Climate-mediated shifts in Neandertal subsistence behaviors at Pech de l’Azé IV and Roc de Marsal (Dordogne Valley, France)

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Abstract

Neandertals disappeared from Europe just after 40,000 years ago, and some hypotheses ascribe this to an end result of numerous population crashes associated with glacial cycles in the late Pleistocene. The goal of this paper is to test the hypothesis that glacial periods stressed Neandertal populations. If cold climates stressed Neandertals, their subsistence behaviors may have changed—requiring intensified use of prey through more extensive nutrient extraction from faunal carcasses. To test this, an analysis of Neandertal butchering was conducted on medium sized bovid/cervid remains composed of predominately red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), and roe deer (*Capreolus capreolus*) deposited during global warm and cold phases from two French sites: Pech de l’Azé IV (Pech IV, Bordes’ excavation) and Roc de Marsal (RDM). Analysis of surface modification on high survival long bones and proximal and middle phalanges, demonstrates that skeletal elements excavated from the cold levels (RDM Level 4, Pech IV Level I2) at each cave have more cut marks and percussion marks than elements from the warm levels (RDM Level 9, Pech IV Level Y-Z) after controlling for fragment size. At both sites, epiphyseal fragments are rare, and although this pattern can result from carnivore consumption, carnivore tooth marks are almost nonexistent (< 0.1%). Alternatively, processing epiphyseal ends for bone grease may have been a Neandertal survival strategy, and epiphyses were more intensively percussed in cold levels than in warm levels at both RDM and Pech IV. The exploitation of low marrow yield elements such as phalanges does not show a consistent pattern relating to climate, but may have been a general Neandertal behavioral characteristic, suggesting that these hominids were regularly on the edge of sufficient nutrient availability even during interglacials. Overall, the faunal assemblages from Roc de Marsal and

Pech IV provide some support for the hypothesis that Neandertals were processing faunal remains more heavily during glacial periods, suggesting a response to increased nutritional stress during colder time periods.

Introduction

The ability of Neandertals to cope with the oscillating climate of the late Pleistocene and the extent to which these changes affected local Neandertal habitats remains unclear. Within the paleoanthropological literature, a dichotomy exists between studies of morphology and paleoecology. Neandertal physiology suggests they were optimally adapted to cold climates (Holliday, 1997; Pearson, 2000; Weaver, 2003, 2009), but archaeologically-based studies indicate that Neandertals often inhabited temperate woodland environments (Shea, 1998, 2007; Boyle, 2000; Davies and Gollop, 2004; Hallin et al., 2012) with large portions of the population dying off during cold glacial periods, suggesting that such times were indeed stressful for Neandertals (Finlayson and Carrion, 2007; Hublin, 2009; Hublin and Roebroeks, 2009). Understanding the influence that climatic instability had on Neandertals is critical for reconstructing the behaviors and demographic patterns of our closest fossil relatives and possibly identifying factors that contributed to their extinction, which appears to have occurred just after 40,000 ka (Higham et al., 2014).

It is now widely recognized that global cold events occurred in rapid succession toward the end of the Pleistocene, especially during MIS 3 (Bond et al., 1993; Dansgaard et al., 1993; Genty et al., 2003; Augustin et al., 2004; Jouzel et al., 2007; Genty et al., 2010), causing environmental fluctuations such as vegetation change that would have affected mammalian density on the landscape (d'Errico and Sánchez Goñi, 2003; Finlayson, 2004; Finlayson et al., 2004; Finlayson and Carrion, 2007; Delagnes and Rendu, 2011). Population levels of large European mammals, specifically mammoths (*Mammuthus primigenius*), woolly rhinos (*Coelodonta antiquitatis*), and large carnivores, decreased at the end of the Pleistocene,

supporting the notion that climatic changes were severe even for cold-adapted mammals (Stewart et al., 2004; Finlayson and Carrion, 2007). It has been hypothesized that this climatic instability and quick succession of multiple cold events contributed to Neandertal extinction by reducing the carrying capacity of the environment, inducing nutritional stress in Neandertal populations, and never allowing them to recover between climatic fluctuations (Finlayson and Giles Pacheco, 2000; Finlayson et al., 2001, 2004, 2008; Finlayson, 2004; Hublin and Roebroeks, 2009). This paper presents a taphonomic analysis of faunal assemblages from the sites of Pech de l'Aze IV and Roc de Marsal in southwestern France and provides a zooarchaeological test of the "climate stress" hypothesis for this region by examining shifts in Neandertal butchering behaviors between glacial and interglacial periods.

Background

The hypotheses that Neandertal extinction was driven in part by the rapid succession of climate changes at the end of the Pleistocene assumes that glacial cycles caused local environmental shifts that negatively impacted Neandertal populations. Hublin and Roebroeks (2009) have argued that Neandertal populations in northern Europe repeatedly died out during times of glaciation, and repeated bottlenecks may have caused the low genetic diversity observed in mitochondrial DNA sampled from Neandertal fossils. Interestingly, Hublin and Roebroeks (2009) have pointed out that this pattern of low genetic diversity in mtDNA is mirrored by carnivores (e.g., otters, wolverines, and lynxes) from northern Europe (Cassens et al., 2000; Walker et al., 2001; Hellborg et al., 2002). Such a pattern suggests that glacial cycles negatively impacted the carnivore guild, probably via the effect that climatic shifts had on their prey

species. In France, a clear pattern of species turnover exists, which signals an ecological shift from glacial to interglacial cycles. The relative abundance of particular species found at archaeological sites changed through time, with *Rangifer* and *Bison* more common during colder time periods and *Cervus* and *Capreolus* more common during warmer interglacials (Laquay, 1981; Delpech, 1983; Grayson and Delpech, 1998; Grayson et al., 2001; Costamagno et al., 2006; Morin, 2008; Delagnes and Rendu, 2011; Discamps et al., 2011; Guérin et al., 2012). Southwestern France has been continuously inhabited from 350 ka to the present (Serangeli and Bolus, 2008; Hublin and Roebroeks, 2009; Mellars and French, 2011). The Pleistocene climate in this region was not severe enough to cause the same population extinctions as in northern Europe. Nevertheless, paleoecological evidence indicates that this region was affected by climate cycles. Mean Annual Temperature (MAT) estimates for MIS 4, are reconstructed at -4 to 6°C, which is 10–15° lower than the current MAT for southwestern France (Van Andel and Tzedakis, 1996). An expansion of global ice sheets during this time caused a decrease in precipitation with an estimated average precipitation rate of 220–370 mm/year, which is 650–800 mm less than current rates (Pons et al., 1992; Van Andel and Tzedakis, 1996). During the stable warm phase of MIS 3 (59–45 ka), temperature estimates are reconstructed as -4 to 0° C in the winter and 12 to 18° C in the summer (Barron et al., 2004).

It is important to note that during glacial periods, southwestern France appears to have become geographically isolated. Environments immediately to the north and south of this region became ecologically hostile. In southern France, the region that parallels the northern extent of the Pyrénées became arid and sparsely vegetated (Bruxelles and Jarry, 2011). Pollen records from sites close to the Mediterranean Sea and from the central Pyrénées show a dominance of steppe or semi-desert vegetation (Jalut et al., 1992). In fact, the Landes de Gascogne, an area

bordering the Atlantic Ocean, became a desert populated by sand dunes (Bertran, 2013). Similarly, in northern France, a lack of pollen recovered from sediments deposited during full glacial periods suggests that northern France was largely unvegetated or tundra during these time periods, which would have made it uninhabitable for many animal species (Fletcher et al., 2010).

Given the wide-spread environmental effects that glacial cycles had on local environments throughout France (and Europe broadly), it is probable that either local Neandertal habitats would have experienced a reduction in primary productivity (and therefore herbivore populations) or late Pleistocene hominids would have crowded into refugium areas resulting in increased population density (a scenario strongly argued against by Hublin and Roebroeks, 2009). However, either case could have resulted in a reduction of food resource abundance capable of inducing nutritional stress. If true, such nutritional stress might have influenced Neandertal subsistence behaviors as a means of compensation. Although an appropriate behavioral response to reduced resource availability could have ultimately moderated stress on Neandertals (possibly even rectifying the situation in the short term), it would nevertheless support the hypothesis that their populations were pushing the limits of their local habitats.

Zooarchaeological assessment of nutritional stress

As explained by King and Murphy (1985: 955), “An animal's nutritional status depends on (1) nutrient accessibility, (2) nutrient demand, and (3) physiological, metabolic, morphological, and behavioral compensations that avert or minimize discrepancies, if any, between the first two.” It is expected that if Neandertals experienced nutritional stress, they

would have modified their behaviors to increase nutrient accessibility and keep pace with nutrient demand. The challenge in detecting nutritional stress is in finding an archaeologically-visible manifestation (a proxy) of those behavioral changes that signal reduced availability of food resources. Elevated butchering intensity (the amount of effort involved in extracting nutrients) should correspond with level of nutritional stress induced by limited game availability because it suggests that hominids made an effort to maximize caloric extraction. Indeed, ethnographic observations (Jenness, 1959; Oswalt, 1966; Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988; Monahan, 1998; Nilssen, 2000) generally indicate that butchering intensity increases when hunter-gatherers are under stress during times of food scarcity. Such behavioral modifications include processing bones for marrow (i.e., by breaking them open), including bones with low marrow yields such as phalanges (Bar-Oz and Munro, 2007), heavily processing epiphyses (Outram, 1999, 2001; Marean, 2005, 2007), and cutting all meat from the bone (Binford, 1978, 1981; Nilssen, 2000).

Researchers interested in the subsistence behaviors of Pleistocene hominids have typically focused on the patterns, placement, and frequency of cut marks and percussion marks on faunal remains to infer butchering practices and butchering intensity (Binford, 1981, 1985; Chase, 1989; Stiner, 1991, 1994; Chase et al., 1994; Grayson and Delpech, 1994, 2003; Mellars, 1996; Marean, 1998; Marean and Kim, 1998; Marean and Assefa, 1999; Boyle, 2000; Burke, 2000a, b; Conard and Prindiville, 2000; Gaudzinski, 2000; Patou-Mathis, 2000; Costamagno et al., 2006). Referring to work with the Nunamuit, Binford (1988:127) states, “My experience suggests that the number of cut marks, exclusive of dismemberment marks, is a function of differential investment in meat or tissue removal. When a butcher who is filleting meat seeks to get all the adhering tissue off the bone, there will be many cut marks; if little effort is made to

clean the bones relatively few cut marks result.” Other indicators of intensive nutrient extraction, such as the exploitation of the relatively difficult-to-access bone marrow, leaves clear signals on bone in the form of fresh breaks and percussion marks from hammer stones (Binford, 1981; Bunn, 1981, 1989; Lyman, 1987; Blumenschine and Salvaggio, 1988, 1991; Capaldo and Blumenschine, 1994; Blumenschine, 1995; Blumenschine et al., 1996; Outram, 2001; Domínguez-Rodrigo and Barba, 2006; Pickering and Egeland, 2006).

One potential caveat is that an exact one-to-one correlation might not exist between the number of cutting or percussing motions and the number of modification marks (Egeland, 2003; Pickering and Egeland, 2006). Pickering and Egeland (2006) point out that a number of factors could inhibit the production of surface modification marks, including the presence of thick portions of periosteum and meat that protect the bone from the tool being used. However, restricting comparisons among samples to animals of similar size and anatomy should mitigate this problem to some degree by ensuring that the animals would have been butchered in a similar manner. Additionally, comparing the number of butchering marks between levels within a site (while controlling for differences among archaeological sites) further accounts for confounding variables. Under these conditions, we assume that a higher frequency of modification marks on long bones between levels at a given site indicates that relatively greater effort was invested in extracting nutrients from carcasses at those time periods.

Surface modification data combined with evidence of the exploitation of difficult-to-access aspects of a carcass, as well as epiphyseal ends for fat and grease extraction, would increase confidence in the inference of intensified butchery likely to occur during times of stress (Outram, 1999, 2001; Egeland and Byerly, 2005; Marean, 2005; Bar-Oz and Munro, 2007; Jin and Mills, 2011). For example, this would include evidence for the processing of bones of

medium sized ungulates with low nutritional value, such as metapodials with low meat value and phalanges with low marrow yields (Bar-Oz and Munro, 2007; Jin and Mills, 2011). Because epiphyseal ends are subject to taphonomic processes that tend to remove them from the archaeological record, these skeletal components are often rare and thus may be difficult to interpret due to low sample sizes. However, of those remaining, it is expected they should show signs of percussion marks if hominids were processing them for nutrient extraction (Marean, 2005). Combining multiple lines of evidence with analyses of the surface modification frequencies should thus provide a more robust picture of overall butchering intensity.

Archaeological sites investigated

Ideally, studies of Neandertal responses to climate change should be conducted on sites that pre-date modern human entrance into Europe, thereby eliminating competition with other hominids as a confounding factor. Here, we focus on the localized effects of climate change on Neandertal subsistence behaviors through zooarchaeological analysis of medium sized bovid/cervid remains excavated from two cave sites—Roc de Marsal (RDM) and Pech de l’Azé IV (Pech IV; Bordes’ 1970–1977 excavation). These sites are located in the Dordogne Valley and date between 100,000–45,000 years ago, thus sampling a long sequence of Neandertal occupation before modern humans entered Europe.

Pech de l’Azé IV In 1952, François Bordes discovered a collapsed cave site about 50 meters above a dry valley floor located approximately 2 km from the Dordogne River (Fig.1). Bordes named the site Pech de l’Azé IV (Pech IV), because it is the fourth site found in a cliff that contained the sites of Pech de l’Azé I, II, and III (Bordes, 1975, 1978). Lithic material

discovered from all four caves played a key role in Bordes' description and formation of Mousterian tool industries and concepts of Mousterian cultural identities (Bordes, 1961, 1973; Bordes and de Sonneville-Bordes, 1970). Bordes ran excavations at Pech IV from 1970 to 1977, excavating a total of 52 m². This massive project exposed a 3 m sequence of Middle Paleolithic deposits, filled with an abundance of Mousterian tools and faunal remains.

A systematic study of Bordes' excavation and curation methods was undertaken between 2000–2003 in order to understand and correct possible biases that may have been introduced into the archaeological assemblage from the time of excavation to its storage at the museum (Dibble et al., 2005). Bordes' excavation techniques were meticulous for the time, and he kept detailed field notes. He excavated in 1 m² with stratigraphic subdivisions within each unit corresponding to the natural geological contours and features as he observed them. When searching through the back dirt generated by Bordes' excavation, very few artifacts were found, and a majority of pieces recovered were less than 5 mm in size (Dibble et al., 2005). The material analyzed in the present study comes from Bordes' original excavations, and it has been determined that stratigraphic levels identified by Bordes align well with levels identified in recent excavations of the site (Dibble et al., 2005). As such, Bordes' original level designations are used throughout the current paper. Specifically, these are Level Y-Z and Level I2, in lieu of Dibble and colleagues' Level 4 and Level 8, respectively. Many of the lithic remains and faunal epiphyseal ends and teeth recovered from the site were point-provenienced with tape measurements. The piece-plotted and numbered materials were then stored in bags organized by square. Specimens that were not large enough to plot were placed in small-finds bags with the elevations documented. It is thus possible to determine the stratigraphic level from which small finds were

excavated. Therefore, while there was a preference for piece-plotting the most identifiable specimens, this bias can and was corrected in this analysis, because small finds were retained.

Recent excavations of Pech IV allowed stratigraphic levels from the site to be dated using thermoluminescence (TL). Six dates have been obtained from the lowest level of the cave site (Level Y-Z) ranging in age from 106.2 ± 11.8 ka to 89.1 ± 9.5 ka, with a weighted mean of 96 ± 5 ka (Richter et al., 2013). These dates place Level Y-Z within the warm interglacial of MIS 5. Charcoal collected from Y-Z revealed that oak (*Quercus*), birch (*Betula*), hornbeam (*Carpinus*), and elm (*Ulmus*) were present (Dibble et al., 2009). These findings confirm paleoenvironmental reconstructions suggesting that deciduous forests existed across France at this time (Van Andel and Tzedakis, 1996). Evidence of randomly distributed artifact orientations, ash layers that preserve calcareous ash crystals, a low percentage of lithic edge damage, and a low frequency of dry bone breaks demonstrate that very few changes have occurred within Y-Z through post-depositional processes (Dibble et al., 2009). Evidence of deciduous trees and thermoluminescence dates broadly corresponding to the MIS 5c interstadial (Johnsen et al., 2001; Välranta et al., 2009) are concordant with the dates and the idea that Y-Z was deposited during a warm interglacial phase. In contrast, two thermoluminescence dates (68.5 ± 6.6 and 71.8 ± 6.7 ka) from Level I2 at Pech IV suggest a deposition age during a colder time period (Richter et al., 2013). The precision of the TL age estimates is sufficient to assign this layer (with reasonable confidence) to the glacial period of MIS 4, but not specifically to a Dansgaard–Oeschger (DO) event.

Roc de Marsal (RDM) is a cave site located on a steep cliff face 80 m above a valley floor. The plain below the cliff is traversed by a small tributary of the Vézère River (Fig. 1). The site was

first excavated from 1953–1971 by Jean Lafille (Lafille, 1961; Turq, 1985; Guérin et al., 2012). During these excavations the articulated skeleton of a two-to-three year old Neandertal child was recovered (Bordes and Lafille, 1962; Legoux, 1963). The site was reopened in 2004 to collect new data from the sequence, reassess its faunal and lithic industries, better understand the site formation processes, and to attempt to provide ages for the deposits (Turq et al., 2009).

Recent excavations of RDM used a total station to plot the location of artifacts in three dimensions as described by Dibble et al. (2007). Three thermoluminescence age estimates (77.4 ± 4.8 ka, 81.4 ± 5.0 ka, 86.7 ± 5.2 ka) were derived from burnt flints associated with Level 9 at the site (Sandgathe et al., 2011). However, these dates are discordant with optically stimulated luminescence age estimates recently published by Guérin et al. (2012), whose results suggest that levels 7–9 were much more recently occupied (70–65 ka). The differences in age estimates and the imprecision surrounding both make it difficult to assign Level 9 to a specific climate event, but the microfaunal composition provide further resolution of the environmental conditions. Microfauna from Level 9 include the field vole (*Microtus agrestis*), garden dormouse (*Eliomys quercinus*), and European pine vole (*Microtus subterraneus*; Sandgathe et al., 2008). These species have broad ecological ranges; however, genetic evidence has shown that during glacial periods, the range of the field vole (*Microtus agrestis*) contracted to areas located primarily in the Carpathian Mountains, the southern Urals or the Caucasus, and the Iberian Peninsula (Jaarola and Searle, 2002). Expansion of field voles into the Dordogne Valley thus indicates relatively warm conditions, and the presence of this taxon supports the interpretation that Level 9 was deposited during an interglacial period (probably late MIS 5a; Sandgathe et al., 2011).

Dates have been obtained for Level 4 at RDM. Guérin et al. (2012) published two TL age estimates (45.4 ± 3.5 ka and 61 ± 6.8 ka). These dates suggest that Level 4 was deposited during

MIS 3. Once again, microfaunal remains help determine the local ecological conditions. The snow vole (*Chionomys nivalis*) is present in Level 4, with a minimum of two individuals represented (Marquet, in Sandgathe et al., 2008). The snow vole lives on rocky substrates usually above tree line in mountainous environments (Janeau and Aulagnier, 1997). However, during glacial periods, when mountains were covered in ice, the range of this species was pushed into lowland environments (Janeau and Aulagnier, 1997). During interglacials, snow vole ranges pushed back above tree line as glacier reduction opened these areas once again (Janeau and Aulagnier, 1997). The presence of this species in the relatively low elevation Dordogne therefore indicates that RDM's Level 4 was deposited during a colder period.

Methods

Sample selection

Data collection took place at the Musée National de Préhistoire, in Les Eyzies, France. The faunal assemblages from RDM and Pech IV are rich in material (total number of faunal remains from each level are as follows: RDM L4 $n = 21,000$; RDM L9 $n = 3658$; Pech IV L I2 $n = 9374$; Pech IV L Y-Z $n = 4847$), including an abundance of cervid and bovid remains. Analyzing all bone fragments from all four levels was not feasible given the detailed procedures to be used. Instead, bone fragments from both levels at each site were sampled at random from all excavation squares. Random sampling was possible due to the curation methods employed for both RDM and Pech IV. At RDM, all archaeological remains were well organized in a tray-box system that allows specimens from specific levels and squares to be selected at random. For Pech IV, fragments were kept in bags with the minimum and maximum elevation, and the unit

(square) recorded on each, thus providing good provenience for each sampled bag. A minimum of 10% of the faunal material was sampled from each level: RDM cold Level 4 $n = 2068$ fragments (~10% of the total sample); RDM warm Level 9 $n = 1922$ fragments (> 50% of the total sample); Pech IV cold Level I2 $n = 910$ (>10% of the total sample); Pech IV warm level Y-Z $n = 727$ bone fragments (>15% of the total sample).

Taxonomic assessment, taxon abundance, and transport strategies From the sampled collection, taphonomic, and taxonomic information was collected on skeletal elements of medium sized artiodactyls in the size 2 (20–113 kg) and 3 (114–340 kg) body size categories, a size range that was dominated by *Cervus*, *Rangifer*, and *Capreolus* in the Pleistocene of southwestern France (Delpech, 1983; Kurtén, 1968; Laquay, 1981). The identification of fragments was as specific as possible and included such categories as size 2 or 3 mammal, size 2 or 3 bovid/cervid, genus, and species (when possible). All fragments identifiable to species and bone element were entered into Microsoft Access, Bone Entry GIS, and Bone Sorter so that the minimum number of individuals for a species could be determined (Marean et al., 2001; Abe et al., 2002). The purpose of focusing on small to medium artiodactyls, and three species of deer specifically, was to control for two variables. First, it has been observed that animals that vary significantly in overall size and anatomy are butchered differently and that butchering marks preserve differently on different species (Binford, 1978; O'Connell et al., 1990; Lyman, 1992, 1995; Monahan, 1998; Egeland, 2003); therefore, restricting analysis to morphologically similar animals helps to control for these factors. Second, because the goal was to investigate butchering intensity, and because Pech IV and RDM are cave sites where carcasses were transported for butchering, it was critical to focus on prey that were likely to have been transported completely or almost completely. The

relationship between skeletal elements transported to butchering sites and the effects of prey body size, hunting group party size, and transport distance is a complex issue (Bunn et al., 1988; O'Connell et al., 1988; O'Connell et al., 1990; Lyman, 1995; Monahan, 1998; Schoville and Otárola-Castillo, 2014). It has been observed that individual hunters can carry complete carcasses of small to medium sized animals (4–113kg) back to a site (Hill and Hurtado, 1996; Monahan, 1998). In addition, Hadza hunting parties (between 2–11 people) will transport complete or nearly complete carcasses of animals as large as 340 kg, regardless of transport distance (Bunn et al., 1988; O'Connell et al., 1988; Monahan, 1998). Therefore, because the transport probabilities of animals up to 340 kg are high, the animals chosen for analysis fit within this size range: *Cervus elaphus* (75–340 kg), *Rangifer tarandus* (91–169 kg), and *Capreolus capreolus* (15–50 kg; Nowak and Wilson, 1999; Miller, 2003).

To examine differences in species abundance among the sites and levels, the Minimum Number of Individuals (MNI) represented for *Cervus*, *Rangifer*, and *Capreolus* was calculated from the Minimum Number of Elements (MNE) following the methods of Abe et al. (2002) and Marean et al. (2001) using bone templates in ArcView GIS. Each identifiable bone fragment was drawn onto the cervid template based on its location in the skeleton. The MNE was then calculated in ArcView GIS as the maximum number of overlapping bone elements. In turn, the MNI of a species was determined as the highest MNE value (between lefts and rights) found out of all elements analyzed.

Once the MNE was known, it was used to calculate the minimum animal units (MAU) and the (%MAU) found in each archaeological layer. The MAU is equivalent to the MNE normalized by the number of times the element appears in the complete skeleton of an animal (see Binford, 1978, 1984; Grayson, 1984). The MAU was calculated by taking the MNE for

each element and dividing it by the number of times that element appears in the body (e.g., MNE of 4 femora/2 femora in the body = MAU of 2). The element with the highest MAU was used as the standard for a normed scale called the %MAU: each skeletal element's MAU was divided by the highest MAU found in the sample and multiplied by 100 (Binford, 1978). Once calculated, the %MAU was then compared to the whole bone standard food utility index (SFUI), which is a calculation of the meat, marrow, and bone grease associated with each skeletal element (Metcalf and Jones, 1988). Plotting the %MAU versus the SFUI for each archaeological level allows for a depiction of the relationship between bone utility and the transport patterns utilized. This relationship was then compared to Binford's theoretical utility curves to determine the transport decisions made by Neandertals at Pech IV and RDM (Binford, 1978; Metcalfe and Jones, 1988). These utility curves include: 1) the bulk strategy, where all portions of a carcass are transported except those of the lowest utility; 2) the gourmet strategy, where only the highest quality portions are transported; and 3) the unbiased strategy, where carcass portions are transported in direct correlation to their utility. Faith and Gordon (2007) have added the unconstrained strategy to this suite of utility curves in which full carcasses are transported, thus all bones are transported equally.

To investigate the transport behaviors of Neandertals at RDM and Pech IV further, data from both sites were compared to expected evenness and Spearman's rho values generated by Faith and Gordon (2007) for the four theoretical utility curves described above. The 95% confidence intervals for each transport strategy were generated by Faith and Gordon (2007) by simulating "population assemblages" composed of 1000 high survival elements that reflected the gourmet, bulk, unbiased, and unconstrained transport strategies. Each of these four "population assemblages" were then resampled without replacement to generate test

assemblages of varying sample sizes ($n = 250$ elements; $n = 150$ elements; $n = 100$ elements; and $n = 50$ elements) with 5000 resampled test assemblages per value of "n." The evenness (using the Shannon evenness index: $\text{evenness} = -\sum p_i \ln p_i / \ln S$, where p_i is the standardized proportion of specimens of the i^{th} element and S is the number of types of elements [e.g., humeri, radioulna, etc.]) and the Spearman's rank correlation (ρ) between % MAU and SFUI were calculated for these assemblages, generating 95% confidence intervals for each of the transport strategies at different sample sizes. An evenness value of one demonstrates that all skeletal elements were transported to the site, which is consistent with the unconstrained transport strategy. Evenness values less than one indicate that some elements were transported more than others, although this measure does not indicate why this is the case. Calculation of Spearman's rank correlation (ρ) between % MAU and SFUI determines if there is a significant correlation between the skeletal elements represented in each archaeological level analyzed and the amount of meat, marrow and bone grease associated with each of those skeletal elements. Thus, both evenness and ρ were calculated here for each faunal sample in an effort to reconstruct the transport decisions of Neandertals that contributed to the accumulation of the assemblages at RDM and Pech IV.

Analysis of nutrient extraction behaviors

From the sampled faunal assemblage, we quantified breakage patterns and surface modification of long bones from the "high survival set" as defined by Marean and Cleghorn (2003): humeri, radioulnae, metacarpals, femora, tibiae, and metatarsals. Focusing on the high

survival set minimizes the impacts of post-discard forces of bone destruction, allowing for increased confidence in comparisons of abundance and modification among different skeletal elements. These are also the bone portions with the highest probability of preservation at levels consistent with their discard (Marean and Frey, 1997; Lam et al., 1999; Marean and Cleghorn, 2003; Cleghorn and Marean, 2004; Faith and Gordon, 2007; Yravedra and Domínguez-Rodrigo, 2008). Analyses of nutrient extraction were conducted on these high survival elements and supplemented with counts on proximal and middle phalanges to provide information on the use of low marrow yielding skeletal regions.

A suite of techniques have been used to observe and quantify processes of intentional nutritive bone breakage (caused by either hominids or carnivores) and non-nutritive dry-bone breakage. These methods were outlined by Villa and Mahieu (1991), who published the set of criteria used here to identify bones that were intentionally broken while in a fresh state for the extraction of marrow, bone grease, and calcium (nutritive bone breaks) versus bones that were broken while in a dry state after most bone grease and marrow were removed (non-nutritive). Such non-nutritive breakage often results from trampling, sediment compaction, rock falls, and processes of excavation and curation. Methods used to record nutritive and non-nutritive bone breakage included recording the fracture angles and outlines observed on the proximal and distal ends of each long bone (Villa and Mahieu, 1991). These techniques aim to evaluate the extent to which hominids and carnivores engaged in nutrient extraction at a site and also the extent of post-depositional processes that took place within an assemblage. This taphonomic approach has been calibrated to experimental studies of breakage patterns caused by humans and carnivores (Marean et al., 2000), and thus can be effectively applied to zooarchaeological remains.

Surface modification analysis

Surface modification analysis (analysis of cut, percussion, tooth marks, etc.) enables evidence of hominid butchering behaviors to be quantified, as well as highlighting the role that carnivores, other animals, and/or taphonomic processes may have played in accumulating and modifying bones in each assemblage. Establishing diagnostic criteria for correctly identifying cut, percussion, and tooth marks has been an intensive area of research within zooarchaeology (Binford, 1981; Brain, 1981; Potts and Shipman, 1981; Blumenschine and Selvaggio, 1988; Blumenschine, 1995; Blumenschine et al., 1996; Egeland et al., 2004; Marean et al., 2004; Pickering et al., 2004; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2009, 2014; McPherron et al., 2010; Pante et al., 2012; Thompson et al., 2015). It has been shown (Blumenschine et al., 1996) through inter-analyst blind tests, that analysts can correctly identify these surface modification marks using incident lighting and low-powered magnification. Detailed criteria have also been developed to help with the identification of chemical etching marks versus tooth marks (Domínguez-Rodrigo and Barba, 2006), trampling marks versus butchering marks (Olsen and Shipman, 1988; Fiorillo, 1989; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2009), and tooth marks created by different carnivores (Domínguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004). The criteria outlined in each of these studies were utilized to record the number of modification marks on each sampled fragment from Pech IV and RDM (including non-identifiable fragments) from size 2–3 mammals using incident lighting and a 45x binocular microscope.

The taxonomic and skeletal element analysis was completed using ArcView GIS. This software was also used to map some surface modification marks to demonstrate general trends in

mark placement. Although the GIS approach can facilitate comparisons among assemblages by standardizing modification mark counts by the total surface area analyzed (Marean et al., 2001; Abe et al., 2002), one drawback is that relying on ArcView GIS templates does not allow the inclusion of surface modification marks when they are observed on unidentifiable fragments, because they cannot be mapped onto a specific bone element or side. In this study, we included fragments that were not necessarily identifiable to a specific element, but were clearly long bones (including proximal or middle phalanges). For statistical comparison between sites and climatic conditions, the cut mark and percussion mark frequencies (proxies for butchering intensity) were standardized using fragment size to correct the per fragment count of the modification marks. This allowed us to include counts of modification marks preserved on all sampled long bone fragments.

Following the recommendation of Jungers et al. (1995), who evaluated a number of techniques to account for size in morphometric analyses, a size proxy for each bone fragment was calculated as the geometric mean of the maximum length and width measurements (measured with calipers). The geometric mean was calculated as the square root of the product of length and width (i.e., an approximation of the bone's surface area, but returned to linear dimension for simplicity). The sampled specimens are highly fragmentary, with little curvature (98–99% of the faunal material in all levels having circumferences < 50% complete); thus, the length and width provide a reasonable estimation of fragment surface area in nearly all cases. Across levels, the average length of fragments ranges from 40.01–43.16 mm, the average width 14.98–15.53 mm.

A generalized linear model was applied to test the hypotheses that cut mark and percussion mark frequencies vary significantly by 1) site (i.e., Pech IV and RDM) and 2)

climatic conditions (i.e., warm vs. cold). The generalized linear model constitutes a family of common statistical tests derived from linear regression, such as analysis of variance (ANOVA) and analysis of covariance (ANCOVA), but which can account for probability functions other than the normal distribution (Myers et al., 2010). Here, the model was designed as an ANCOVA, which included site and climate as independent variables (or "treatment effects") and the number of surface modification marks (cut or percussion) as the dependent (or "response") variable. The geometric mean of fragment length and width was incorporated as a covariate in the model to control for the effects of fragment size on cut and percussion mark count across sites and climatic conditions. This was done by calculating the least-squares mean for cut mark and percussion mark count for each assemblage based on the linear covariation between fragment size and cut and percussion mark count. The ANCOVA thus permits a single test of the effects of the two independent variables and the size covariate on the number of surface modification marks (cut marks or percussion marks), thereby preserving statistical power (Zar, 2010).

The statistical analysis of the surface modification data was designed to address the following question: for each site, is the mean number of modification marks per bone fragment (which we assume is a proxy for butchering intensity) greater in the cold-climate levels than it is in the corresponding site's warm-climate levels? Possible alternative outcomes were that 1) there is no significant difference in the per fragment mark count by either site or climatic condition (the null hypothesis); 2) per fragment mark counts differ significantly between the two sites, but climate has no significant effect (i.e., an interaction effect); 3) the effect of climate is significant at one site but not at the other (an interaction effect); or 4) the per fragment count is significantly higher in colder climates at one site, but significantly higher in the warm level of the other (an interaction effect). Because surface modification marks comprise count data (and

for some fragments counts of zero), the model assumed a Poisson distribution (Zar, 2010), which is beneficially applied to ranges of values that include small numbers (Whitaker, 1914).

Significant effects were considered at $p < 0.05$. All statistical analyses were conducted using Statistica software. For this analysis, fragments with surfaces obscured by cemented sediments were not used—only bone fragments with surfaces that were greater than 20% visible were included.

Results

Taxonomic representation and transport strategies

Table 1 shows the number of bone fragments identified as specifically as possible to mammalian group. The term “size 2–3 bovid/cervid” is used to indicate bone fragments identified to the following groups: nonidentifiable size 2–3 bovid/cervids, size 2–3 cervid, *Capreolus capreolus*, *Cervus elaphus*, and *Rangifer tarandus*. A consequence of randomly sampling fragments is that some fragments attributed to larger species (e.g., *Equus*, *Bison*) were drawn from levels 4 and 9 at RDM and I2 and Y-Z at Pech IV. These specimens are listed as “other taxa” in Table 1. Data were collected on these specimens, but for present purposes, bones from these larger animals were not included in the analysis. They are mentioned here simply to demonstrate that other taxa were present at the site. Table 2 lists the number of identifiable skeletal elements assigned to size 2–3 bovid/cervids. Only high survival skeletal elements were used in the calculations of the MNE and %MAU, which inform the analyses of the transport strategies used. The high survival long bones were also strictly used in the surface modification

analysis; however, it is important to note that low survival and/or low utility elements of size 2–3 bovid/cervids were recovered at both sites.

The taxonomic analysis of size 2–3 bovid/cervid fragments shows that *Rangifer* were more abundant in levels deposited during glacial cycles, while (within a site) *Cervus* and *Capreolus* were more abundant in levels deposited during interglacials (Fig. 2, Table 1). The calculated MNIs from these identifiable fragments further indicate that there was a shift in species abundance between warmer and colder levels at each site (Table 3). Table 3 summarizes the MNI values calculated from all identifiable long bone, mandible, and cranial fragments mapped into ArcView GIS. Although MNI values are low overall, *Rangifer* were more abundant in the glacial levels at both sites, while *Cervus* and *Capreolus* were more abundant in the warmer levels. For illustrative purposes, Figure 3 shows an example of the ArcView GIS templates for tibial fragments of *Rangifer* and *Cervus*.

Figure 4 shows the percent minimum animal units (%MAU) of each high survival element plotted against the standard food utility index (SFUI), which is a measure of the caloric value (e.g., meat, marrow, and bone grease) associated with different body parts (see Metcalfe and Jones, 1988). Each level falls between Binford's bulk and unbiased transport strategies, suggesting a mixed transport strategy whereby Neandertals are sometimes transporting high utility elements and leaving behind lower utility elements, and at other times transporting elements in direct proportion to their utility (Binford, 1978). The raw data for these analyses are shown in Tables 4a-d where all bone fragments drawn into ArcView GIS for each species were combined, allowing the MNE for all size 2–3 bovid/cervids to be derived for each level of interest at RDM and Pech IV. These tables also present the results for the %MAU both with and

without teeth for comparative purposes (see Binford, 1978, 1984; Grayson, 1984), along with the evenness index and Spearman's rho for all levels analyzed (see Faith and Gordon, 2007).

The use of the bulk or unbiased transport strategies is supported when the evenness values are calculated for each of the high survival skeletal elements from Pech IV and RDM and compared to experimental 95% confidence intervals established for the gourmet, unbiased, bulk, and unconstrained transport strategies (from Faith and Gordon, 2007; using their results with sample sizes of 50). The evenness values for all levels (Tables 4a-d, Fig. 5) fall within Faith and Gordon's 95% confidence intervals for both the unbiased strategy (95% CI: 0.767–0.937) and the bulk strategy (95% CI: 0.899–0.987). None of the Spearman's rank correlation tests between %MAU and SFUI are statistically significant. However, Faith and Gordon (2007) found that small sample sizes and transport strategies with relatively even skeletal element abundances (i.e., the bulk transport strategy) frequently return erroneous nonsignificant results. Thus, the nonsignificant rho values are reported in Tables 4a-d, but should be interpreted cautiously. Overall, the data from all assemblages most closely match either the bulk or unbiased strategies based on evenness and either the bulk or unconstrained based on the rho values.

Taphonomy and post-depositional destruction

Table 5 shows the frequency of nutritive and non-nutritive bone breaks in each archaeological level analyzed. The results for the archaeological assemblages (Figs. 6 and 7) were compared with actualistic experimental samples from the literature (Blumenschine, 1988; Capaldo, 1995; Marean et al., 2000, 2004). The actualistic assemblages represent the end-

members of the accumulating processes for large mammals. Comparative samples labeled “Carnivore Only” include data from experiments in which carnivores had exclusive access to carcasses and “Hominid Only” refers to experiments for which humans were fully responsible for butchering the carcasses. “Hominid to Carnivore” is a situation where humans modified bones first and then carnivores were allowed to feed on them. Bone breakage patterns are broadly similar among the experimental conditions; thus, these breakage variables have little utility for inferring a specific agent of accumulation (Marean et al., 2000). However, results from this analysis demonstrate a high frequency of nutritive bone breaks (typified by curve or V-shaped outlines and oblique angles) at both RDM and Pech IV, suggesting that effort was exerted to remove internal bone nutrients from faunal remains at both sites (Fig. 6). Conversely, the frequencies of non-nutritive bone breaks are low in all archaeological levels. Non-nutritive bone breakage (Fig. 7) typified by right angle breaks and transverse outlines most often occur when all nutrients have been removed from the bones and the bones have dried (Villa and Mahieu, 1991). These breaks can occur from a variety of post-depositional processes, such as sediment compaction and trampling. However, a small percentage of these types of breaks do occur while bones are being processed for nutrient extraction by either humans or carnivores (Marean et al., 2000). At Pech IV and RDM, frequencies of transverse outline and right angle breaks do not exceed those that occur when humans and/or carnivores actively remove nutrients from long bones. These results demonstrate that both sites are well preserved and did not suffer high levels of post-depositional damage (e.g., from trampling or sediment compaction).

In contrast to the bone breakage types, the relative abundance of shaft fragments and epiphyseal ends is more sensitive to the intensity of carnivore modification. Assemblages in which carnivores are involved (either primarily or secondarily) preserve much lower frequencies

of epiphyses (< 10%) than those in which hominids are the only accumulators (approximately 25%; Marean et al., 2000). Table 6 shows the frequency of shaft fragments and epiphyseal fragments from each level from Pech IV and RDM. These sites exhibit very high frequencies of shaft fragments (> 80% overall) and very low frequencies of epiphyseal ends (< 8% overall). The destruction of epiphyses can result from numerous destructive processes, including human processing, carnivore consumption, post-depositional destruction, etc. An analysis of tooth mark frequencies presented below allows us to exclude carnivores, and the analysis of breakage frequencies just presented makes post-depositional destruction an unlikely process for this rarity of epiphyses.

As done with the prior variables, the percentage of percussion marks versus the percentage of tooth marks found on long bone fragments at Pech IV and RDM was compared to data from actualistic studies where humans, carnivores, and both humans and carnivores extracted nutrients from long bones (Blumenschine, 1988, 1995; Marean and Bertino, 1994; Capaldo, 1995, 1997; Marean et al., 2000, 2004). At RDM, (Table 7, Fig. 8) tooth marks were present on six long bone fragments from Level 4 and one long bone fragment from Level 9. At Pech IV, one long bone fragment was found to have a tooth mark in Level I2, while no tooth marks were observed on long bones fragments from Level Y-Z. We conclude that carnivores did not modify the vast majority of long bones at RDM or Pech IV. Other researchers have found similar results in studies of faunal remains from Pech IV and RDM that included bones of the axial skeleton (Dibble et al., 2009; Turq et al., 2009; Sandgathe et al., 2011).

When taken as a whole, the taphonomic analyses show that archaeological assemblages at Pech IV and RDM are primarily anthropogenic in origin and that little post-depositional destruction has occurred. These results demonstrate that corrections for post-depositional

damage or the effects of carnivore modification are unnecessary. The lack of carnivore activity at these two sites is interesting given that so few epiphyseal ends were sampled from each level. If carnivores were not highly active at Pech IV and RDM, then one possible reason for the lack of epiphyseal ends in each level is that long bones were subjected to heavy processing. In light of such taphonomic information and especially the results from the breakage analysis (showing high frequencies of nutritive bone breaks), Neandertals themselves might have put considerable effort into extracting marrow and bone grease from long bones, and this is examined in more detail below.

Bone surface modification by hominids

In an effort to quantify how intensely Neandertals were processing skeletal elements in each level and to understand if Neandertal processing intensity changed between warm and cold climatic cycles, a generalized linear model was applied to the surface modification counts on long bone fragments including the proximal and middle phalanges from size 2–3 bovid/cervids from each site. Results from this analysis show that for both cut mark (Fig. 9) and percussion mark (Fig. 10) frequencies there was a significant effect of both site and climate, as well as an interaction between these two factors. Bones excavated from levels deposited during colder climates (Level 4 at RDM and I2 at Pech IV) had more cut marks (Wald $\chi^2 = 78.44$, $p < 0.001$) and percussion marks (Wald $\chi^2 = 67.88$, $p < 0.001$) than bones excavated from levels deposited during warmer time periods. For cut marks, the significant effect of climate appears to be driven by the frequency of cut marks found on long bones and proximal and middle phalanges from

RDM, because the 95% confidence intervals (CI) of the least-square means overlap at Pech IV. Indeed, site was also a significant effect on the per specimen number of cut marks (Wald $\chi^2 = 34.40$, $p < 0.001$) and the interaction effect of climate by site was significant (Wald $\chi^2 = 51.33$, $p = < 0.001$). Consequently, the effect of climate on per specimen cut mark frequency was greater at RDM than at Pech IV (Fig. 9).

Climate also had a significant effect on the number of percussion marks per specimen (Wald $\chi^2 = 4.92$, $p = 0.02$). There was also a significant effect of site on the percussion marks, but the pattern was the opposite of that seen for the cut mark analysis, with Pech IV showing an overall greater frequency of marks per specimen (Wald $\chi^2 = 337.25$, $p < 0.001$; Fig. 10). Furthermore, the effect of climate on the percussion mark count is more pronounced at Pech IV than RDM (Fig. 10). This pattern in the percussion mark data is reflected in the significant interaction effect between site and climate (Wald $\chi^2 = 4.93$, $p = 0.03$).

The analyses above demonstrate that percussion marks were more common in levels deposited during colder time periods. Moreover, the frequencies of percussion marked long bones in all levels (RDM 4 = 21%; RDM 9 = 12%; Pech I2 = 43%; Pech Y-Z = 31%) closely matched expected values from actualistic studies where 100% of marrow was extracted (mean = 27.6%, lower 95% CI = 15.4, Upper 95% CI = 39.8; Blumenschine, 1988; Marean et al., 2000). This suggests that during both warm and cold climate oscillations, Neandertals were processing within-bone nutrients, but they were doing so more intensively during cold climates. Bolstering this pattern of intensive nutrient extraction is the finding that while identifiable long bone epiphyseal ends are rare in all levels (Tables 6 and 8), the epiphyseal ends that are present exhibit percussion marks (Table 8). These percussion-marked epiphyseal ends are more frequent in the cold levels than in the warm levels.

To further investigate the processing of epiphyseal ends, fragments from the small-finds bags were analyzed (Table 9). For this analysis, small-finds bags were randomly sampled from hundreds of small-finds bags from RDM Level 4 and Level 9 and Pech IV Level I2 and Level Y-Z. Once pulled from a collection, all small finds within a bag were analyzed. Analyzing small finds was important because it has been suggested that if Neandertals were processing epiphyseal ends for bone grease, that activity should have created small fragments of spongy bone, unless they were consuming epiphyseal ends directly (Marean, 2005). Findings from this analysis show that at RDM, small pieces of spongy bone were present in a higher abundance in Level 4 (cold level) than in Level 9. However, the reverse pattern is seen at Pech IV, where Level Y-Z (warm level) had a higher frequency of spongy bone (Fig. 11).

Finally, the fact that phalanges were modified along with the other long bones in the body demonstrates that Neandertals were thoroughly processing herbivore skeletons for nutrients. Although only a small number of proximal and middle phalanges are found at each site, a portion of those phalanges also contain cut marks and percussion marks (Table 10). In fact, the frequency of percussion marks on these low-marrow yielding elements shows that proximal phalanges with percussion marks are represented at similar frequencies to bones with higher marrow-yields (e.g., long bones from the high survival set; Fig. 12).

Discussion

The results of the taxonomic analysis suggest that climate may have influenced the abundance of different species, with *Rangifer* most abundant in the colder levels and *Cervus*

more abundant in the warmer levels. This is interesting, given that transport patterns were largely consistent across time at Pech IV and RDM for size 2–3 bovid/cervids. Optimal foraging theory predicts that as search time and/or distance to prey increases and/or encounter rates decrease more field processing should take place so that lower utility parts will be left at the field processing sites, while higher utility parts will be transported to home base sites (Binford, 1978; Metcalfe and Barlow, 1992; Barlow and Metcalfe, 1996; Bettinger et al., 1997; Bird and Bliege Bird, 1997; Cannon, 2001, 2003; Bird et al., 2002; Faith, 2007). The consistent strategies for transporting small to medium bovid/cervids at Pech IV and RDM suggest that while species abundances may have shifted (e.g., *Rangifer* vs. *Cervus*), encounter rates or search times of animals in this body size range may not have changed. It might be argued that if encounter rates did not change, then perhaps Neandertals were not nutritionally stressed. For this interpretation to be compelling, a broader analysis of animals in multiple body size ranges is needed to capture the range of transport strategies utilized by Neandertals at these sites over time. While it is possible that transport strategies truly remained static, it is important to remember that in this study, the anatomy and the body size of the species analyzed was controlled in an effort to limit variation in butchering behaviors associated with animals with different anatomy that might have been transported differently. The fact that transport patterns for size 2–3 bovid/cervids are similar across levels at both sites (Figs. 4 and 5) suggest that our efforts to control this variation worked. In this case, it also shows that although size 2–3 bovid/cervids were transported similarly among sites and climatic regimes, butchering strategies varied, with more butchering marks produced in colder time periods.

The taphonomic analysis showing very low frequencies of non-nutritive breakage (Table 5, Fig. 7) suggests that the archaeological deposits were well protected from post depositional

processes that would break bones. The presence of small fragments of spongy bone (Table 9, Fig. 11) and the nearly complete lack of tooth marks on long bone fragments (Table 7, Fig. 8) demonstrate that carnivores rarely consumed bones at Pech IV and RDM. Hyena coprolites have been found in low frequencies in Level 4 at RDM, and a few carnivore teeth (especially canid teeth) have been found at both RDM and Pech IV. However, all faunal analyses reported by other researchers who have studied the RDM and Pech IV collections are in agreement with the analysis presented here, having identified very few tooth marks on bone fragments and little evidence for acid etching of bones (Dibble et al., 2009; Turq et al., 2009; Sandgathe et al., 2011). Similarly, low levels of carnivore modification have been reported at other Neandertal sites in southern France including Grotte XVI (Grayson and Delpech, 2003), Jonzac (Jaubert et al., 2008; Niven et al., 2012), Abri Peyrony (Soressi et al., 2013), and Pech de l'Azé I (Rendu, 2010). This lack of carnivore modification may be the result of a general tendency for Neandertals to heavily process animal carcasses. If Neandertals removed most nutrients from the bones, the resulting processed fragments may not have been attractive to carnivores. Indeed, experiments of carnivore consumption have shown that carnivores tend to ignore bone fragments that are stripped of meat and bone marrow (Blumenschine, 1988; Marean and Spencer, 1991). Another possibility is that Neandertals were occupying sites year round, limiting carnivore occupation and access to bone accumulations.

Overall, the results show that Neandertals intensively extracted nutrients from prey carcasses across time, as demonstrated by an abundance of nutritive bone breaks (Fig. 6), cut marks, and percussion marks on long bone fragments in all levels analyzed (Figs. 9 and 10). While it is clear that Neandertals were accessing internal bone nutrients under varying climatic conditions, the quantitative comparisons provide some support for the hypothesis that

Neandertals increased their processing efforts during colder periods. The strongest evidence for this comes from the statistical analysis of the number of cut marks (Fig. 9) and percussion marks (Fig. 10) found on all size 2–3 bovid/cervid long bone fragments including proximal and middle phalanges. This analysis shows that bone fragments deposited during colder climates had more cut marks at both RDM and Pech IV, but that the magnitude of the difference was affected by the site being analyzed. At RDM, Level 4 (cold level) had significantly more cut marks than Level 9 (warm level). At Pech IV, bones deposited in Level I2 (colder level) also contained more cut marks than Level Y-Z (the warmer level), but the 95% confidence intervals overlap, so the difference is not as pronounced as at RDM. The frequency of percussion marks at both sites also showed that bone fragments deposited during colder climates have more percussion marks on average than levels deposited during warmer climates (Fig. 10). Again though, there was an effect of site, as the difference between warm and cold levels was more pronounced in the Pech IV assemblage. However, it is clear for both sites that the frequency of percussion marks per bone was significantly greater in the levels deposited during cold climates than in warm climates. Why Pech IV showed an overall greater number of modification marks than RDM is unclear. It could be argued that Pech IV evinced greater signs of nutritional stress in both cold and warm periods, but this assumes that across sites (rather than simply within sites but at different levels) higher frequencies of butchery marks indicates greater stress. The sites were not necessarily occupied during the exact same time periods or under the same ecological conditions, and the factors driving these site-based results warrant further investigation. Nevertheless, when comparing within a single site, percussion mark frequency (and to a lesser extent, cut mark frequency) was greater in the colder levels, suggesting increased butchering intensity during these times.

The data on epiphyseal processing provides mixed evidence that Neandertals were processing bones more intensively in colder climates. Epiphyseal ends are rare in all levels (Tables 6 and 8), as expected due to density mediated destruction of these elements (Marean et al., 1992; Lyman, 1994; Lam et al., 1998, 2003). Nevertheless, of the epiphyseal fragments that remain, percussion marks are fairly common (Table 8); therefore, the destruction of epiphyses cannot be solely attributed to sediment compaction, burning, or other taphonomic forces. This finding matches expectations published by Marean (2005) for what an archaeological assemblage would be like if hominids were processing epiphyseal ends for consumption without the aid of hot-rock bone-boiling technology. Furthermore, more percussion marks were found on those deposited during colder periods than those deposited during interglacials (Table 8). That said, the absolute fragmentation of epiphyses (as determined through the analysis of the small-finds bags) did not show a consistent pattern with regard to climate. At RDM, small fragments of spongy bone were found in higher abundance in the small-finds bags from Level 4 (the cold level) than from Level 9 (the warm level). However, this pattern was not found at Pech IV, where fragments of spongy bone are more frequent in the warm Level Y-Z than from the cold level I2 (Fig. 11, Table 9).

The final criterion for inferring the intensive processing of skeletal elements for nutrient extraction is that bones with low marrow yields should show evidence of processing (Bar-Oz and Munro, 2007). Bar-Oz and Munro (2007) specifically singled out phalanges for this type of analysis. Table 10 shows that while few phalanges are present in the current sample, some of these do contain surface modification marks. The frequency of percussion marked proximal phalanges at RDM is higher in the cold level than in the warm level, but this pattern does not hold at Pech IV (Table 10). As such, the phalangeal data might actually suggest that heavy

processing of carcasses was a general Neandertal behavioral trait, possibly indicating that these hominids were regularly on the edge of nutrient sufficiency. However, given that the surface modification data (cut marks and especially percussion marks) from the skeleton as a whole shows an uptick during cold periods, these efforts appear to have been intensified even further during such times when populations would have been more susceptible to nutritional stress.

Conclusion

Results from this study provide some indication that Neandertals processed bones more thoroughly during cold climates than they did during warmer time periods at Pech IV and RDM in southwestern France. Overall, skeletal elements from glacial periods at RDM and Pech IV exhibit higher frequencies of surface modification (cut marks and especially percussion marks), suggesting that Neandertals intensified their efforts to extract calories from prey resources during these periods. The practice of breaking open low marrow yield bones such as phalanges appears to have been a general Neandertal behavior independent of climatic conditions, although it may indicate that Neandertals were regularly nutritionally stressed even during interglacial periods. Nevertheless, given that the overall frequency of cut marks and percussion marks increased in glacial periods at two separate archaeological sites (from different time periods), this suggests that more intensive butchering may have been a common Neandertal behavioral response to climate stress in southwestern France. These results are consistent with the hypothesis that cold climates were associated with nutritional stress in these hominids. Further testing of this hypothesis by analyzing the intensity of nutrient extraction at other Neandertal sites may be a

productive research focus for zooarchaeologists interested in Neandertal behavioral ecology throughout Eurasia. If similar results are obtained across the Neandertal range, it would support the broader hypothesis that climate changes negatively affected Neandertal populations and may have contributed to their extinction.

Acknowledgments

Funding was provided by the National Science Foundation (BCS-9242224) and Arizona State University's School of Human Evolution and Social Change, Institute of Human Origins, and Graduate and Professional Students Association. We thank the directors, researchers, and staff at Musée National de Préhistoire in France: Jean-Jacques Cleyet-Merle, Stéphane Madelaine, Peggy Jacquement, Marie-Pierre Regal, and Bernard Nicolas and many others. Kaye Reed, Lilian Spencer, Kelly Knudson, Ben Schoville and Caley Orr provided helpful comments throughout this research. We also thank William Doyle and Danielle Mercure for lending support. Finally, we thank the editors and four anonymous reviewers for their helpful feedback and constructive criticism that improved the manuscript.

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Figure legends

Figure 1. Map of Dordogne Valley of France showing the location of Roc de Marsal and Pech de l’Azé IV. This map has been modified from Sandgathe et al. (2011). Dark gray lines indicate rivers and black lines indicate modern roads. Les Eyzies de Tayac, Domme, and Sarlat la Canéda are local towns.

Figure 2. Categorized number of identifiable faunal remains from Levels 4 and 9 at RDM and Levels I2 and Y-Z at Pech IV. See footnote in Table 1 for an explanation of the groupings.

Figure 3. Fragments of tibiae of *Rangifer* (left) and *Cervus* (right) analyzed from the Roc de Marsal and Bordes’ excavation of Pech de l’Azé IV. Each fragment was drawn into ArcView GIS, where it was then mapped onto the same template and fragment overlaps were used to identify elements from different individuals. The darkest areas on each element indicate the highest number of overlaps; similarly, the color bars to the right of each element indicate the number of overlaps along each element with the bottom black bar indicating the highest number of overlaps (minimum number of elements [MNE]). The MNI of a species is equal to the highest MNE value (between lefts and rights) found for all elements analyzed of a particular species. These MNI values are shown in Table 5.

At RDM Level 4 = cold, Level 9 = warm

At Pech Level I2 = cold, Level Y-Z = warm

Figure 4. The relationship between the relative abundance of high survival skeletal elements (% Minimum Animal Units) and their Standardized Food Utility Index (SFUI) for levels 4 and 9 at Roc de Marsal and I2 and Y-Z at Pech IV. A distance-weighted least squares curve was fitted to the data points from each level. Utility curves proposed by Binford (1978) are plotted with the data for comparison.

Figure 5. The Spearman’s rank correlation (ρ) between % Minimum Animal Units and Standard Food Utility Index and the evenness values of high survival skeletal elements at Roc de Marsal and Pech IV. These data are plotted against the expected values for assemblages with a sample size of 50 that were accumulated using the gourmet, unbiased, bulk, and unconstrained transport strategies (from Faith and Gordon, 2007).

Figure 6. The frequency of long bone fragments from size 2-3 bovid/cervids with oblique breakage angles versus the frequency of fragments with curved and V-shaped outlines. These separately coded variables describe two independent aspects of nutritive bone breaks and follow the definitions of Villa and Mahieu (1991). Data are compared to experimental and naturalistic assemblages where nutrients were extracted by hominids only, hominids then modified by carnivores, and carnivores only (Marean et al., 2000). The cold levels from RDM and Pech IV are indicated by the gray icons and warm levels are indicated by the black.

Figure 7. The frequency of long bone fragments from size 2-3 bovid/cervids with right angle breaks versus the frequency of fragments exhibiting breaks with transverse outlines. These separately coded variables describe two independent aspects of non-nutritive bone breaks and follow the definitions of Villa and Mahieu (1991). Data are compared to experimental and naturalistic assemblages where nutrients were extracted by hominids only, hominids then modified by carnivores, and carnivores only (Marean et al., 2000). The cold levels from RDM and Pech IV are indicated by the gray icons and warm levels are indicated by the black.

Figure 8. The percentage of long bone shafts with percussion marks versus the percentage with tooth marks. Data are compared to experimental and naturalistic assemblages broken by hominids only, hominids then modified by carnivores, and carnivores only (Blumenschine, 1988, 1995; Marean and Spencer, 1991; Marean et al., 1992, 2000; Marean and Bertino, 1994; Capaldo, 1995, 1997). The ellipses are used for illustration, but have no statistical meaning.

Figure 9. Comparison of the number of cut marks per fragment (long bones and phalanges) from Roc de Marsal (RDM) and Pech IV (Bordes' excavations). The central bars are the least-squares means calculated based on the covariation between the number of cut marks and fragment size. The error bars are the 95% confidence intervals for that mean. The lines connecting the layers at each site show the interaction effect between site and climatic regime as tested in the analysis of covariance model (see methods). Parallel lines indicate no interaction effect (i.e., a consistent effect of climate at both sites), whereas divergent or crossed lines indicate interaction between these variables (i.e., a different effect of climate at each site).

Figure 10. Comparison of the number of percussion marks per fragment (long bones and phalanges) from Roc de Marsal (RDM) and Pech IV (Bordes' excavations). The central bars are the least-squares means derived from the linear covariation between the number of percussion marks and fragment size (i.e., the mean number of percussion marks per fragment increases with fragment size). The error bars are the 95% confidence intervals of the least-squares mean. The lines connecting the layers at each site show the interaction effect between site and climatic regime as tested in the analysis of covariance model (see text). Parallel lines indicate no interaction effect (i.e., a consistent effect of climate at both sites), whereas divergent or crossed lines indicate interaction between these variables (i.e., a different effect of climate at each site).

Figure 11. The frequency of spongy bone fragments found in small finds bags from Roc de Marsal (RDM) and Pech IV.

Figure 12. The frequency of percussion marks found on bone fragments and proximal phalanges from Pech IV and RDM.

Figure 1

Figure 2

Figure 3

Figure 4

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Figure 8

Figure 9

Figure 10

Figure 11

Figure 12

Table 1. Number of dental and skeletal remains identified to each taxonomic group.

Taxon*	RDM L4	RDM L9	Pech IV I2	Pech IV Y-Z
Bovid/Cervid	778	368	143	148
Cervid	28	11	21	13
<i>Capreolus capreolus</i>	24	43	21	29
<i>Cervus elaphus</i>	76	133	69	208
<i>Rangifer tarandus</i>	436	24	253	1
Non-ID mammal	540	1269	291	288
Other Taxa	186	74	112	40
Total Bones Analyzed	2068	1922	910	727

*When identifiable, fragments from size 2–3 bovid/cervids were assigned to a specific taxon (*Capreolus*, *Cervus*, or *Rangifer*). When not fully identifiable, they were assigned to either “bovid/cervid” or “cervid” depending on how distinguishable the remains were. Remains that could be specifically assigned to non-cervid taxa (e.g., *Equus*) were grouped together as “other taxa.” These specimen counts include fragments with surfaces that may have been obscured by cement/sediment and thus may not be included in the surface modification analysis.

Table 2. Number of identifiable specimens (NISP) identified to specific skeletal elements or as long bone fragments for size 2–3 bovid/cervids.

NISP skeletal element	RDM L4	RDM L9	Pech IV I2	Pech IV YZ
Cranial bones	21	15	8	6
Maxillary single teeth	18	30	18	20
Mandible	41	19	31	16
Mandibular single teeth	39	34	43	50
Humerus	66	24	34	29
Radioulna	86	24	35	24
Metacarpal	46	45	24	30
Femur	65	31	31	18
Tibia	98	51	74	37
Metatarsal	118	60	104	69
Metapodial	62	39	22	30
Prox Phalanges	3	7	8	5
Middle Phalanges	2	2	3	5
Distal Phalanges	4	1	2	1
Long bone Fragments	534	172	29	37
Atlas	0	1	0	0
Axis	0	0	0	0
Cervical	8	1	0	0
Thoracic	10	1	1	1
Lumbar	5	2	2	1
Sacrum	2	1	0	0
Rib	53	4	15	3
Scapula	8	2	9	3
Sternabra	4	1	0	0
Carpals	4	0	9	8
Tarsals	13	1	5	4
Pelvis	6	2	5	1
Patella	1	0	0	0

Table 3. Minimum number of individuals calculated for long bones, mandibles, and crania from ArcView GIS for each species of cervid analyzed from RDM and Pech IV.

Taxon	RDM L4	RDM L9	Pech IV I2	Pech IV Y-Z
<i>Rangifer tarandus</i>	11	2	9	0
<i>Cervus elaphus</i>	3	4	4	10
<i>Capreolus capreolus</i>	1	3	2	1

Table 4a. The minimum number of skeletal elements and the minimum animal units calculated using ArcView GIS of size 2–3 bovid/cervids from Roc de Marsal Level 4.

RDM Level 4 Size 2-3 Bovid/Cervids								
Element	MNE L	With Teeth	MNE R	With Teeth	MAU MAU	MAU Teeth	SFUI	% MAU With Teeth
Cranial	2	same	N/A	N/A	1	1	9.1	8
Mandible	5	same	3	same	4	4	11.5	32
Humerus	7		8		7.5		36.8	60
Radioulna	10		5		7.5		25.8	60
Metacarpal	2		1		1.5		5.2	12
Femur	4		8		6		100	48
Tibia	14		11		12.5		62.8	100
Metatarsal	3		4		3.5		37	28
Total Sample Size without teeth			87					
Total Sample Size with teeth			Same					
Evenness Value			0.89					
Spearman's rho			0.63					

Table 4b. The minimum number of skeletal elements and the minimum animal units calculated using ArcView GIS of size 2–3 bovid/cervids from Roc de Marsal Level 9.^a

RDM Level 9 Size 2-3 Bovid/Cervids								
Element	MNE L	With Teeth	MNE R	With Teeth	MAU	MAU Teeth	SFUI	% MAU With Teeth
Cranial	0	2	N/A	N/A	0	1	9.1	15
Mandible	2	4	2	same	2	3	11.5	46
Humerus	3		4		3.5		36.8	54
Radioulna	4		4		4		25.8	62
Metacarpal	2		0		1		5.2	15
Femur	3		4		3.5		100	54
Tibia	8		5		6.5		62.8	100
Metatarsal	2		2		2		37	31
Total Sample Size without teeth			45					
Total Sample Size with teeth			49					
Evenness Value			0.92					
Spearman's rho			0.67					

^aNote that the MNE of both cranial remains and left mandibles increase by two when all teeth were included in the analysis, increasing the total sample size by four. The Evenness and Rho values were calculated using the %MAU derived from the MNE with teeth.

Table 4c. The minimum number of skeletal elements and the minimum animal units calculated using ArcView GIS of size 2–3 bovid/cervids from Pech IV Level I2.^a

Pech IV Level I2 Size 2-3 Bovid/Cervids								
Element	MNE L	With Teeth	MNE R	With Teeth	MAU	MAU Teeth	SFUI	% MAU With Teeth
Cranial	1	2	N/A	N/A	0.5	1	9.1	11
Mandible	5	7	6	same	5.5	6.5	11.5	72
Humerus	6		6		6		36.8	67
Radioulna	5		3		4		25.8	44
Metacarpal	2		0		1		5.2	11
Femur	5		4		4.5		100	50
Tibia	9		9		9		62.8	100
Metatarsal	1		6		3.5		37	39
Total Sample Size without teeth			68					
Total Sample Size with teeth			71					
Evenness Value			0.91					
Spearman's rho			0.56					

^aNote that the MNE of cranial remains increases by one and the MNE of left mandibles increase by two when all teeth were included in the analysis, increasing the total sample size by three. The Evenness and Rho values were calculated using the %MAU derived from the MNE with teeth.

Table 4d. The minimum number of skeletal elements and the minimum animal units calculated using ArcView GIS of size 2–3 bovid/cervids from Pech IV level Y-Z.^a

Pech IV Level Y-Z Size 2-3 Bovid/Cervids								
Element	MNE L	With Teeth	MNE R	With Teeth	MAU MAU	MAU Teeth	SFUI	% MAU With Teeth
Cranial	0	3	N/A	N/A	0	1.5	9.1	21
Mandible	2	4	4	10	3	7	11.5	100
Humerus	6		6		6		36.8	86
Radioulna	2		3		2.5		25.8	35
Metacarpal	1		0		0.5		5.2	7
Femur	3		2		2.5		100	36
Tibia	4		4		4		62.8	57
Metatarsal	3		1		2		37	29
Total Sample Size without teeth			41					
Total Sample Size with teeth			52					
Evenness Value			0.90					
Spearman's rho			0.14					

^aNote that the MNE of cranial remains increases by three, the MNE of left mandibles increases by two, and the MNE of right mandibles increases by six when all teeth were included in the analysis, increasing the total sample size by 11. The Evenness and Rho values were calculated using the %MAU derived from the MNE with teeth.

Table 5. Number of long bone ends with nutritive bone breaks (e.g., oblique angle breaks and curved outlines) and non-nutritive bone breaks (e.g., right angle breaks and transverse outlines; following Villa and Mahieu, 1991).^a

Nutritive Bone Breaks					
Level	Oblique	%	Curved	%	Total Long Bone Ends
RDM 4	2000	92.59	1977	91.53	2160
RDM 9	837	91.98	837	91.98	910
Pech IV I2	603	82.83	600	82.42	728
Pech IV Y-Z	477	83.98	477	83.98	568
Non-Nutritive Bone Breaks					
Level	Right	%	Transverse	%	Total Long Bone Ends
RDM 4	29	1.34	45	2.08	2160
RDM 9	20	2.20	24	2.64	910
Pech IV I2	24	3.30	27	3.71	728
Pech IV Y-Z	23	4.05	23	4.05	568

^aFresh breaks that occurred during the excavation/curation process and indeterminate ends covered in concretions were not included in the analysis.

Table 6. Summary of the number of long bone shaft fragments (including the proximal and middle phalanges) and epiphyseal ends from Pech IV and RDM.^a

Level	Climatic Reconstruction	Long Bone Shaft Fragments	% Total sample	Long Bone Epiphyses	% Total sample	Total size 2-3 Bovid/ Cervid Postcranial Remains
RDM L4	Cold	1080	85.71	24	1.90	1260
RDM L9	Warm	455	89.92	13	2.57	506
Pech IV I2	Cold	364	80.71	30	6.65	451
Pech IV Y-Z	Warm	284	86.59	24	7.32	328

^aLong bone shaft fragments include mid-shaft fragments and near-epiphysis fragments. The percentages of long bone fragments and epiphyses do not total to 100% because these were calculated from the total number of postcranial remains, which include other elements (e.g., vertebrae). The total size 2–3 bovid/cervid postcranial remains is the sample of fragments with surface visibility >25%.

Table 7. Raw data for the number of size 2–3 bovid/cervid long bone fragments including phalanges with at least one percussion mark (PM) or one tooth mark (TM).^a

	RDM L4	RDM L9	Pech I2	Pech Y-Z	RDM L4	RDM L9	Pech I2	Pech Y-Z
Element	PM	PM	PM	PM	TM	TM	TM	TM
Humerus	19	5	18	9	0	0	0	0
Radioulna	16	6	12	6	3	0	1	0
Metacarpal	5	6	11	7	0	0	0	0
Femur	22	4	11	7	0	0	0	0
Tibia	29	10	40	13	0	0	0	0
Metatarsal	20	8	44	22	0	1	0	0
Metapodial	14	1	7	2	0	0	0	0
Prox Phalanges	1	0	1	1	0	0	0	0
Mid. Phalanges	0	0	0	0	0	0	0	0
Long Bones	105	15	12	23	3	0	0	0

^aNote no bones were observed with both PM and TM.

Table 8. Raw data of the number of long bone epiphyseal ends recovered from each level along with the number of epiphyseal ends with at least one percussion mark (PM).^a

Level	Climatic reconstruction	Total Long Bone Epiphyseal Ends	Number with PM	% of Epiphyseal Ends with PMs
RDM L4	Cold	24	6	25%
RDM L9	Warm	13	2	15%
Pech IV I2	Cold	30	6	20%
Pech IV Y-Z	Warm	24	2	8%

^aMany bones' surfaces were covered in concretions. Only fragments with surfaces that were greater than 25% visible were included.

Table 9. Number of cortical and spongy bone fragments analyzed from small-finds bags from Roc de Marsal and Pech IV.

Level	Bags Sampled	Cortical Bone	% Cortical	Spongy Bone	% Spongy	Total Fragments
RDM L4	13 bags	5754	92.64	457	7.36	6211
RDM L9	7 bags	7132	96.60	251	3.40	7383
Pech IV I2	9 bags	1112	97.89	24	2.11	1136
Pech IV Y-Z	6 bags	3172	94.40	188	5.60	3360

Table 10. The number of identifiable proximal and middle phalanges with cut marks (CM) and percussion marks (PM) from Pech IV and RDM.

Proximal Phalanges						Middle Phalanges				
	NISP	N with CM	%	N with PM	%		N with CM	%	N with PM	%
RDM L4	3	2	66.67	1	33.33	2	0	0.00	0	0.00
RDM L9	7	0	0.00	0	0.00	2	0	0.00	0	0.00
Pech IV I2	8	1	12.50	1	12.50	3	1	33.33	0	0.00
Pech IV Y-Z	5	2	40.00	1	20.00	5	2	40.00	0	0.00