic artifacts is particularly problematic

given their critical role for prehistoric human ecology and the cost of ensuring that sufficient stone was available when needed. Again, this characteristic of stone artifacts must have kept human technological behaviors under strong selection pressure to devise ways to extend short use-life of available stone.

Lithic Technology Is Messy

When archaeologists began to carry out quantitative replicative experiments of lithic technology, one result of flint-knapping was immediately apparent: making any artifact rapidly and easily produces a very large number of flakes, fragments, and pieces of debris, only some of which are useful for many tasks (e.g., Amick and Mauldin 1989; Magne and Pokotylo 1981; Shott 1994). Even assuming that most sharp-edged flakes of reasonable size potentially served as tools, creating even flakes produces a large amount of debris.

Given the strong constraints on lithic artifacts described above, the messiness of lithic reduction technology meant that people whose activities required them to move their residence regularly would be under considerable selection pressure to carry with them only those pieces of stone with the most usable edges and least amount of waste, rather than carrying entire nodules and the heavy, unusable waste that they produce (Kelly 1983; Kuhn 1994; Surovell 2009). They would only discard these pieces of stone into the archaeological record (i.e., the trash) after trying to extend their use-lives as much as possible through rejuvenating the tool edges. On the other hand, people whose activities allowed them to reside in a single locality for longer and accumulate a stockpile of stone, could break rocks with abandon, replacing short-lived tools with fresh ones instead of resharpening them, and amassing great quantities of lithic debris in the process (Parry and Kelly 1987). Because such temporarily sedentary groups did not have to worry as much about portability and did not have to pay the cost of transporting waste stone, lithic debris could accumulate rapidly at residential localities.

Implications for the Archaeological Record

These inherent characteristics of flaked-stone technology have important implications for the archaeological record created from the trash generated by lithic production and use (Shott 1998, 2008). Human foragers who exhibit high residential mobility should be expected to transport and discard relatively few stone artifacts because stone is heavy but important for survival. In order to extend the short use-lives of the relatively few stone artifacts they

carry, lithics discarded by residentially mobile foragers should also exhibit regular evidence of edge rejuvenation. That is, a comparatively higher proportion of the discarded artifacts should be retouched. On the other hand, logistically organized hunter-gatherers (i.e., those practicing central place foraging) have the opportunity to accumulate stone at regularly visited base camps, which they can occupy for longer stays. Lithic refuse at such sites should be characterized by larger quantities of lithic debris and fewer retouched artifacts.

At most Paleolithic sites that are recognized as such by archaeologists—that is, recognized because of the quantity of ancient refuse (mostly stone artifacts and animal bones)—single occupations by residentially or logistically organized foragers are not easily discernable. When they are, they are very difficult to interpret due to the low number of clearly associated artifacts (Aldeias et al. 2012). In fact, most assemblages that we study are probably time-averaged palimpsests of the trash of repeated human occupations of a locale (Barton et al. 2004; Barton and Clark 1993; Riel-Salvatore and Barton 2004). Hence, we would expect to see variable mixtures of residues from the different mobility strategies discussed above. The more that refuse from transiently sedentary base camps is represented, the greater the overall density of lithic debris that should be found, but the lower the relative frequency of retouched pieces in the assemblage. Conversely, the more that residentially mobile foragers contributed their lithic trash to an assemblage, the more it should be characterized by a lower overall density of discarded lithic materials per volume of excavated sediment and by a higher frequency of retouched pieces. If the largely inherent properties of lithic technology and selection pressures on human technological behaviors described above hold true, we would expect to see a strong negative relationship between retouch frequency and total lithic artifact volumetric density in assemblages. In fact, in a series of papers published over the past decade, we have shown this to be the case repeatedly in assemblages across southern Europe (Barton 1998; Barton and Riel-Salvatore 2012; Barton et al. 2011; Riel-Salvatore and Barton 2004; Riel-Salvatore and Barton 2007), and others have further replicated these results (Clark 2008, 2015; Kuhn 2004; Kuhn and Clark 2015; Sandgathe 2006). Furthermore, a series of recently published experiments using agent-based models have lent further support to these studies (Barton and Riel-Salvatore 2014); in fact, so far, only in exceptional cases have these expectations not been met (e.g., Conard and Will 2015). These complementary studies and lines of evidence lend strong support to our hypothesis that this relationship between retouch frequency and artifact density (which we have elsewhere termed the "whole assemblage behavioral indicator," or WABI) serves as robust proxy for human land-use strategies. In

addition, recent comparisons between the results of WABI values and detailed morphological analysis of individual artifacts further support these conclusions (Riel-Salvatore 2007, 2009).

Building on this work, we use this proxy record of human land-use to investigate large-scale human ecological dynamics during the Upper Pleistocene across southern Europe and the Near East. It is clear from our work and that of others that, because retouch frequency and artifact volumetric density are predicted to be negatively highly correlated—and indeed often are—we only need to use one of these two measures as a proxy for past land-use strategies. As noted in our prior work (Riel-Salvatore and Barton 2004), lithic volumetric density can vary with deposition processes across space and time, and so does not provide a comparable measure for synthesizing large-scale behavioral patterns beyond a particular depositional context, while retouch frequency is a normalized measure that is not affected by such depositional processes. Hence, we focus here on the frequency of retouched artifacts within entire lithic assemblages as a proxy for human land-use strategies.

ECOLOGICAL DYNAMICS FOR WESTERN EURASIA

The syntheses presented here are based on data from 167 assemblages, recovered from 31 localities distributed geographically from Gibraltar to southern Jordan (figure 2.1, table 2.1). Temporally, they span the entire Upper Pleistocene from the last Interglacial through the end of the Pleistocene. In terms of standard typological assignment, these assemblages include Middle Paleolithic, Upper Paleolithic, and what are sometimes called "transitional" (e.g., Uluzzian) industries. While not comprehensive of all sites known across western Eurasia, of course, this sample still represents a large spatial, temporal, and industrial range and is sufficient to display robust patterning discussed below.

Our prior work suggests a general trend through the Upper Pleistocene toward reduced variation in land-use strategies, as indicated by retouch frequency and an accompanying trend toward an emphasis on logistical mobility, and suggests further that variation in land-use strategies is responding to environmental change (Barton 1998; Barton and Riel-Salvatore 2012; Barton et al. 2011; Riel-Salvatore and Barton 2004, 2007; Riel-Salvatore et al. 2008). While reliable radiometric dates are available for only a few of the assemblages (unfortunately, the norm for most of the Upper Pleistocene archaeological record), we are able to assign all 167 assemblages to an Oxygen Isotope Stage (OIS; figure 2.2). At this temporal resolution, the pattern toward reduced variability is clear, as is the trend from variable mobility strategies toward a focus
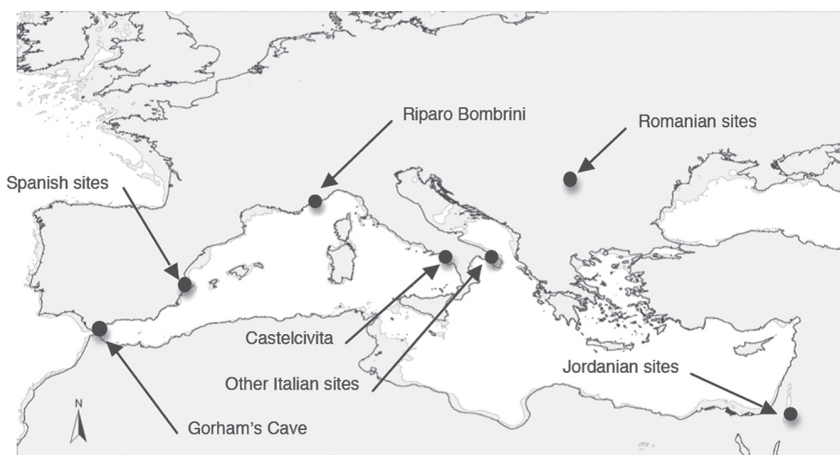
FIGURE 2.1. *Locations of sites that produced assemblages used in analyses. Map shows Pleistocene coastlines (at −100 m bmsl) in gray, with modern coastlines as black line.*

primarily on logistical mobility by the Last Glacial Maximum (LGM) (figures 2.2 and 2.3).

In a recent, detailed analysis of assemblages and paleoenvironmental data from OIS 3 in Italy, Riel-Salvatore suggests that the amount of environmental variation is as important as general environmental trends as a driver of human land-use changes during the Upper Pleistocene (Riel-Salvatore 2007:87–92; Riel-Salvatore 2010). That is, increased unpredictability over much shorter time frames and consequent risk of resource shortfalls in the period leading up to the LGM created a fitness landscape strongly favoring flexible logistical mobility strategies. These allowed humans to concurrently target a wider range of potential resources, over a much larger spatial extent, than could residentially mobile strategies that cycled sequentially through more predictable, seasonally variable resources. Indeed, studies of recent hunter-gathers show that logistical strategies are more common at high latitudes, with high spatiotemporal variance in resource distribution and abundance, while residential mobility predominates at low latitudes (Binford 1980; Grove 2010; Kelly 1995).

We use a high-resolution proxy for global climatic change—$^{18}O/^{16}O$ ratios from the GISP2 (Greenland Ice Sheet Project) ice core (Meese et al. 1997)—to represent climate change at large scales. A simple comparison of retouch frequency for dated assemblages and $\delta^{18}O$ (figure 2.4) shows some degree of correspondence, but it is not visually compelling. However, the combination of environmental variance with the maximum range of $^{18}O/^{16}O$ values within

TABLE 2.1. Assemblages used in analyses.

Country	Site	Industry	Number of Assemblages
Gibraltar	Gorham's Cave	Upper Paleolithic	4
Gibraltar	Gorham's Cave	Middle Paleolithic	6
Italy	Capelvenere	Middle Paleolithic	11
Italy	Castelcivita	Proto-Aurignacian	2
Italy	Castelcivita	Uluzzian	4
Italy	Marcello Zei	Middle Paleolithic	3
Italy	Mario Bernardini	Uluzzian	3
Italy	Mario Bernardini	Middle Paleolithic	21
Italy	Riparo Bombrini	Proto-Aurignacian	2
Italy	Riparo Bombrini	Middle Paleolithic	8
Italy	Serra Cicora	Proto-Aurignacian	2
Italy	Serra Cicora	Uluzzian	2
Italy	Serra Cicora	Middle Paleolithic	3
Italy	Torre dell'Alto	Middle Paleolithic	6
Italy	Uluzzo	Epigravettian	3
Italy	Uluzzo	Uluzzian	2
Italy	Uluzzo C	Uluzzian	3
Italy	Uluzzo C	Middle Paleolithic	17
Jordan	Ain al-Buhira	Late Ahmarian	1
Jordan	Ain al-Buhira	Ahmarian	1
Jordan	Tabaqa	Late Epipaleolithic	1
Jordan	Tor al-Tareeq	Middle Epipaleolithic	1
Jordan	Tor al-Tareeq	Early Epipaleolithic	2
Jordan	Tor Sadaf	Early Ahmarian	1
Jordan	Tor Sadaf	Transition	2
Jordan	Tor Sageer	Early Epipaleolithic	1
Jordan	WHS 621	Middle Paleolithic	1
Jordan	WHS 634	Middle Paleolithic	1
Jordan	Yutil al-Hasa	Late Epipaleolithic	1
Jordan	Yutil al-Hasa	Early Epipaleolithic	1

TABLE 2.1—*continued*

Country	Site	Industry	Number of Assemblages
Jordan	Yutil-al-Hasa	Late Ahmarian	2
Romania	Baia de Fier-Pestera Muierii	Middle Paleolithic	1
Romania	Borosteni-Pestera Cioarei	Middle Paleolithic	4
Romania	Cosava-Cuca	Aurignacian	2
Romania	Nandru-Pestera Curata	Middle Paleolithic	5
Romania	Nandru-Pestera Spurcata	Middle Paleolithic	1
Romania	Ohaba Ponor	Aurignacian	1
Romania	Ohaba Ponor	Middle Paleolithic	4
Romania	Pestera Moieciu-Pestera Mare	Upper Paleolithic	2
Romania	Pestera Moieciu-Pestera Mare	Middle Paleolithic	1
Romania	Pestera Valea Coacazei	Middle Paleolithic	1
Romania	Rasnov-Gura Cheii	Middle Paleolithic	1
Romania	Romanesti-Dumbravita	Aurignacian	1
Spain	Beneito	Solutreo-Gravettian	1
Spain	Beneito	Gravettian	1
Spain	Beneito	Aurignacian	1
Spain	Beneito	Middle Paleolithic	1
Spain	Cova del Salt	Middle Paleolithic	6
Spain	Cova Negra	Middle Paleolithic	15
Total	31 sites		167

each OIS provides a measure of the extremes of environmental variation that hominins faced during the Upper Pleistocene in western Eurasia. In fact, these values are highly correlated with mean retouch frequency values for the 167 assemblages (figure 2.5).

Moreover, there is a general tendency for the resource forays of logistically mobile hunter-gatherers to extend over a much greater geographical area than the territories occupied by residentially mobile foragers (Binford 2001; Grove 2009; Kelly 1983). That is, even though residentially mobile foragers may move more often during the course of a year, they tend to do so within an area of limited spatial extent. On the other hand, logistically organized hunter-gatherers may travel less frequently but acquire resources over a region of much greater geographic extent on an annual and lifetime basis. The geographic range over
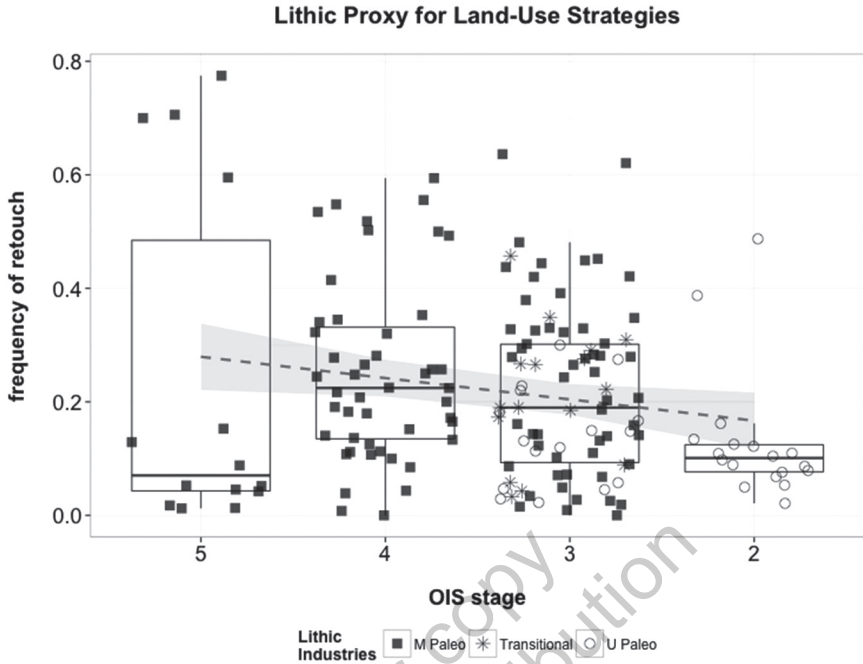
Lithic Proxy for Land-Use Strategies

FIGURE 2.2. *Retouch frequencies for all sites, by Oxygen Isotope Stage (N = 167 assemblages). Box plots show median and mid-spread. Dashed regression line shows overall trend in retouch frequencies over the Upper Pleistocene; grey shading shows 95% confidence intervals around the trend line.*

which hunter-gatherers forage also affects the size of their potential mating network (sensu Wobst 1974; see Amick 1996 for an extreme case) with potential consequences for biocultural evolution that are discussed below.

DISCUSSION

These results have interesting and potentially important implications for biobehavioral change during the Upper Pleistocene of western Eurasia. One way to interpret this evidence would be to say that Neanderthals were residentially mobile foragers, and were replaced by logistically mobile anatomically modern humans (AMH), whose flexible land-use strategies were favored by deteriorating climate approaching the LGM. However, while this story makes for an appealing narrative, it is overly simplistic and is not supported by the evidence presented here.
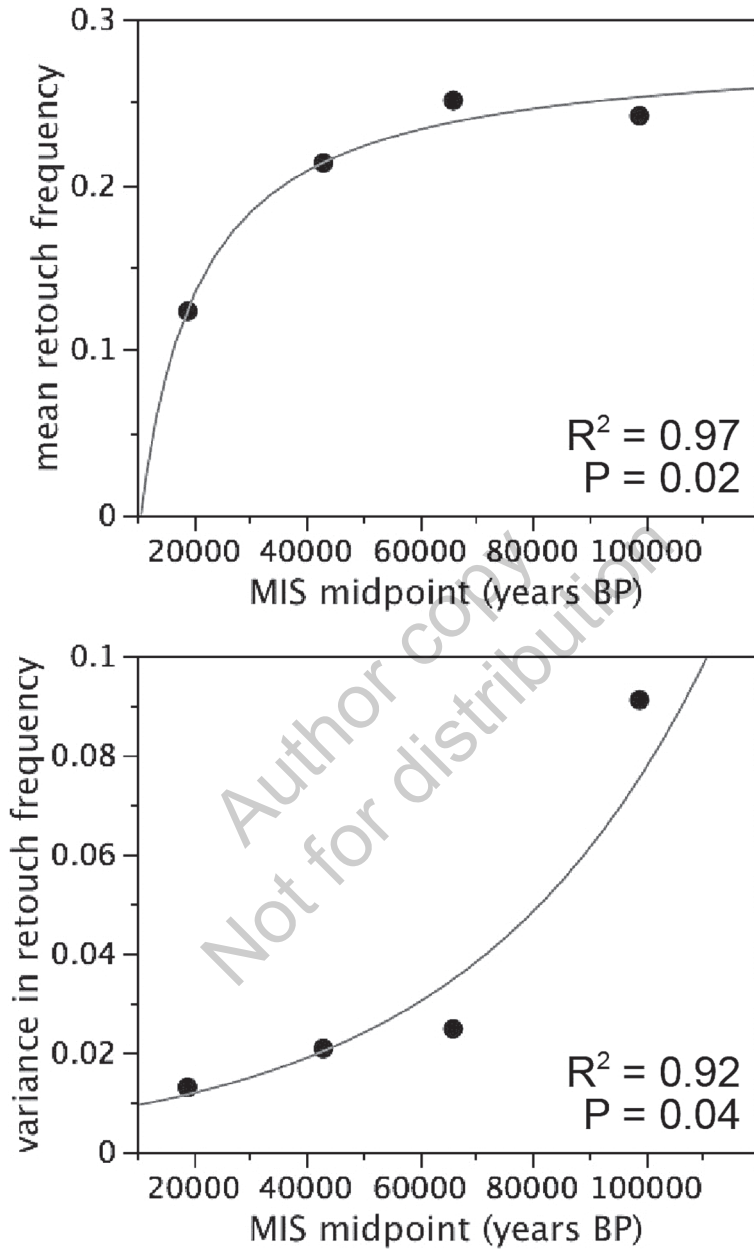
Figure 2.3. *Least-squares regression of temporal trends in retouch frequency and variance in retouch frequency seen in figure 2.1.*
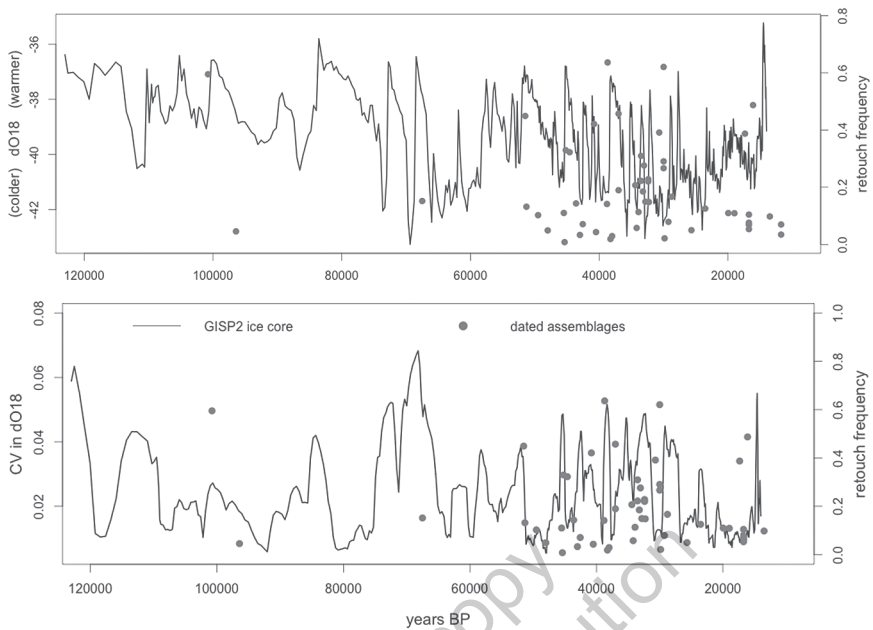
FIGURE 2.4. *(Top) GISP2 δ¹⁸O and retouch frequency for all dated sites (N = 55 assemblages). (Bottom) Retouch frequency for dated assemblages and temporal variation in environments, as shown by coefficient of variation for 100–year rolling mean of GISP2 δ¹⁸O.*

Indeed, during OIS 5–4 all the lithic assemblages in the assemblages studied are classified as Middle Paleolithic and the only human remains in western Europe, at least, are classified as Neanderthal. Similarly, during OIS 2, all the lithic assemblages studied are classified as Upper Paleolithic and the only human remains found are classified as AMH. But these observations tell us nothing about the nature of the changes in human behavior and biology that transpired during the Upper Pleistocene nor their causes. During OIS 3, when human remains classified as both Neanderthal and AMH are found, as well as lithic assemblages classified as Middle and Upper Paleolithic, there is still much debate over which "kind" of hominin made which "kind" of assemblage at this time (Hublin 2013). But, it is likely that most Middle Paleolithic and Transitional assemblages were made by hominins classified as Neanderthals and that most assemblages labeled Upper Paleolithic were made by hominins considered AMH (Riel-Salvatore and Clark 2007; Zilhão and d'Errico 2003).

Looking at the points and graphs in figure 2.2, it is obvious that logistical strategies have been practiced since OIS 5–3 by hominins who made
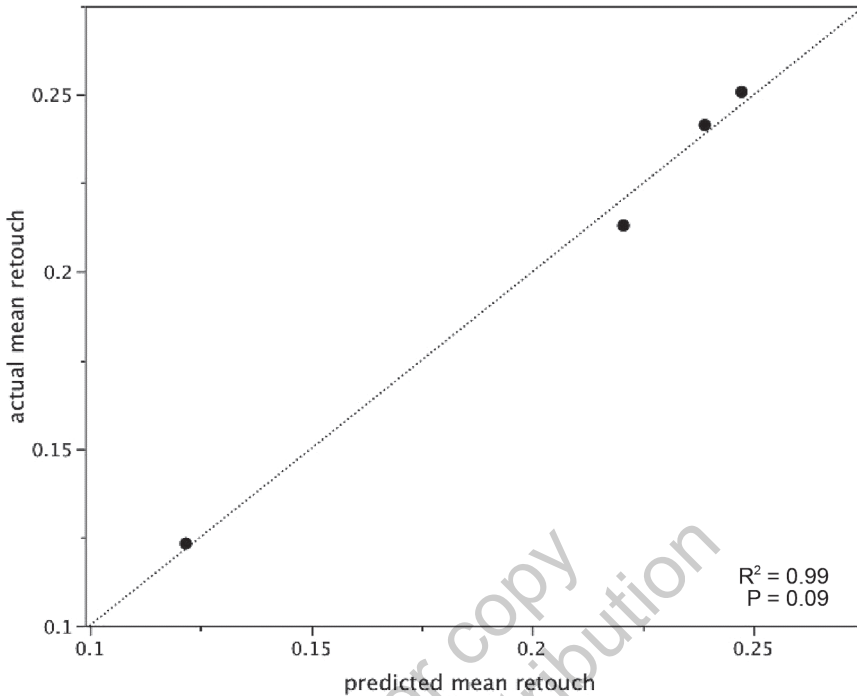
Figure 2.5. *Least-squares multiple regression of mean retouch frequency (x-axis) vs. combination of range plus variance in δ¹⁸O in the GISP2 for OIS 5–2 (y-axis).*

assemblages classified as Middle Paleolithic (cf. Lieberman and Shea 1994). What changed over the course of the Upper Pleistocene was the frequency of highly residentially mobile strategies. This decline is seen from OIS 3–2 among assemblages classed as Upper Paleolithic as well as in those classed as Middle Paleolithic during OIS 5–3. That is, the vectored changes in lithic industries that we have documented across western Eurasia in the Upper Pleistocene cross-cut the typological classifications of Middle and Upper Paleolithic. This is especially clear if we look at the distribution of retouch frequency separately in assemblages classed as Middle Paleolithic, Transitional, and Upper Paleolithic within OIS 3, when all are found (figure 2.6).

By definition, we classify as Upper Paleolithic assemblages those that contain higher frequencies of artifacts that were probably hafted in compound tools, such as backed blades. Such compound tools, being lightweight and maintainable (sensu Torrence 1989) should be more commonly associated with logistical land-use strategies. Conversely, we classify as Middle Paleolithic those
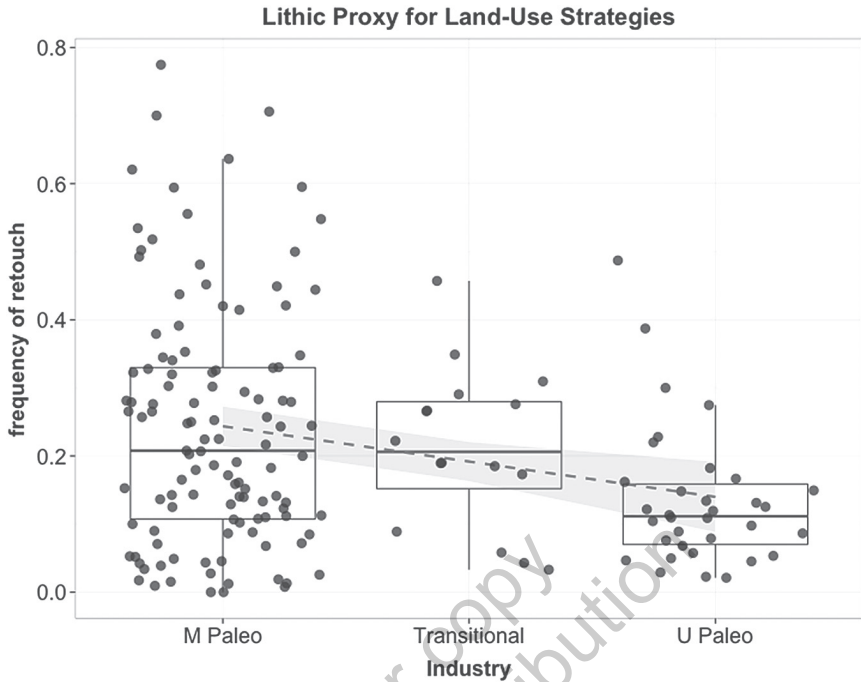
Lithic Proxy for Land-Use Strategies

FIGURE 2.6. *Retouch frequencies for OIS 3 assemblages from western Eurasia classified as Middle Paleolithic, Transitional, and Upper Paleolithic. Individual assemblages shown as black dots. Box-plots in gray show median, mid-spread, and range. Dashed line shows linear regression for industries; grey shaded zone shows 95% confidence interval.*

assemblages dominated by flake artifacts that were less likely to be hafted and more likely to be ad hoc tools typical of residentially mobile foragers (Nelson 1991). Yet while the mean values for retouch frequency differ for the Upper and Middle Paleolithic assemblages shown in figure 2.6, there is complete overlap in the distributions of both groups. That is, during OIS 3, both Middle and Upper Paleolithic assemblages range from ones indicating high levels of logistical mobility to ones indicating moderate amounts of residential mobility.

Returning to human biology, even if only Neanderthals were the makers of Middle Paleolithic and Transitional assemblages, and only AMH made Upper Paleolithic assemblages, the trends we discuss would cross-cut these biological differences as they do lithic classifications. If, as is increasingly suggested by paleogenetic data (e.g., Fu et al. 2015; Hawks and Throckmorton 2013; Hershkovitz et al. 2015), the relationships between human skeletal

morphology, human behavior, and the forms of discarded stone artifacts and production debris are more complex than this, the data we have presented offer a new window into the dynamics of human biogeography and behavior during this time of rapid environmental change (cf. Green et al. 2010).

The increased prevalence of logistical mobility strategies across the span of the Upper Pleistocene, regardless of how assemblages are classified or who may have made and used them, means that *all* hominins were undertaking an increasing number of longer distance forays to collect resources to return to a home base. This would have brought members of *all* western Eurasian hominin groups in contact with a larger and more diverse number of other humans. This resulting increase in opportunities for social and biological interactions across much wider geographic regions would have had profound impacts on human biological variation.

The very small sample of human fossils known even in western Eurasia, means that paleoanthropologists still have virtually no information about the nature of biological variation within real hominin populations (i.e., contemporaneous individuals and social groups within delimited regions) in the Upper Pleistocene. But those individuals that have been found in western Eurasia especially (i.e., those classified as Neanderthals) seem to have developed and maintained a suite of derived characteristics of skeletal morphology from sometime in the Middle Pleistocene into OIS 3 (Harvati 2007; Hublin 2009; Klein 2003; Wolpoff et al. 2004). The presence of a biologically distinctive regional population in this region is not surprising, given its geography as a long, narrow peninsula, especially during periods of continental and Alpine ice sheets. This geography would have left western European hominins semi-isolated, allowing them to emerge as a regionally distinctive population (Serangeli and Bolus 2008). It would also be easier for western European hominins to maintain these distinctive characteristics when residential mobility within spatially delimited "territories" was the common land-use strategy, limiting the social and biological interaction of any group to its immediate neighbors. This scenario is congruent with Voisin's characterization of Neanderthals and the AMH as ring species, with gene flow between adjacent populations but considerable genetic differences between geographically distant populations (Voisin 2006; see also Holliday 2006). Greater long-distance mobility, resulting from increasing reliance on logistical land-use strategies, would have considerably reduced the limitations to gene flow and cultural transmission imposed by geography and residential mobility patterns in this region.

In other animals (and plants), a biogeographical change that increases interactions among members of different variant populations or even sister species

(e.g., removal of a geographic barrier or transportation by humans of one taxon into the range of another) commonly results in increased hybridization rates, leading to a rapid disappearance of one of them as a recognizably distinct variant or species (Epifanio and Nielsen 2001; Wolf 1990). Recent DNA sequencing of a 38,000-year-old Neanderthal specimen, estimates that the last common ancestor of modern humans and Neanderthals lived between 670,000 and 120,000 years ago (95% CI), with a mean at 370,000 (Noonan et al. 2006), and other estimates of the time of divergence fall within this range (Garrigan and Kingan 2007; Green et al. 2006; Krause et al. 2007; Harvati 2007). Mammalian rates of evolution of hybrid inviability are considerably faster than other vertebrates, but still average 2–4 million years (Fitzpatrick 2004), considerably longer than the time since the Neanderthal/modern human divergence. This means that Neanderthals and the ancestors of modern humans probably could have produced viable hybrids during OIS 3 (50,000–27,000 years ago). Recent sequencing of Neanderthal DNA and comparisons with modern (i.e., twenty-first century) human genomes indicates that such genetic exchange did take place between Neanderthals and AMH in western Eurasia (Green et al. 2010).

However, even viable hybrids often exhibit decreased or increased fertility with respect to one or both of the ancestral populations that can have significant impacts on parent populations (especially if the parent populations have had the opportunity to diverge to some degree evolutionarily), regardless of whether they are different species or different populations of the same species (Demuth and Wade 2007). Increased hybridization, coupled with decreased hybrid fertility will reduce the overall fertility of a parent population by siphoning off reproductive capacity into the production of low fertility (or even sterile) hybrids. On the other hand, increased hybridization accompanied by the higher fertility of "hybrid vigor" can ultimately replace all of one parent population with hybrids. Such extinction through hybridization is sufficiently common in nature to be an important concern in conservation biology with significant impacts on rare and endangered species (Epifanio and Nielsen 2001; Wolf 1990). The fact that hybrids are often difficult to distinguish from one of the ancestral species without genetic analysis (Brisbin 1995) exacerbates these problems. The increased biological and cultural interaction between Neanderthal populations and other hominin variants, due to the changes in land-use patterns documented here, is sufficient to account for the disappearance of Neanderthal skeletal morphology (i.e., extinction) across western Eurasia through significantly increased hybridization rates without invoking interpopulation or interspecific competition or other mechanisms. But as Brisbin (1995) points out, obvious skeletal evidence for the existence

of recognizable hybrids may be difficult to come by in spite of new genetic evidence for such interactions (Fu et al. 2015).

A model of extinction of Neanderthals through hybridization also helps explain otherwise puzzling features of their spatiotemporal distribution in OIS 3 (Smith et al. 2005). With direct competition for resources between human groups, the most effective competitors end up with the most productive lands, and the less effective competitors are relegated to marginally productive areas. This has regularly been the case when agriculturalists competed with hunter-gatherers, and even when immigrating hunter-gatherers encounter long-established hunter-gatherers in a region (Fiedel 2004). However, recognizable Neanderthal remains from OIS 3 are found across the southern and south-western fringes of Europe. Especially as global climate cooled, and became increasingly unpredictable and continental ice sheets and tundra spread across northern Europe, morphological Neanderthals occupied the most mesic areas of Europe with the most diverse and easily procured resources. The earliest specimens of AMH, in contrast, are found in the much more challenging (i.e., comparatively marginal) areas of central/eastern Europe and the steppe south of the ice (Finlayson and Carrión 2007; Finlayson et al. 2006; Nigst et al. 2014; Trinkaus 2005; van Andel et al. 2003; Zilhão 2007). At a high cost in organization and technology, these human groups managed to survive and (eventually) flourish in these rigorous environments in spite of their being especially challenging ecologically for hunter-gatherers originating in Africa. But they did not apparently displace Neanderthals, who were supposedly much less effective competitors, from glacial Europe's prime real estate for millennia.

However, if Neanderthals disappeared due to hybridization rather than being out-competed in some as yet unspecified way, the spatiotemporal distributions of Pleistocene hominins makes more sense. The newcomers to western Eurasia (i.e., AMH) were initially relegated to marginal environments of the more frigid north and east by the established and well-adapted local populations (i.e., Neanderthals). We have not compiled lithic data on Upper Paleolithic assemblages from eastern/central Europe (but cf. Riel-Salvatore et al. 2008). However it would not be surprising if an analysis like the one presented here shows that OIS 3 hominins in these area faced environmental pressures to shift their land-use strategies toward logistical mobility somewhat earlier than populations to the more mesic south. Furthermore, as immigrants into a relatively new (i.e., for Upper Pleistocene hominins) and expanding ecosystem that was also devoid of other human competitors, that of the mammoth steppe south of growing ice sheets, there also are ecological reasons to expect higher mobility and longer distance moves in these groups (Barton et al. 2004).

As increasingly unpredictable and extreme environmental oscillations during OIS 3 favored logistical land-use strategies more broadly, previously isolated Neanderthals in the European heartland came to interact biologically and culturally to a much greater degree with other human groups to the east and north. These even more mobile fringe populations would have been transmitting genes and ideas over even longer distances and served as constantly replenishing reservoirs of a geographically more extensive "modern" human gene pool. Once the process passed a critical threshold of genetic interchange, recognizably distinct Neanderthal populations could have disappeared comparatively rapidly, falling victim to genetic "globalization" (Smith et al. 2005). Given the geography of Europe, we would expect this process to move through the population from the east to the most isolated westernmost tip of the European peninsula. In fact, traditionally, the latest dates for morphologically recognizable Neanderthals have been argued to come from the Iberian Peninsula (Jordá Pardo 2007; Zilhão 2006), although recent data have admittedly challenged this and proposed a relatively sudden shift across Europe (Higham et al. 2014).

Because humans are cultural animals, with much behavioral information transmitted by nongenetic means, we would expect hybridization to likewise occur in behavioral residues, including lithic refuse, at an increasing rate from OIS 3 onwards. Given the expected difficulties in recognizing hybrid hominins, we should not be surprised to find Middle Paleolithic artifacts made by individuals who appear to be morphologically modern or Upper Paleolithic artifacts made by individuals who resemble Neanderthals. We might or might not find mosaics of traits in some specimens—if we were certain which traits were indeed ancestral Neanderthal and which were ancestral non-Neanderthal.

In conclusion, we want to point out two other implications of the model of human ecological dynamics that we have presented here. The first is that, if Neanderthals disappeared due to hybridization, it means that at least some Neanderthal genetic material may survive in modern populations, but it is no longer clustered into a recognizable constellation of morphological traits. Recent comparisons between Neanderthal and modern genomes suggest as much as 4 percent or even more of western European genes may have Neanderthal origins (Green et al. 2010; Hawks and Throckmorton 2013; Wall et al. 2009). In this respect, it is interesting that modern Europeans and their descendants are quite distinct from the rest of humanity in their lack of pigmentation, ever-growing dense facial hair in males and general hirsuteness, and a tendency toward mid-facial prognathism—with similar characteristics also distinguishing Neanderthals from other contemporaneous hominins

(Lalueza-Fox et al. 2007; Wolpoff et al. 2004). The second is that the model we have developed to explain robust, large-scale spatiotemporal patterning in Upper Pleistocene lithic assemblages across western Eurasia is based on evidence that suggests *all* hominins in this region, including Neanderthals, responded in a similar fashion to significant environmental change. If Neanderthals became extinct due to hybridization, it was because they effectively adapted to the environmental uncertainty of the Upper Pleistocene. That is, their disappearance was not due to being ineffective competitors, but rather a result of their success in adapting to the challenges of global climate change.

REFERENCES

Aldeias, Vera, Paul Goldberg, Dennis Sandgathe, Francesco Berna, Harold L. Dibble, Shannon P. McPherron, Alain Turq, and Zeljko Rezek. 2012. "Evidence for Neandertal Use of Fire at Roc de Marsal (France)." *Journal of Archaeological Science* 39(7):2414–2423. http://dx.doi.org/10.1016/j.jas.2012.01.039.

Amick, Daniel. 1996. "Regional Patterns of Folsom Mobility and Land-Use in the American Southwest." *World Archaeology* 27(3):411–426. http://dx.doi.org/10.1080/00438243.1996.9980317.

Amick, Daniel, and Raymond P. Mauldin, eds. 1989. *Experiments in Lithic Technology*. BAR International Series 528. Oxford: British Archaeological Reports.

Andrefsky, William, Jr. 2009. "The Analysis of Stone Tool Procurement, Production, and Maintenance." *Journal of Archaeological Research* 17(1):65–103. http://dx.doi.org/10.1007/s10814-008-9026-2.

Barton, C. Michael. 1990. "Beyond Style and Function: A View from the Middle Paleolithic." *American Anthropologist* 92(1):57–72. http://dx.doi.org/10.1525/aa.1990.92.1.02a00040.

Barton, C. Michael. 1991. "Retouched Tools: Fact or Fiction? Paradigms for Interpreting Chipped Stone." In *Perspectives on the Past: Theoretical Biases in Mediterranean Hunter-Gatherer Research*, ed. Geoffrey A. Clark, 143–163. Philadelphia: University of Pennsylvania Press.

Barton, C. Michael. 1998. "Looking Back from the World's End: Paleolithic Settlement and Mobility at Gibraltar." In *Las Culturas del Pleistoceno Superior en Andalucía*, ed. J. L. Sanchidrián Torti and M. D. Simón Vallejo, 13–23. Nerja, Spain: Patronato de la Cueva de Nerja.

Barton, C. Michael, Joan Bernabeu, Aura, Oreto Garcia, Lluis Molina, and Steven Schmich. 2004. "Historical Contingency, Nonlinearity, and the Neolithization of the Western Mediterranean." In *Current Issues in Mediterranean Landscape Archaeology*,

ed. LuAnn Wandsnider and Effie Athanassopoulos, 99–124. Philadelphia: University of Pennsylvania Press. http://dx.doi.org/10.9783/9781934536285.99.

Barton, C. Michael, and Geoffrey A. Clark. 1993. "Cultural and Natural Formation Processes in Late Quaternary Cave and Rockshelter Sites of Western Europe and the Near East." In *Formation Processes in Archaeological Context*, ed. Paul Goldberg, David T. Nash, and Michael D. Petraglia, 33–52. Madison, WI: Prehistory Press.

Barton, C. Michael, and Julien Riel-Salvatore. 2012. "Agents of Change: Modeling Biocultural Evolution in Upper Pleistocene Western Eurasia." *Advances in Complex Systems* 15(1–2):1150003-1–1150003-24.

Barton, C. Michael, and Julien Riel-Salvatore. 2014. "The Formation of Lithic Assemblages." *Journal of Archaeological Science* 46:334–352. http://dx.doi.org/10.1016/j.jas.2014.03.031.

Barton, C. Michael, Julien Riel-Salvatore, John M. Anderies, and Gabriel Popescu. 2011. "Modeling Human Ecodynamics and Biocultural Interactions in the Late Pleistocene of Western Eurasia." *Human Ecology* 39 (6): 705–725. http://dx.doi.org/10.1007/s10745-011-9433-8.

Binford, Lewis R. 1980. "Willow Smoke and Dogs' Tails: Hunter-Gatherer Settlement Systems and Archaeological Site Formation." *American Antiquity* 45(1):4–20. http://dx.doi.org/10.2307/279653.

Binford, Lewis R. 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter-Gatherer and Environmental Data Sets*. Berkeley: University of California Press.

Brisbin, I. L. 1995. "Conservation of the Wild Ancestors of Domestic Animals." *Conservation Biology* 9(5):1327–1328. http://dx.doi.org/10.1046/j.1523-1739.1995.09051327.x.

Clark, Amy E. 2008. "Changes in Occupation Intensity During the Lower and Middle Paleolithic at Tabun Cave, Israel." Master's Thesis, University of Arizona, Tucson.

Clark, Amy E. 2015. "Changes in Land Use and Occupation Intensity at the Onset of the Middle Paleolithic? A View from Tabun Cave, Israel." In *Settlement Dynamics of the Middle Paleolithic and Middle Stone Age,* Volume IV, ed. Nicholas J. Conard and Anne Delagnes. Tübingen Publications in Prehistory. Tübingen: Kerns Verlag.

Conard, Nicholas J., and Manuel Will. 2015. "Examining the Causes and Consequences of Short-Term Behavioral Change during the Middle Stone Age at Sibudu, South Africa." *PLoS One* 10(6):e0130001. http://dx.doi.org/10.1371/journal.pone.0130001.

Demuth, J. P., and Michael J. Wade. 2007. "Population Differentiation in the Beetle *Tribollium castaneum*. I. Genetic Architecture." *Evolution: International Journal of Organic Evolution* 61(3):494–509. http://dx.doi.org/10.1111/j.1558-5646.2007.00048.x.

Dibble, Harold L. 1987. "The Interpretation of Middle Paleolithic Scraper Morphology." *American Antiquity* 52(1):109–117. http://dx.doi.org/10.2307/281062.

Epifanio, John, and Jennifer Nielsen. 2001. "The Role of Hybridization in the Distribution, Conservation and Management of Aquatic Species." *Reviews in Fish Biology and Fisheries* 10(3):245–251. http://dx.doi.org/10.1023/A:1016729132297.

Fiedel, Stuart J. 2004. "Rapid Migrations by Arctic Hunting Peoples: Clovis and Thule." In *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogeography*, ed. C. Michael Barton, Geoffrey A. Clark, David R. Yesner, and Georges A. Pearson, 79–84. Tucson: University of Arizona Press.

Finlayson, Clive, and José S. Carrión. 2007. "Rapid Ecological Turnover and Its Impact on Neanderthal and Other Human Populations." *Trends in Ecology & Evolution* 22(4):213–222. http://dx.doi.org/10.1016/j.tree.2007.02.001.

Finlayson, Clive, Francisco Giles Pacheco, Joaquin Rodriguez-Vidal, Darren A. Fa, José María Gutierrez López, Antonio Santiago Pérez, Geraldine Finlayson, Ethel Allue, Javier Baena Preysler, Isabel Cáceres, et al. 2006. "Late Survival of Neanderthals at the Southernmost Extreme of Europe." *Nature* 443(7113):850–853. http://dx.doi.org/10.1038/nature05195.

Fitzpatrick, Benjamin M. 2004. "Rates of Evolution of Hybrid Inviability in Birds and Mammals." *Evolution; International Journal of Organic Evolution* 58(8):1865–1870. http://dx.doi.org/10.1111/j.0014-3820.2004.tb00471.x.

Frison, George C. 1968. "A Functional Analysis of Certain Chipped Stone Tools." *American Antiquity* 33 (2): 149–155. http://dx.doi.org/10.2307/278516.

Fu, Qiaomei, Mateja Hajdinjak, Oana Teodora Moldovan, Silviu Constantin, Swapan Mallick, Pontus Skoglund, Nick Patterson, Nadin Rohland, Iosif Lazaridis, Birgit Nickel, et al. 2015. "An Early Modern Human from Romania with a Recent Neanderthal Ancestor." *Nature* (June):22; advance online publication.

Garrigan, Daniel, and Sarah B. Kingan. 2007. "Archaic Human Admixture: A View from the Genome." *Current Anthropology* 48(6):895–902. http://dx.doi.org/10.1086/523014.

Gould, Richard A. K., D. A. Koster, and A. H. L. Sontz. 1971. "The Lithic Assemblage of the Western Desert Aborigines of Australia." *American Antiquity* 36(2):149–168. http://dx.doi.org/10.2307/278668.

Green, Richard E., Johannes Krause, Adrian W. Briggs, T. Maricic, U. Stenzel, M. Kircher, N. Patterson, H. Li, W. Zhai, M. H. Y. Fritz, et al. 2010. "A Draft Sequence of the Neandertal Genome." *Science* 328(5979):710–722. http://dx.doi.org/10.1126/science.1188021.

Green, Richard E., Johannes Krause, Susan E. Ptak, Adrian W. Briggs, Michael T. Ronan, Jan F. Simons, Lei Du, Michael Egholm, Jonathan M. Rothberg, Maja

Paunovic, et al. 2006. "Analysis of One Million Base Pairs of Neanderthal DNA." *Nature* 444(7117):330–336. http://dx.doi.org/10.1038/nature05336.

Grove, Matt. 2009. "Hunter-Gatherer Movement Patterns: Causes and Constraints." *Journal of Anthropological Archaeology* 28(2):222–233. http://dx.doi.org/10.1016/j.jaa .2009.01.003.

Grove, Matt. 2010. "Logistical Mobility Reduces Subsistence Risk in Hunting Economies." *Journal of Archaeological Science* 37(8):1913–1921. http://dx.doi.org/10 .1016/j.jas.2010.02.017.

Harmand, Sonia, Jason E. Lewis, Craig S. Feibel, Christopher J. Lepre, Sandrine Prat, Arnaud Lenoble, Xavier Boës, Rhonda L. Quinn, Michel Brenet, Adrian Arroyo, et al. 2015. "3.3-Million-Year-Old Stone Tools from Lomekwi 3, West Turkana, Kenya." *Nature* 521 (7552): 310–15. http://dx.doi.org/10.1038/nature14464.

Harvati, Katerina. 2007. "Neanderthals and Their Contemporaries." In *Handbook of Paleoanthropology*, ed. Winifred Henke and Ian Tattersall, 1717–1748. http://dx.doi .org/10.1007/978-3-540-33761-4_56.

Hawks, John, and Zach Throckmorton. 2013. "The Relevance of Archaic Genomes to Modern Human Origins." In *The Origins of Modern Humans: Biology Reconsidered*, ed. Fred H. Smith and James C. Ahern, 339–354. Hoboken, New Jersey: Wiley-Blackwell. http://dx.doi.org/10.1002/9781118659991.ch10.

Hershkovitz, Israel, Ofer Marder, Avner Ayalon, Miryam Bar-Matthews, Gal Yasur, Elisabetta Boaretto, Valentina Caracuta, Bridget Alex, Amos Frumkin, Mae Goder-Goldberger, et al. 2015. "Levantine Cranium from Manot Cave (Israel) Foreshadows the First European Modern Humans." *Nature* 520(7546):216–219. http://dx.doi.org/10.1038/nature14134.

Higham, Tom, Katerina Douka, Rachel Wood, Christopher Bronk Ramsey, Fiona Brock, Laura Basell, Marta Camps, Alvaro Arrizabalaga, Javier Baena, Cecillio Barroso-Ruíz, et al. 2014. "The Timing and Spatiotemporal Patterning of Neanderthal Disappearance." *Nature* 512(7514):306–309. http://dx.doi.org/10.1038 /nature13621.

Holliday, T. 2006. "Neanderthals and Modern Humans: An Example of a Mammalian Syngameon?" In *Neanderthals Revisited: New Approaches and Perspectives*, ed. Katerina Harvati and Terry Harrison, 281–297. Dordrecht, Netherlands: Springer. http://dx.doi.org/10.1007/978-1-4020-5121-0_16.

Hublin, Jean-Jacques. 2009. "The Origin of Neandertals." *Proceedings of the National Academy of Sciences of the United States of America* 106(38):16022–16027. http://dx.doi .org/10.1073/pnas.0904119106.

Hublin, Jean-Jacques. 2013. "The Makers of the Early Upper Paleolithic in Western Eurasia." In *Origin of Modern Humans: Biology Reconsidered*, ed. Fred H. Smith

and James C. Ahern, 223–252. Hoboken, New Jersey: Wiley-Blackwell. http://dx .doi.org/10.1002/9781118659991.ch6.

Jordá Pardo, Jesús F. 2007. "The Wild River and the Last Neanderthals: A Palaeoflood in the Geoarchaeological Record of the Jarama Canyon (Central Range, Guadalajara Province, Spain)." *Geodinamica Acta* 20(4):209–217. http://dx .doi.org/10.3166/ga.20.209-217.

Kelly, Robert L. 1983. "Hunter-Gatherer Mobility Strategies." *Journal of Anthropological Research* 39:277–306.

Kelly, Robert L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.

Kimbel, W. H., R. C. Walter, D. C. Johanson, K. E. Reed, J. L. Aronson, Z. Assefa, C. W. Marean, G. G. Eck, R. Bobe, E. Hovers, et al. 1996. "Late Pliocene Homo and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia." *Journal of Human Evolution* 31(6):549–561. http://dx.doi.org/10.1006/jhev.1996.0079.

Klein, Richard G. 2003. "Paleoanthropology: Whither the Neanderthals?" *Science* 299(5612):1525–1527. http://dx.doi.org/10.1126/science.1082025.

Krause, Johannes, Carles Lalueza-Fox, Ludovic Orlando, Wolfgang Enard, Richard E. Green, Hernán A. Burbano, Jean-Jacques Hublin, Catherine Hänni, Javier Fortea, Marco de la Rasilla, et al. 2007. "The Derived FOXP2 Variant of Modern Humans Was Shared with Neandertals." *Current Biology* 17(21):1908–1912. http://dx.doi.org/10.1016/j.cub.2007.10.008.

Kuhn, Steven L. 1992. "On Planning and Curated Technologies in the Middle Paleolithic." *Journal of Anthropological Research* 48:185–214.

Kuhn, Steven L. 1994. "A Formal Approach to the Design and Assembly of Mobile Toolkits." *American Antiquity* 59(3):426–442. http://dx.doi.org/10.2307/282456.

Kuhn, Steven L. 2004. "Middle Paleolithic Assemblage Formation at Riparo Mochi." In *Processual Archaeology: Exploring Analytical Strategies, Frames of Reference and Culture Process*, ed. Amber Lynn Johnson, 31–60. Westport, CT: Greenwood Publishing Group.

Kuhn, Steven L., and Amy E. Clark. 2015. "Artifact Densities and Assemblage Formation: Evidence from Tabun Cave." *Journal of Anthropological Archaeology* 38:8–16. http://dx.doi.org/10.1016/j.jaa.2014.09.002.

Lalueza-Fox, Carles, Holger Rompler, David Caramelli, C. Staubert, G. Catalano, D. Hughes, N. Rohland, E. Pilli, L. Longo, S. Condemi, et al. 2007. "A Melano- cortin 1 Receptor Allele Suggests Varying Pigmentation Among Neanderthals." *Science* 318(5855):1453–1455. http://dx.doi.org/10.1126/science.1147417.

Laville, Henri, Jean-Philippe Rigaud, and James Sackett. 1980. *Rock Shelters of the Perigord*. New York: Academic Press.

Lieberman, Daniel E., and John J. Shea. 1994. "Behavioral Differences between Archaic and Modern Humans in the Levantine Mousterian." *American Anthropologist* 96 (2): 300–332. http://dx.doi.org/10.1525/aa.1994.96.2.02a00030.

Magne, Martin P., and David Pokotylo. 1981. "A Pilot Study in Bifacial Lithic Reduction Sequences." *Lithic Technology* 10:34–47.

McCall, Grant S. 2012. "Ethnoarchaeology and the Organization of Lithic Technology." *Journal of Archaeological Research* 20(2):157–203. http://dx.doi.org/10.1007/s10814-011-9056-z.

McPherron, Shannon P., Zeresenay Alemseged, Curtis W. Marean, Jonathan G. Wynn, Denné Reed, Denis Geraads, René Bobe, and Hamdallah A. Béarat. 2010. "Evidence for Stone-Tool-Assisted Consumption of Animal Tissues before 3.39 Million Years Ago at Dikika, Ethiopia." *Nature* 466(7308):857–860. http://dx.doi.org/10.1038/nature09248.

Meese, D. A., A. J. Gow, R. B. Alley, G. A. Zielinski, P. M. Grootes, M. Ram, K. C. Taylor, P. A. Mayewski, and J. F. Bolzan. 1997. "The Greenland Ice Sheet Project 2 Depth-Age Scale: Methods and Results." *Journal of Geophysical Research* 102(C12):26411–26423. http://dx.doi.org/10.1029/97JC00269.

Nelson, Margaret C. 1991. "The Study of Technological Organization." In *Archaeological Method and Theory*, vol. 3. ed. Michael B. Schiffer, 57–100. Tucson: University of Arizona Press.

Nigst, Philip R., Paul Haesaerts, Freddy Damblon, Christa Frank-Fellner, Carolina Mallol, Bence Viola, Michael Götzinger, Laura Niven, Gerhard Trnka, and Jean-Jacques Hublin. 2014. "Early Modern Human Settlement of Europe North of the Alps Occurred 43,500 Years Ago in a Cold Steppe-Type Environment." *Proceedings of the National Academy of Sciences of the United States of America* 111(40):14394–14399. http://dx.doi.org/10.1073/pnas.141220111.

Noonan, James P., Graham Coop, Sridhar Kudaravalli, D. Smith, J. Krause, J. Alessi, F. Chen, D. Platt, S. Paabo, J. K. Pritchard, et al. 2006. "Sequencing and Analysis of Neanderthal Genomic DNA." *Science* 314(5802):1113–1118. http://dx.doi.org/10.1126/science.1131412.

Nowell, April, and Iain Davidson. 2010. *Stone Tools and the Evolution of Human Cognition*. Boulder: University Press of Colorado.

Otten, Jennifer J., Jennifer Pitzi Hellwig, and Linda D. Meyers, eds. 2006. *Dietary Reference Intakes: The Essential Guide to Nutrient Requirements*. Washington, DC: National Academies Press.

Parry, William J., and Robert L. Kelly. 1987. "Expedient Core Technology and Sedentism." In *The Organization of Core Technology*, ed. Jay K. Johnson and Carol A. Marrow, 284–304. Boulder: Westview Press.

Riel-Salvatore, Julien. 2007. "The Uluzzian and the Middle-Upper Paleolithic Transition in Southern Italy." PhD dissertation, Arizona State University, Tempe.

Riel-Salvatore, Julien. 2009. "What Is a "Transitional" Industry? The Uluzzian of Southern Italy as a Case Study." In *Sourcebook of Paleolithic Transitions: Methods, Theories, and Interpretations*, ed. Marta Camps and Parth Chauhan, 377–396. New York: Springer. http://dx.doi.org/10.1007/978-0-387-76487-0_25.

Riel-Salvatore, Julien. 2010. "A Niche Construction Perspective on the Middle–Upper Paleolithic Transition in Italy." *Journal of Archaeological Method and Theory* 17(4):323–355. http://dx.doi.org/10.1007/s10816-010-9093-9.

Riel-Salvatore, Julien, and C. Michael Barton. 2004. "Late Pleistocene Technology, Economic Behavior, and Land-Use Dynamics in Southern Italy." *American Antiquity* 69(2):257–274. http://dx.doi.org/10.2307/4128419.

Riel-Salvatore, Julien, and C. Michael Barton. 2007. "New Quantitative Perspectives on the Middle-Upper Paleolithic Transition: The View from the Northern Mediterranean." In *Early Upper Paleolithic "Transitional" Industries: New Questions, New Methods*, ed. Julien Riel-Salvatore and Geoffrey A. Clark. BAR International Series 1620. Oxford: British Archaeological Reports.

Riel-Salvatore, Julien, and Geoffrey A. Clark, eds. 2007. *New Approaches to the Study of Early Upper Paleolithic "Transitional" Industries in Western Eurasia: Transitions Great and Small*. BAR International Series S1620. Oxford: British Archaeological Reports.

Riel-Salvatore, Julien, Gabriel Popescu, and C. Michael Barton. 2008. "Standing at the Gates of Europe: Human Behavior and Biogeography in the Southern Carpathians during the Late Pleistocene." *Journal of Anthropological Archaeology* 27(4):399–417. http://dx.doi.org/10.1016/j.jaa.2008.02.002.

Sandgathe, Dennis M. 2006. *Examining the Levallois Reduction Strategy from a Design Theory Point of View*. BAR International Series 1417. Oxford: British Archaeological Reports.

Semaw, S., P. Renne, J. W. K. Harris, C. S. Feibel, R. L. Bernor, N. Fesseha, and K. Mowbray. 1997. "2.5-Million-Year-Old Stone Tools from Gona, Ethiopia." *Nature* 385(6614):333–336. http://dx.doi.org/10.1038/385333a0.

Serangeli, Jordi, and Michael Bolus. 2008. "Out of Europe - The Dispersal of a Successful European Hominin Form." *Quartär* 55:83–98.

Shott, Michael J. 1994. "Size and Form in the Analysis of Flake Debris: Review and Recent Approaches." *Journal of Archaeological Method and Theory* 1(1):69–110. http://dx.doi.org/10.1007/BF02229424.

Shott, Michael J. 1998. "Status and Role of Formation Theory in Contemporary Archaeological Practice." *Journal of Archaeological Research* 6(4):299–329. http://dx.doi.org/10.1007/BF02446082.

Shott, Michael J. 2008. "Lower Paleolithic Industries, Time, and the Meaning of Assemblage Variation." In *Time in Archaeology: Time Perspectivism Revisited*, ed. Simon Holdaway and LuAnn Wandsnider, 61–75. Salt Lake City: University of Utah Press.

Smith, Fred H., Ivor Jankovic, and Ivor Karavanic. 2005. "The Assimilation Model, Modern Human Origins in Europe, and the Extinction of Neandertals." *Quaternary International* 137(1):7–19. http://dx.doi.org/10.1016/j.quaint.2004.11.016.

Surovell, Todd A. 2009. *Toward a Behavioral Ecology of Lithic Technology: Cases from Paleoindian Archaeology*. Tucson: University of Arizona Press.

Torrence, Robin. 1989. "Tools as Optimal Solutions." In *Time, Energy and Stone Tools*, ed. Robin Torrence, 1–6. Cambridge: Cambridge University Press.

Trinkaus, Erik. 2005. "Early Modern Humans." *Annual Review of Anthropology* 34(1):207–230. http://dx.doi.org/10.1146/annurev.anthro.34.030905.154913.

van Andel, T. H., S. W. Davies, and B. Wening. 2003. "The Human Presence in Europe during the Last Glacial Period I: Human Migrations and the Changing Climate." In *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*, ed. T. H. van Andel and S. W. Davies, 31–56. Cambridge: McDonald Institute for Archaeological Research.

Voisin, J.-L. 2006. "Speciation by Distance and Temporal Overlap: A New Way of Understanding Neanderthal Evolution." In *Neanderthals Revisited: New Approaches and Perspectives*, ed. K. Harvati and T. Harisson, 299–314. New York: Springer. http://dx.doi.org/10.1007/978-1-4020-5121-0_17.

Wall, Jeffrey D., Kirk E. Lohmueller, and Vincent Plagnol. 2009. "Detecting Ancient Admixture and Estimating Demographic Parameters in Multiple Human Populations." *Molecular Biology and Evolution* 26(8):1823–1827. http://dx.doi.org/10.1093/molbev/msp096.

White, J. Peter, and David H. Thomas. 1972. "What Mean These Stones? Ethno-taxonomic Models and Archaeological Interpretations in the New Guinea Highlands." In *Models in Archaeology*, ed. David L. Clarke, 275–308. London: Methuen.

Wobst, H. Martin. 1974. "Boundary Conditions for Paleolithic Social Systems: A Simulation Approach." *American Antiquity* 39(2):147–178. http://dx.doi.org/10.2307/279579.

Wolf, Eric R. 1990. "Distinguished Lecture: Facing Power—Old Insights, New Questions." *American Anthropologist* 92(3):586–596. http://dx.doi.org/10.1525/aa.1990.92.3.02a00020.

Wolpoff, Milford H., B. Mannheim, A. Mann, John Hawks, Rachel Caspari, Karen Rosenberg, David Frayer, George Gill, and Geoffrey Clark. 2004. "Why Not the

Neandertals?" *World Archaeology* 36(4):527–546. http://dx.doi.org/10.1080/00438240 42000303700.

Zilhão, João. 2006. "Chronostratigraphy of the Middle-to-Upper Paleolithic Transition in the Iberian Peninsula." *Pyrenae* 37:7–84.

Zilhão, João. 2007. "The Emergence of Ornaments and Art: An Archaeological Perspective on the Origins of Behavioral 'Modernity.'" *Journal of Archaeological Research* 15(1):1–54. http://dx.doi.org/10.1007/s10814-006-9008-1.

Zilhão, João, and Francesco d'Errico, eds. 2003. *The Chronology of the Aurignacian and of the Transitional Technocomplexes: Dating, Stratigraphies, Cultural Implications*. Lisbon: Instituto Portugues de Arqueologia.