How Did Hominins Adapt to Ice Age Europe without Fire?

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Online enhancements: supplemental figures

Analyses of archaeological material recovered from several Middle Paleolithic sites in southwest France have provided strong corroborating data on Neanderthal use of fire. Both direct and indirect data show that Neanderthals in this region were frequently and/or intensively using fire during warmer periods, but such evidence declines significantly in occupations that took place during colder periods. One possible explanation for this pattern is that it reflects the inability of Western European Neanderthals to make fire, simply because natural sources of fire occur much more frequently during warmer climatic periods. Regardless of the explanation, the long periods of diminished evidence of fire shows that, unlike modern humans, these hominins were not obligate fire users, and this fact in itself raises important questions of how they adapted, physiologically and/or technologically, to the generally harsh glacial conditions of the middle latitude of Europe and to reduced energy returns typical of raw food. As a corollary, it also raises questions regarding their need for and use of fire during the warmer periods.

Throughout history, pyrotechnology, a uniquely human technological innovation, has been seen as a major factor in allowing humans to adapt to a wide range of environmental circumstances. But as noted recently by Shimelmitz et al. (2014:196), "only when fire use became a regular part of human behavioral adaptations could its benefits be fully realized and its evolutionary consequences fully expressed." Recently a series of papers was published (Aldeias et al. 2012; Goldberg et al. 2012; Sandgathe et al. 2011*a*, 2011*b*) looking at the evidence for combustion features at two sites in southwest France, Roc de Marsal and Pech de l'Azé IV. At both sites two patterns were apparent. First, there were long periods of time when, in spite of extensive evidence for ongoing occupation, evidence for the use or presence of fire was lacking. Second, as indicated by the dates and faunal remains, these periods of little or no use of fire reflected a time of increasingly cold conditions. Given an abundance of evidence for fire use earlier in the sequences of both sites during the warmer periods of MIS 5, the lack of evidence during the colder periods was especially surprising. Earlier, we suggested (Sandgathe et al. 2011*a*) that these European hominins lacked the ability to start fires, relying instead on natural fires. This suggestion was based on the fact that most wildfires are caused by lightning strikes and that lightning occurs much more frequently during warmer and wetter periods and more rarely during cold, dry periods. Regardless of the reason for the long hiatus, however, if fire were not being used during long periods of occupation at these sites, this raises important questions regarding the role of fire in the overall

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 0011-3204/2017/58S16-0011$10.00. DOI: 10.1086/692628

adaptation of these hominins to the colder conditions of MIS 4 and MIS 3. Some of these questions will be addressed later in this paper. First, however, it is important to review the evidence from these two sites and others that have been studied subsequently, taking into account some results of recent laboratory experiments on the transfer of heat from surface fires to underlying sediments (Aldeias 2017; Aldeias et al. 2016).

Evidence for Presence and Absence of Fire at Pech de l'Azé IV and Roc de Marsal

Pech de l'Azé IV (Pech IV) and Roc de Marsal are two Mousterian cave sites in the Dordogne region of southwest France (fig. A1; figs. A1–A7 available online) recently excavated by the same multidisciplinary team from 2000 to 2010 (Dibble et al. 2009; McPherron, Soressi, and Dibble 2001; Sandgathe et al. 2008; Turq et al. 2009, 2011). Both sites span the period of time from mid to late MIS 5 into MIS 3. At both sites there is clear evidence for fire use in the basal layers and very limited evidence of it in the upper layers.

Pech IV contains several major geological strata of Pleistocene-age sediments (fig. A2). The lowermost, Layer 8, lies directly on bedrock (see Dibble et al. 2009) and is dated by thermoluminescence (TL) and optically stimulated luminescence (OSL) to approximately 95 ± 5 kya, or MIS 5c (Gibbard and van Kolfschoten 2005; Jacobs et al. 2016; Richter et al. 2012; Winograd et al. 1997). In keeping with these dates, the associated fauna also suggests a warm, humid climatic regime (Dibble et al. 2009; Laquay 1981; Niven 2013). Evidence for fire, including clear organic- and ash-rich units, burned bone, burned lithics, and rubefied (reddened) sediments is abundant in this layer.

In the overlying layers, there is little direct evidence of fire. Following the heavily disturbed Layer 7, Layer 6 is also associated with a faunal assemblage (fig. A3) that reflects a relatively temperate wooded environment and dates to approximately 77 kya (Jacobs et al. 2016). Although in his earlier excavation of the site, Bordes (1975) did observe some limited traces of fire residues in this layer, our own excavations did not. Following another partially disturbed layer (5B), Layer 5A represents the beginning of a colder period, with a significant increase in reindeer, and this trend to colder conditions continues through Layer 4, which dates to around the beginning of MIS 4. The final Pleistocene layer, Layer 3, is dated by a number of methods (see also McPherron et al. 2012) to around 50 kya, or MIS 3. Virtually no direct evidence of fire was seen in Layers 4 and 5, although burned bones were observed in thin section and some dispersed charcoal occurred in Layer 3.

Another Middle Paleolithic site excavated by the same team is Roc de Marsal, which is located about 20 km west of Pech IV (Turq et al. 2009). Here excavations recognized 13 stratigraphic layers (fig. A4). At the base, Layers 13 through 10 represent locally mobilized sediments from weathering of the limestone bedrock. Layer 10 contains some limited archaeological materials ($n = 129$ lithics), but these may be mostly or entirely intrusive. Artifact densities in Layers 9 through 2 are very high (e.g., $n = 8{,}100$ lithics for Layer 9). Layer 1 is a disturbed Holocene deposit.

Layers 9 through 5 comprise a single lithostratigraphic unit with significant interbedded darker anthropogenic components including major concentrations of ash, charcoal, and burned objects. The faunal data (fig. A5) indicate temperate conditions with an abundance of forest species, suggesting a late MIS 5a date (Marquet in Sandgathe et al. 2008). The overlying layers, Layers 4 through 2, show increasingly colder and drier conditions that would correspond to MIS 3 (see Castel et al. 2016; Guérin et al. 2012, 2016; Sandgathe et al. 2008).

As at Pech IV, direct evidence for fire (see Aldeias 2017) is found not throughout the Roc de Marsal sequence but rather only in the earliest layers. This evidence includes discrete charcoal and ash units, burned or calcined bone, burned lithics, and rubefied sediments (Aldeias et al. 2012; Goldberg et al. 2012). In Layers 7 and 9 localized examples of "stacked" hearths are clearly visible in section view (fig. A6), which indicates that individual hearths were repeatedly constructed in more or less the same location throughout the duration of each of these stratigraphic components. However, not all of the lower layers exhibit direct and intensive evidence for fire and in fact, such evidence alternates: Layers 5, 7, and 9 are rich in such features, while Layers 6 and 8 have little or no direct evidence for them. Abundant hearths in the lower levels of the site were also mentioned in the unpublished notes of the previous excavator, J. Lafille.

To summarize (and as shown in fig. A7), the Middle Paleolithic occupations of Pech de l'Azé IV and Roc de Marsal overlap considerably in time, with initial occupations during a temperate period followed by occupations that occurred during a marked deterioration in climate. At both sites unmistakable hearth features occur in their lower layers and indicate that fire was certainly used at this time, that is, during the time of relatively warmer conditions. But it is equally clear from both sites that fire use was not a constant element in the occupations. At Roc de Marsal, for example, the lower layers seem to alternate between those with clear fire residues and those without. At both sites, however, the upper Mousterian layers (Layers 4 through 2 at Roc de Marsal and Layers 5 and 4 at Pech IV) contain no identifiable fire features, including no concentrations of charcoal or ash and limited quantities of burned bone or flint. At best, very rare and very small fragments (<0.5 cm) of charcoal were noted, and these were primarily confined to Layer 3 of Pech IV (where there are also slightly more heated flints).

How Good Are These Data?

The primary question to be addressed first is whether or not the absence of direct evidence for fire is indeed evidence of fire's absence. With regard to taphonomic factors, strong arguments can be made to show that postdepositional processes were not significant factors in removing the direct evidence.

First of all, at both sites well-preserved fire residues occur both inside the caves as well as beyond what would have been the drip lines at the time of occupation. Therefore the degree of overhead cover is not a factor. Furthermore, there is no evidence in the form of edge damage on the lithic artifacts, preferred orientations of objects, winnowing of smaller objects, or micromorphological studies of the sediments to indicate significant post-depositional disturbances or erosion in the upper layers of either site. Thus, no site formation processes have been identified that could have removed the fire residues.

Nonetheless, even if direct evidence for fire may be have been removed, there should be indirect evidence due to the effects that heat has on lithics, bones, and even the sediment, and all of these should remain (Aldeias 2017). When flint is exposed to heat, color changes can be visible at temperatures starting at 250°C, a distinctive luster begins to develop at temperatures of approximately 350°C, and crazing can occur starting at 320°C (Julig et al. 1999:838 and citations within; Rottländer 1983). These effects are not limited to objects that are actually in the fire. A series of actualistic experiments (Sievers and Wadley 2008; Stiner et al. 1995; Werts and Jahren 2007), as well as more highly controlled ones (Aldeias 2017; Aldeias et al. 2016), has suggested that the heat from fires can transfer to underlying sediments, though exactly how far down and the rate of transfer are dependent on several variables. For example, figure 1 below shows the results of two heat experiments at two different temperatures (950°C and 600°C) at the ground surface, with additional temperature readings at depths of 2, 6, 10, and 20 cm. Even at the cooler surface temperature of 600°C, objects 2 cm below the surface will heat to 300°C within an hour, and at higher temperatures and with longer duration, temperatures as high as 200°C will be reached at even 10 cm below the surface. Thus, even relatively small and/or brief fires will affect underlying objects.

Instead of simply noting the presence of burned flints in the two sequences, the number of proximal and complete pieces showing signs of burning is expressed as a percentage of all proximal and complete pieces (in both cases counts are for pieces larger than 2.5 cm; see fig. 2). At both sites the percentage of burned lithics and fauna decreases through the sequence, reaching minima of 1%–2% in the upper layers. As shown in Sandgathe et al. (2011*a*), the numbers are a function of neither varying sample size nor artifact density. Even if the direct evidence for the combustion features were removed, it is highly unlikely that the same processes would remove the objects that were either in direct association with the fire or embedded in sediments directly below the fire.

At both sites, then, the percentage of burned lithic objects, which is not subject to preservation issues, generally agrees with the direct evidence of fire residues in that the use of fire

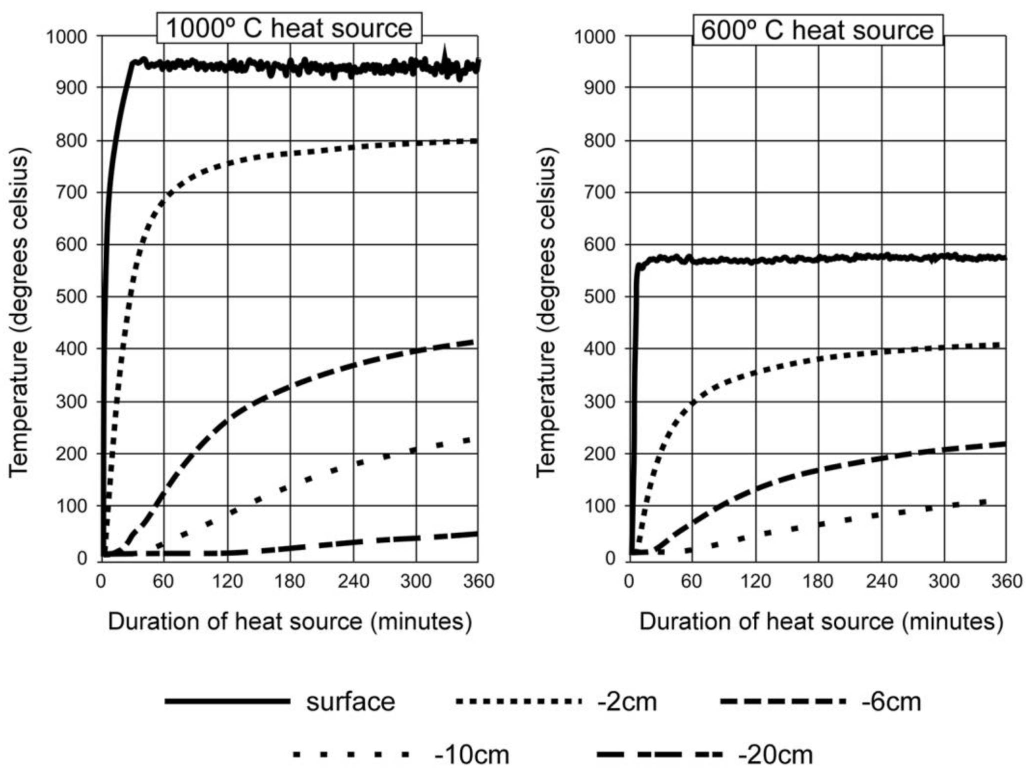

Figure 1. Results of controlled experiments on heat transfer from ground surface down into the substrate (in this case sand). The experiment was run with the surface heat source set at 950°C and again at 600°C. Temperatures were continually recorded at the ground surface and at 2, 6, 10, and 20 cm beneath the heat source (see Aldeias et al. 2016).

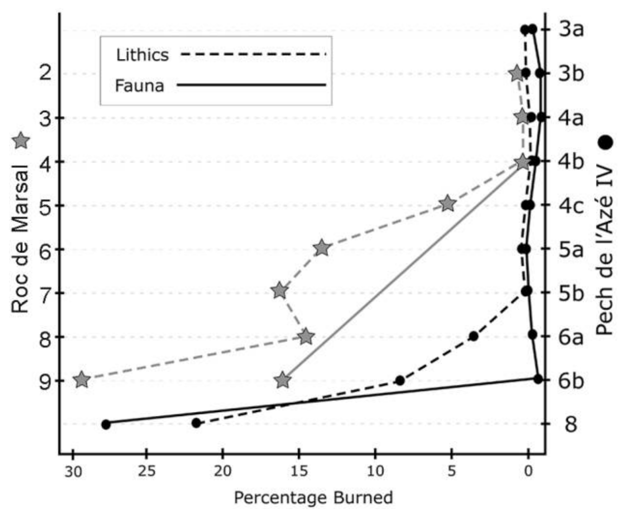

Figure 2. Frequencies of burned lithics (as a percentage of all platform-bearing lithics) in each layer at both Pech de l'Azé IV and Roc de Marsal.

drops off significantly, if not completely, during the later occupations. It can be noted too that the same trends are apparent among the fauna and small finds. Two notable exceptions are Layers 6 and 8 at Roc de Marsal, where the percentage of heated flints remains high even though there are no visible hearths in these layers. Although it might be suggested that the elevated percentage of heated flints might represent some vertical movement of lithics, there is currently no micromorphological or field evidence for this. Likewise, generally there are some clear time-related patterns in these layers (9–5) that are not expected if substantial mixing had occurred. The far more likely explanation is that heat from fires in overlying layers moved down through the sediments (i.e., the fires in Layers 5 and 7 modified some of the lithics of Layers 6 and 8, respectively; see Aldeias 2017; Aldeias et al. 2016).

It is also unlikely that during the later occupations fires were constructed at other lateral and as yet unexcavated locations at the sites. At Roc de Marsal, the majority of the site has now been excavated (when combining our own excavations with the previous excavations of Lafille). The morphology of the cave in relation to the remaining sediments makes it very unlikely that evidence of fire remains to be detected there by some future excavation. Our own excavations extended along the entire length of deposits from well in front of the drip line to the rear of the cave, as well as laterally across the width of the cave. If there had been any other fire residues (including burned flints), they would have been detected. This issue is a bit more problematic at Pech de l'Azé IV because our own excavations were concentrated on the western section of the excavated area, that is, the side that is closest to the original (and now collapsed) entrance of the cave (Turq et al. 2011). However, observation of the eastern section remaining from Bordes's (1975) earlier excavation clearly indicates the same level of burning in the basal deposits and a similar lack of such traces in the upper layers. Furthermore, analysis of Bordes's entire collection, which represents a much larger area than our own, shows an identical pattern of decreasing percentages of burned lithics through the sequence (see fig. 2). Moreover, these two excavations were concentrated directly in the middle of the major part of the deposits, as determined by topographic relief.

In summary, both Pech IV and Roc de Marsal have excellent preservation, and the correlation is high between the presence or absence of direct evidence for fire (i.e., ash, charcoal or burned bone, rubefied sediments) and the indirect evidence of burned artifacts (see Aldeias 2017). This relationship is not surprising given the causal nature of one to the other, but it means that the presence of fire can be detected even though various taphonomic processes may have obliterated the more direct evidence. Therefore, in the absence of both direct and indirect evidence, the conclusion that fire was not present at particular times during the occupation of these two sites is much stronger than it would be by relying on the direct evidence alone. It would seem unavoidable to conclude, therefore, that, while fire was being used frequently and/or intensely during the earlier occupations, its use drops to near zero in the upper occupations. While evidence for the use of fire does not disappear entirely, on the basis of the very low frequency of burned flints, this evidence represents an insignificant aspect of these later occupations.

How Can We Explain These Patterns?

What has been shown is that at these two sites fire was absent over significant periods of time, potentially over thousands of years of repeated occupation and use of the sites. Is it possible to argue that how these sites were used changed over time? The answer to this question would appear to be no. For both Pech de l'Azé IV and Roc de Marsal, while understanding the duration and intensity of individual occupation events is difficult at best, it is clear that these were both consistently used as occupation sites. The significant concentrations of stone tools (made and used in all components of both sites) and heavily butchered faunal remains throughout the entire sequences (Castel et al. 2016; Hodgkins et al. 2016; Niven 2013) are evidence of this. It would be very difficult to argue that at times, the sites served more ephemeral purposes (e.g., that they were kill sites or secondary butchery sites) where the use of fire may have been less likely. In addition, the alternating pattern in the basal layers of Roc de Marsal—with fires present in Layers 5, 7, and 9 and absent in Layers 6 and 8—provides another argument against fires being associated with only certain kinds of site use (see figs. 3, 4). Both the burned and unburned layers show virtually identical technological and typological characteristics.

Although faunal data are incomplete for Roc de Marsal, it is clear that while the prey species varies throughout both site sequences, the kinds of anatomical elements represented are virtually indistinguishable in layers with fire versus those

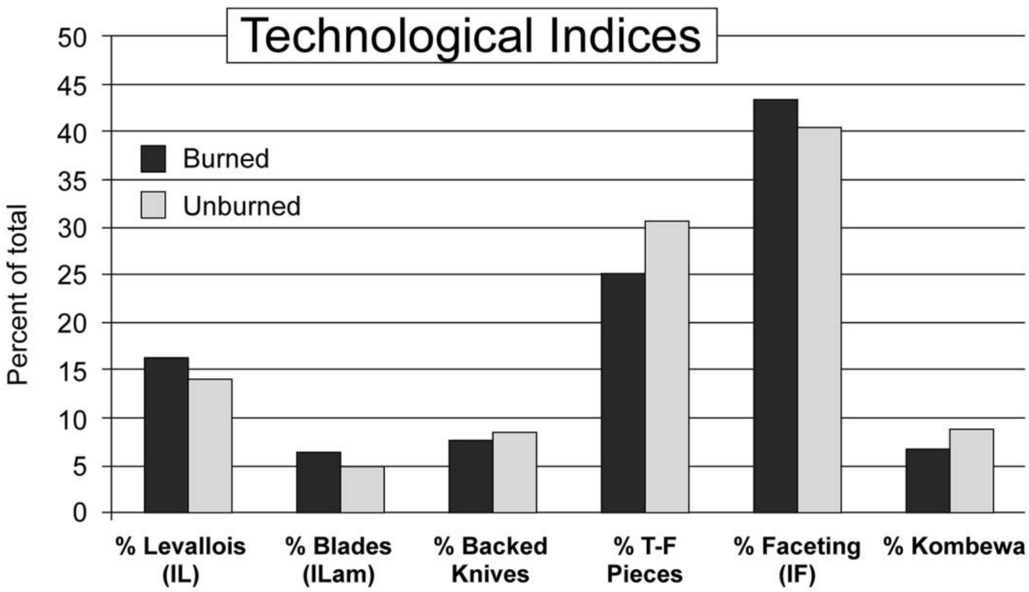

Figure 3. Percent frequencies of technological types in burned layers (layers with significant evidence for use of fire) compared to unburned layers (layers with little or no evidence for use of fire) at both Pech de l'Azé IV and Roc de Marsal.

without (see fig. 5; Castel et al. 2016; Hodgkins et al. 2016; Dibble et al. 2017, pt. 3). Again, this suggests that the presence or absence of fire does not appear to reflect changes in site use. Likewise, while there is no evidence either for or against the use of fire for cooking, the arguments of Wrangham (2009) concerning the benefits that could be derived from cooking suggest that if fire were available, it would tend to be used for this purpose under all circumstances. In other words, it would be difficult to argue that these Neanderthals simply changed their tastes in food preparation for millennia.

Since one of the primary uses of fire ethnographically is for warmth, it is especially ironic that in these two sites the use of fire drops off significantly during colder periods. This pattern is repeated at several sites in the region where we have comparable data. At Combe-Capelle Bas, which was excavated and analyzed using identical techniques, there was also no direct

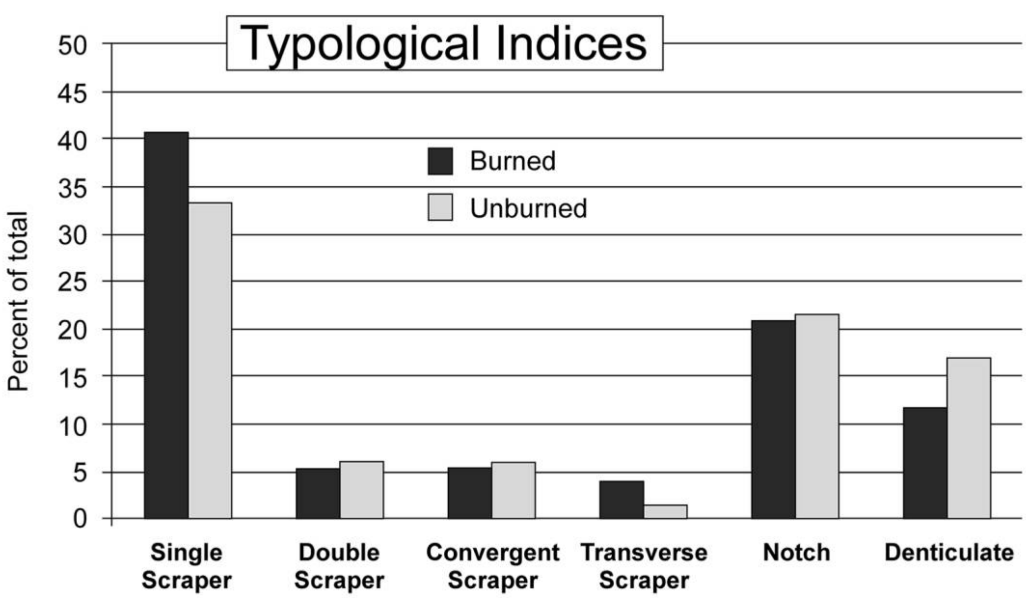

Figure 4. Percent frequencies of major tool types in burned layers (layers with significant evidence for use of fire) compared to unburned layers (layers with little or no evidence for use of fire) at both Pech de l'Azé IV and Roc de Marsal.

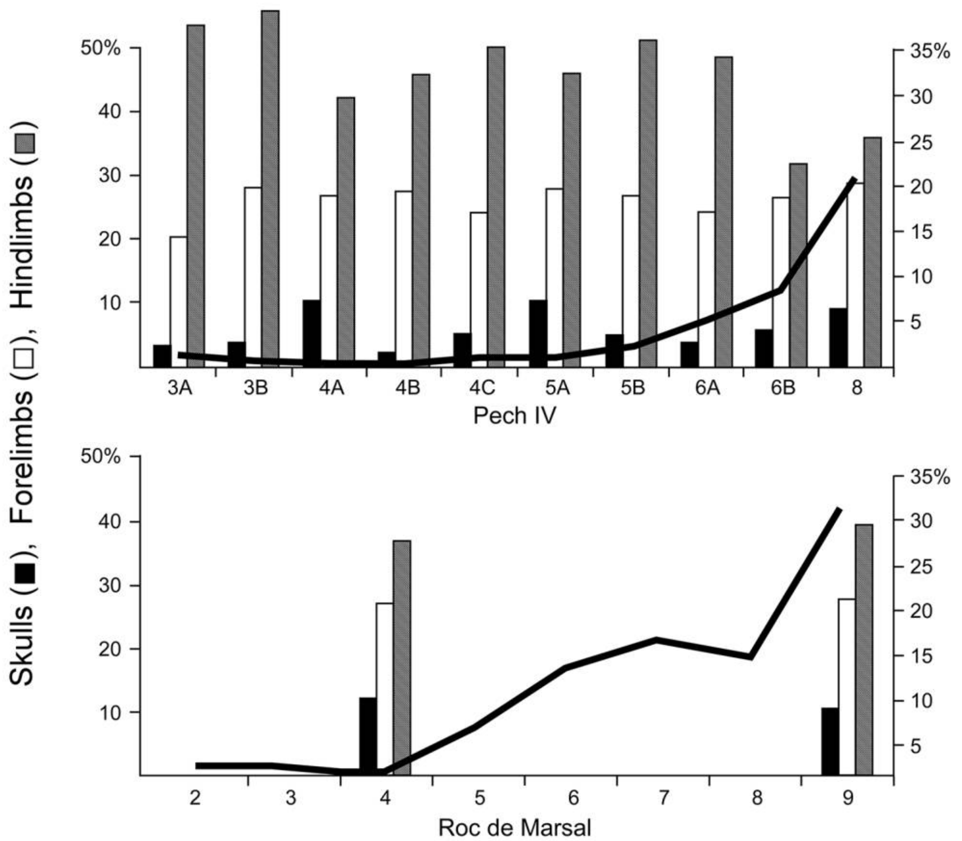

Figure 5. Relative frequencies of different anatomical components (skull portions, forelimb portions, and hind limb portions) compared to frequencies of burned lithics in each layer at both Pech de l'Azé IV (Pech IV; Niven 2013; L. Niven, personal communication) and Roc de Marsal (Hodgkins et al. 2016; J. Hodgkins, personal communication).

evidence of fire residues, and the percentage of burned flints remained at <2% for the entire sequence (Dibble and Lenoir 1995). This site, which contains Quina Mousterian assemblages, has been dated to MIS 3 (Valladas et al. 2003) and is thus contemporary with the nonfire occupations from Pech de l'Azé IV and Roc de Marsal. Similarly, the Quina layers at Jonzac and La Quina (Bierwirth 1996; McPherron et al. 2006; Niven et al. 2012) are associated with very high percentages of reindeer, and the percentage of heated flints is less than 0.5%. At Jonzac, the Quina layers have been TL dated to MIS 4 (Richter et al. 2013). In the overlying layers at these two sites, heated flints are never more than 4% of the assemblage, and they generally are much less. A similar pattern is noted at La Ferrassie, which exhibits Levallois industries similar to those at Roc de Marsal, little evidence of fire, and again occupations occurring during cold periods (Guérin 2015).

One of the best sites in the region for testing a correlation of fire and climate is Combe Grenal, where some 64 layers likely represent deposits from late MIS 6 through MIS 3. Data from Bordes's collection (the site is currently being reexcavated) also indicates a correlation between climatic regime and frequency of fire use. This is based on percentages of burned flints recorded for 23 of the 64 layers identified by Bordes (Bordes, Laville, and Paquereau 1966). As can be seen in table 1, there is a general tendency, with some exceptions, for frequencies of burned flints to increase in those layers that were identified, through associated fauna (see Chase 1986) and sedimentology (Guadelli and Laville 1988), as being associated with warmer and wetter climatic periods. These data provide some of the comparable quantitative data called for by Sorensen (2017) but contradict his conclusions for this important site based on the number of observations (e.g., presence of purported fires in particular layers, heated bedrock, burned bones taken for AMS dating, TL samples taken for dating, etc.). More work is needed to reconcile these differences, but it should be emphasized that comparable proxies on relative scales are preferable to presence or absence data and that techniques such as micromorphology and FTIR (Fourier transform infrared spectroscopy) are preferable for identifying fire features. This said, we also acknowledge that curation issues with the Combe Grenal collection may impact proxies based on counting heated flints (Dibble et al. 2009).

We cannot exclude the possibility that all of these nonfire occupations were limited to summer months and that what we are seeing at these sites is a switch in seasonality wherein southwest France was only occupied during warm months. It

Table 1. Climate and frequency of burned flints in sampled layers of the Middle Paleolithic site Combe Grenal in southwest France

Layer	Climate	% lithics burned	*N* lithics
1–4	Very cold, very dry	No data	No data
5	Very cold, very dry	.0	19
6	Very cold, very dry	.0	170
7–8	Less cold, humid	.0	430
9	Cold and dry	1.9	160
10	Cold and dry	No data	No data
11–13	Less cold, humid	No data	No data
14	Very cold, very dry	1.9	1,227
15–16	Very cold, very dry	No data	No data
17	Less cold, humid	4.5	1,099
18–19	Less cold, humid	No data	No data
20	Mild, humid	21.7	1,395
21–22	Mild, humid	No data	No data
23	Very cold, very dry	1.2	1,490
24–25	Very cold, very dry	No data	No data
26–35	Cold and humid	No data	No data
36–37	Cold, very dry	No data	No data
38	More mild, humid	6.9	1,643
39	More mild, humid	No data	No data
40	Cold and very dry	.8	491
41–43	Temperate and humid	.3	725
44–49	Cold and dry	No data	No data
50a	Temperate and humid	11.8	678
50	Temperate and humid	14.7	2,878
51	Temperate and humid	10.6	1,710
52	Temperate and humid	15.5	1,255
53	Cold and humid	29.0	93
54–55	Cold and humid	No data	No data
56–57	Cold and dry	No data	No data
58	Less cold, humid	.0	402
59	Cold and very dry	No data	No data
60–61	Cold and very dry	1.2	1,294
62	Less cold, humid	.0	83
63–64	Cold and dry	No data	No data

Note. Climate descriptions from Guadelli and Laville (1988) and Chase (1986).

would be difficult, however, to imagine that these sites were consistently used only in one season for the tens of thousands of years represented by those layers that have little evidence for fire. That said, even during the warm months, conditions were still far cooler than today's and, again, modern hunter-gatherers in even substantially warmer environments still rely on fire to warm themselves, especially at night.

For all of these reasons, it was suggested by Sandgathe et al. (2011*a*) that the presence or absence of fire was due to the inability to start fires and, therefore that fire would be more likely to be present when it was naturally available. If the primary natural source of fires is lightning strikes, then the apparent pattern seen in these two sites—fires present during warm periods, absent during cold periods—would reflect the fact that lightning strikes occur more frequently in warmer and more humid climates and much less frequently in colder and drier ones.

Obviously, arguments based on negative evidence are fraught with difficulties, and admittedly, there are many potential explanations—both behavioral and natural—for an absence of evidence for fire in these sites. The hypothesis that this absence is due to an inability to start fires will require quantitative data from many other sites that are adequately dated and for which both indirect and direct evidence for fire is noted (Aldeias et al. 2012; Goldberg et al. 2012; Sandgathe et al. 2011*a*). This is only a hypothesis advanced to explain the cyclical pattern apparent in the data. The more important finding is that fire is not as ubiquitous as it should be, given that virtually all recent hunter-gatherer populations, even prior to access to matches and lighters, used fire daily for a wide range of applications and at almost every location where people spend any time at all. Thus, the main conclusion to be drawn from the evidence at hand is that use of fire by Western European Neanderthals is sporadic at best, and for any particular site—even those with relatively dense or intensive occupations—fire may be virtually absent for long periods of time. What we are suggesting, therefore, is that during the European Late Pleistocene there is simply not enough evidence of fire to assume that Neanderthals used fire, especially for warmth and for cooking, to a degree equivalent to that seen among extant humans. At a minimum, this may mean that fire had a very different role in Neanderthal adaptations in Western Europe than at, say, Kebara, Tabun (Schiegl et al. 1996; Shimelmitz et al. 2014), or Qesem Cave in Israel (Barkai et al. 2017) and that there may have been extended periods of time when fire was not used to a great extent. Thus, the available data we do have for this region of France indicates that Neanderthals were not obligate fire users (contra Sorensen 2017), and such evidence might constitute a significantly different behavioral adaptation than those seen in more recent modern human occupations (see Henry 2017).

Implications for Considering the Role of Fire in Western European Neanderthal Adaptations

The primary focus of this paper is to emphasize the quality of the data presented to show that fire was not present for long periods of time in this particular region. We are not arguing that Neanderthals, as a species, were fire incapable, always ate raw food, and never used fire for heat. Rather we are simply presenting quantitative evidence (rather than simple presence or absence) that at times and for long periods they did not make extensive use of fire. Admittedly, this is based on only a few Middle Paleolithic sites, and given the lack of comparable data available in the literature (see Sandgathe 2017; Sandgathe et al. 2011*b*; Roebroeks and Villa 2011), it is still unknown to what extent this pattern holds true for many other times and places during the Pleistocene. But the evidence available from a number of sites is strong enough to make us question our assumption that once we find evidence of fire in the archaeological record, it automatically means that it was an essential part of human behavior and adaptation from that point forward (cf. Barkai et al. 2017) and throughout the world.

If this assumption is not valid, and the use of fire was much more limited than previously believed, this does raise important questions regarding European hominin behavior and adaptation in the Pleistocene. One of the more important questions concerns the ability of hominins to survive during the colder periods. Among modern human groups, it would be impossible for foragers to inhabit more northerly latitudes without fire unless they had very well-developed clothing and shelter technology. However, anatomically modern humans are relative newcomers to higher latitudes, unlike Neanderthals who, along with their direct ancestors, have a potential time depth in Europe of several hundred thousand years. While it is possible that Neanderthal populations migrated to some extent in response to major climatic changes and did not always inhabit the most northerly European latitudes during colder periods (e.g., Roebroeks 2006; Steegmann, Cerny, and Holliday 2002), the presence of significant numbers of occupations in Europe during full glacial conditions indicates that Neanderthals were adapted to such conditions.

The question is to what extent was theirs a physiological adaptation versus a cultural or technological one? While we do see the advent of bone needles during the Gravettian of late MIS 3 and early MIS 2, evidence for tailored clothing prior to this is virtually nonexistent (Collard et al. 2016). It has been argued that simply draping or wrapping untailored animal hides around a person has very limited thermal effectiveness (e.g., Gilligan 2007; Wales 2012). Although there is ongoing discussion about how much of the difference in morphology between Neanderthals and their African contemporaries is due to active selective pressures and how much is mainly due to random genetic drift (e.g., Weaver, Roseman, and Stringer 2007), it has long been accepted that Neanderthals have significant cold-adapted features such as their short, squat, heavy bodies with shorter, stockier limbs (e.g., Holliday 1997; Ruff et al. 1993; Steegmann, Cerny, and Holliday 2002; Trinkaus 1981).

Assuming that an absence of fire means an absence of cooking, there are also implications for Neanderthal energetics. This is an area where Neanderthals differed significantly from anatomically modern humans and one with behavioral consequences that may have played a role in the replacement of the former by the latter. It is argued that due to their larger body mass and unique shape, Neanderthals would have had a higher basal metabolic rate than anatomically modern humans and therefore a proportionally larger total energy expenditure (e.g., Aiello and Wheeler 2003; Sorensen and Leonard 2001; Steegmann, Cerny, and Holliday 2002). Conservative estimates suggest a 10% difference between Neanderthals and middle Upper Paleolithic humans (Churchill and Rhodes 2009; Froehle and Churchill 2009; Macdonald, Roebroeks, and Verpoorte 2009). This estimate is based on the premise that Neanderthals and anatomically modern humans derived the same caloric benefits from the food consumed, and it means that if Neanderthals and early anatomically modern humans had the same diet composition, Neanderthals would have been obliged to consume more. This in turn may have necessitated more frequent moves (Macdonald, Roebroeks, and Verpoorte 2009; Verpoorte 2006).

Moreover, given that cooking raises the nutritional and energetic value of food (e.g., Carmody and Wrangham 2009; Wrangham 2009), then an inability to cook their food for extended periods would further increase the amount of calories required by Neanderthals to meet their daily energetic needs. Lower overall energy requirements could have given anatomically modern humans competitive advantages over Neanderthals in terms of reproductive success and demographic expansion (Froehle and Churchill 2009). There is considerable evidence that Middle Paleolithic populations relied particularly heavily on sources of fat in their diet. This is especially apparent in the breakage of long bones, presumably for the extraction of marrow, and the intense, intentional fragmentation of cancellous bone, presumably to extract bone grease (Castel et al. 2016; Hodgkins et al. 2016). In the face of increased caloric requirements for Neanderthals, and especially increased fat requirements, cooking meat may have taken on an especially important role under certain conditions.

Besides increasing net caloric returns, cooking can also reduce the danger presented by bacterial and parasitic loads in meat. As the evidence from sites like Roc de Marsal and Pech IV clearly indicates that meat was not always cooked, it seems likely that consumption of raw meat was relatively common during the Lower Paleolithic and during at least certain periods in the Middle Paleolithic. This might not present any major problems during colder climatic periods when meat acquired by hominins would tend to remain unspoiled longer and, during some cold periods in some regions, was likely more easily acquired and in greater quantities due to the prevalence of large numbers of herd animals like reindeer, horse, and bison. During warmer climatic periods when the fauna was dominated by mainly smaller and less gregarious woodland species (like red deer, roe deer, and wild pigs), meat was likely generally less available (Hodgkins et al. 2016). Meat would also tend to spoil faster during warmer periods, and it is possible that simple meat preservation techniques, like smoking, could have been practiced. However, there is no evidence for such practices, and it may be that, if meat spoilage was a consideration for Neanderthals, they were simply cooking it to make it safe for consumption. Along with increased availability of natural fire, such a pattern of behavior would also help explain the apparent association between increased fire use and warmer climatic periods.

Conclusions

Much of the current evidence suggests that as recently as the latter half of the Late Pleistocene, Neanderthals were not using fire all the time, especially not during cold climatic periods. This raises important questions about how these hominins were able to adapt to high-latitude glacial conditions both in terms of their physiology and their technology.

Roebroeks and Villa (2011) make an important point that there is no evidence supporting the idea that fire was requisite to the initial colonization of Europe. Although they conclude that the use of fire became "habitual" during the European Middle Paleolithic, the data from Roc de Marsal and Pech IV show that hominins occupied or used these sites for long periods of time without using fire. Whether or not these results are applicable to the entire European Middle Paleolithic is currently unknown, since quantified data (rather than simply presence or absence), both direct and indirect, on the degree of fire use is largely unreported (see Sandgathe 2017). The same problem applies to the Upper Paleolithic as well. For a long time, it has been assumed that once the advantages of fire were discovered, its use would spread quickly. But as the evidence is examined more closely, and as we try to evaluate the degree of fire use, it is becoming fair to say that we simply do not know when fire use became a regular, integral, and, eventually, necessary component of hominin adaptations.

Acknowledgments

This paper is based on research funded by the National Science Foundation, the Leakey Foundation, the Conseil General de la Dordogne, the Max Planck Society, the Service Régional de l'Archéologie (Agquitaine), and the University of Pennsylvania Research Foundation and University of Pennsylvania Museum. It was also made possible by the considerable support of the National Museum of Prehistory at Les Eyzies, France, in particular the director, Cleyet-Merle, and curator, Stephen Madeleine, for helping us access collections held there. Thanks also to our colleague Alain Turq for all of his help and support and to Virginie Sinet-Mathiot for running our field lab. We would like to thank the Wenner-Gren Foundation for providing the funding for the symposium that led to this volume and give a very special thank you to Leslie Aiello, president of the Wenner-Gren Foundation, and Laurie Obbink, conference program associate, for organizing and hosting the symposium so effectively and so graciously. We also acknowledge the constructive reviews of two anonymous referees.

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