Tracking Climate-Driven Changes in Neandertal Subsistence Behaviors and Prey Mobility Patterns

by

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ABSTRACT

The ability of Neandertals to cope with the oscillating climate of the late Pleistocene and the extent to which these climate changes affected local Neandertal habitats remain unanswered anthropological topics of considerable scientific interest. Understanding the impact of climatic instability on Neandertals is critical for reconstructing the behaviors of our closest fossil relatives and possibly identifying factors that contributed to their extinction. My work aimed to test the hypotheses that 1) cold climates stressed Neandertal populations, and 2) that global climate changes affected local Neandertal habitats. An analysis of Neandertal butchering on *Cervus elaphus*, *Rangifer tarandus*, and *Capreolus capreolus* skeletal material deposited during global warm and cold phases from two French sites – Pech de l'Azé IV and Roc de Marsal – was conducted to assess the impact of climate change on butchering strategies and resource extraction. Results from a statistical analysis of surface modification on all marrow yielding long bones, including the 1st phalanx, demonstrated that specimens excavated from the cold levels at each cave have more cut marks (Wald χ^2= 51.33, p= <0.001) and percussion marks (Wald χ^2= 4.92, p= 0.02) than specimens from the warm levels after controlling for fragment size. These results support the hypothesis that Neandertals were nutritionally stressed during glacial cycles. The hypothesis that global climates affected local habitats was tested through radiogenic strontium isotopic reconstruction of large herbivore mobility patterns (e.g., *Bison*, *Equus*, *Cervus* and *Rangifer*), because it is known that in the northern hemisphere, mammals migrate less in warm, well-vegetated environments, but more in cold, open environments. Identifying isotopic variation in mammalian fossils enables mobility patterns to be inferred, providing an indication of whether environments at Pech de l'Azé IV and Roc de Marsal tracked global climates. Results from this study indicate that Neandertal prey species within the Dordogne Valley of France did not undertake long distance round-trip migrations in glacial or interglacial cycles, maintaining the possibility that local habitats did not change in differing climatic cycles. However, because Neandertals were nutritionally stressed the most likely conclusion is that glacial cycles decreased herbivore populations, thus stressing Neandertals.

To Caley, with abandon.

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CHAPTER 1: INTRODUCTION, BACKGROUND, AND HYPOTHESES

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, remain unanswered paleoanthropological topics of considerable scientific interest. Within the paleoanthropological literature, a dichotomy exists between studies of Neandertal morphological traits, which portray Neandertals as hominids optimally adapted to cold climates (e.g., Holliday, 1997; Pearson, 2000; Weaver, 2003, 2009); and studies of Neandertal archaeological remains that suggest that Neandertals often inhabited temperate woodland environments (e.g., Shea, 1998, 2007, Boyle, 2000; Davies and Gollop, 2004; Hallin et al., 2012) with large portions of the population dying off during cold glacial cycles (Finlayson and Carrion, 2007; Hublin, 2009; Hublin and Roebroeks, 2009). Understanding the impact 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.

It is now widely recognized that global cold events occurred in rapid succession at the end of the Pleistocene (see Bond et al., 1993; Dansgaard et al., 1993; Genty et al., 2003, 2010; Augustin et al., 2004; Jouzel et al., 2007), and it has been hypothesized that these cold events may have driven Neandertal extinction by reducing the carrying capacity of Neandertal environments, thereby nutritionally stressing Neandertal populations and never allowing them to recover between climatic fluctuations (Finlayson and Giles Pacheco, 2000; Finlayson et al., 2001, 2002; Finlayson, 2004; Stewart et al., 2004; Finlayson and Carrion, 2008). Population levels of other large European mammals, specifically mammoths, woolly rhinos and large carnivores, also decreased at the end of the Pleistocene, supporting the notion that climatic changes were severe even for cold-adapted mammals (Stewart et al., 2004). Currently, insufficient data exist about how climate change impacted Neandertals and their prey—a short-coming that will be addressed in this dissertation.

The hypotheses that Neandertal extinction was driven by rapid climate changes at the end of the Pleistocene has two major assumptions. The first is that cold climates stressed Neandertal populations. If true, then ecological stress may have influenced Neandertal subsistence behaviors. Under nutritional stress, modern (Binford, 1978) and archaeological (Outram, 1999; Bar-Oz and Munro, 2007) hunter-gatherer groups intensify nutrient extraction behaviors. Such behavioral modifications include processing bones for marrow, including low marrow yield bones such as phalange (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). The second assumption is that global-scale climate changes affected Neandertal habitats at the local level; if true, that change should have affected the migration patterns of Neandertal prey. Within the northern hemisphere, in warm, well vegetated environments, large ungulates are non-migratory in the sense that they do not undertake long distance round trip migrations. In cold, open, and resource-poor environments, many large herbivores do undertake long distance round trip migrations (Johnson et al., 2002). If for example, if it is shown that Neandertal prey were not migratory, it would be consistent with some archaeological evidence suggesting that Neandertals primarily occupied forested areas of Europe (e.g., Shea, 1998, 2007, Boyle, 2000; Davies and Gollop, 2004; Hallin et al., 2012), which is where non-migratory large herbivores live today. If Neandertal habitats changed in accordance with global climatic shifts (cold-warm oscillations), then it might be expected that their prey species would show evidence of responding accordingly with regard to these different migratory behaviors. It should be noted that throughout this dissertation the word *migration* will be used to refer to the long distance round trip movements of herbivores. Thus, reconstructing the migrations of herbivores excavated from Neandertal cave sites provides an independent environmental proxy for discovering whether Neandertal habitats tracked global climatic changes. Understanding the mobility patterns of Neandertal prey is also critical for understanding the hunting behaviors of Neandertals. Zooarchaeological and isotope-based migration analyses each provide methods for interpreting climate-mediated changes in the archaeological record, but the strength of the current dissertation project is the combined use of these methods to serve as independent proxies for the influence of environment on Neandertal behavior.

If climate change was stressful enough to drive Neandertals to extinction, then Neandertals should show signs of stress during all major cold phases. Ideally, studies of Neandertal response 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 in analyses attempting to determine if climate change caused Neandertals to shift their subsistence behaviors. Therefore, the goal of this dissertation is to test the two major assumptions of the climate stress hypothesis: 1) that cold climates stressed Neandertal populations, and 2) that local habitats of Neandertals in the Dordogne Valley of France changed in reaction to short-term climate change, thus possibly driving Neandertals to extinction when such events occurred in rapid succession later in the Pleistocene.

The first aspect of the project focuses on the localized effects of climate change on Neandertal subsistence behaviors through zooarchaeological analysis of cervid remains (red deer (*Cervus elephus*), reindeer (*Rangifer tarandus*), and roe deer (*Capreolus capreolus*)) 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. The second assumption of the model is tested directly for the Dordogne Valley through isotope-based migration studies of multiple mammalian taxa (*Equus, Cervus, Rangifer, and Bison*) excavated from each cave site. Studying the mobility patterns of mammals provides an independent environmental proxy for the Dordogne Valley, of the vegetation that was present, the seasonal availability of Neandertal prey, and the possible mobility patterns used by Neandertals themselves.

Background

The subsistence practices of Neandertals have been a topic of prolific research in anthropology, incorporating a multitude of subjects including the examination of Neandertal hunting (e.g., Chase, 1986, 1989; Chase et al., 1994; Grayson and Delpech, 1994; Mellars, 1996; Marean, 1998; Marean and Kim, 1998; Marean and Assefa, 1999; Boyle, 2000; Burke, 2000; Conard and Prindiville, 2000; Gaudzinski, 2000; Patou-Mathis, 2000; Steele, 2004; Bocherens, 2005) and/or scavenging abilities (e.g., Binford, 1981, 1985, 1988; Stiner, 1991, 1994), their prey choice (e.g., Grayson and Delpech, 1998, 2003; Grayson et al., 2001; Stiner and Munro, 2002; Costamagno et al., 2006), and their the seasonal use of cave sites, mobility patterns and landscape-use patterns (e.g., Dibble and Rolland, 1992; Lieberman and Shea, 1994; Speth and Tchernov, 2001; Rivals et al., 2009; Barton et al., 2011; Delagnes and Rendu, 2011, Barton and Riel-Salvatore, 2012). A number of studies have also compared the subsistence behaviors of Neandertals and modern humans (e.g., Binford, 1985; Lieberman and Shea, 1994; Marean and Kim, 1998; Marean, 2005, 2007; Stiner, 1991, 1993, 1994; Steele, 2004; Stiner and Kuhn, 2006, Barton and Riel-Salvatore, 2012).

The extensive research on Neandertal subsistence has led to a consensus view that these late Pleistocene hominids were adept hunters (Marean 1998, 2005, 2007; Marean and Kim, 1998; Marean and Assefa, 1999; Boyle, 2000; Burke, 2000; Conard and Prindiville, 2000; Gaudzinski, 2000; Patou-Mathis, 2000; Steele, 2004; Bocherens, 2005). In fact, isotopic evidence has revealed that the Neandertal diet was largely carnivorous, incorporating meat from multiple species of herbivores including mammoth and wooly rhino (Richards et al., 2000; Bocherens, 2005, 2009; Richards and Trinkaus, 2009). Recently, however, analyses of microfossils preserved in Neandertal dental calculus have found that Neandertals did also consume some plant foods (Henry et al., 2010). Despite the vast amounts of literature on Neandertals, few reports have directly addressed whether Neandertal butchering behaviors and the mobility patterns of their prey changed in accordance with specific climatic oscillations corresponding to marine isotope stages. Understanding if and how Neandertals changed their butchering behaviors during oscillating climatic cycles is important for reconstructing how these hominids lived in northern latitudes for hundreds of thousands of years, and ultimately for gaining insight into why they were replaced by modern humans ~30,000 years ago. As mentioned previously, changes in prey use and butchering intensity are documented in this dissertation using rigorous zooarchaeological methods at two cave sites in southwestern France.

Geographical location

Western Europe (and France in particular) is a geographic region that has been well studied by paleoanthropologists. It is generally thought that Neandertals evolved in western Europe through anagenesis from earlier Middle Pleistocene hominids typically referred to the taxon *Homo heidelbergensis* (Dean et al., 1998; Harvati, 2007; although see Bermúdez de Castro et al., 2011), with evidence for the first hominids in western Europe stretching back to 1.2 Ma (Carbonell et al., 2008). Hominin remains, identified as “Pre-Neandertal”, “Early Neandertal” and “Classic Neandertal” have been described from Spain to Russia, but France is home to the vast majority (with more than 50 sites) (Serangeli and Bolus, 2008; Mellars and French, 2011). Of these, most sites are located in the limestone cliffs and caves of southwestern France (Serangeli and Bolus, 2008; Mellars and French, 2011). The dominance of Neandertal sites in this location is partially a product of the fact that this region has been open and easily accessible for scientific study for the last 200 years (with the exception of World War I and II): a time period in which the field of paleoanthropology was defined and set into practice. The taphonomy of the region has also made it amenable to study, because mammalian and lithic remains are well preserved. While the factors listed above have the potential to over-emphasize the role of this geographic location in Neandertal evolution, it has also become clear that Neandertals and their ancestors did continuously inhabit this area over time, surviving several hundred thousand years of glacial and interglacial cycles. Therefore, the time depth of deposits, the preservation of archaeological material, and the knowledge gained from years of study within Southern France enables a uniquely focused view to be obtained of Neandertal evolution and behavioral variability.

Neandertal skeletal remains have been found in a number of limestone caves and rock shelters in southern France. The most notable sites include La Ferassie, La Chapelle-aux-Saints, La Quina, Le Moustier, Regourdou, Combe Grenal, St. Césaire, Pech de l'Azé I and Roc de Marsal (see Mellars, 1996; Serangeli and Bolus, 2008). Faunal remains are also extremely well preserved and abundant at each of these sites and numerous other sites excavated from the region. Species lists have been reported from many archaeological sites including

Grotte Vaufrey; Le Portel, La Quina, Lazaret, Grotte des Cedres, Adaouste, Les Canalettes, Hortus, Salpêtre de Pompignan, Mauran, Tournal, Grotte XVI, Pech l'Azé 1, Pech l'Azé IV, Le Flageolet, Jonzac, La Ferrassie) (see Laquay, 1981; Delpech, 1983, 1996, 2007; Grayson and Delpech, 1994, 2003; Gardeisen, 1999; Boyle, 2000; Stewart et al., 2004; Rendu, 2010; Delagnes and Rendu, 2011; Discamps et al., 2011). Table 1.1 is a species list compiled from each of the cave sites previously listed. The range of species found (presence/absence data) at these sites remained fairly constant over time (Delpech, 1983; Grayson and Delpech, 2003; Discamps et al., 2011). However, the relative abundance of particular species found at archaeological sites does appear to have changed through time, with *Rangifer* and *Bison* more common during glacial time periods and *Cervus* and *Capreolus* more common during interglacials (Laquay, 1981; Delpech, 1983; Grayson and Delpech, 1998; Grayson et al., 2001; Costamagno et al., 2006; Morin, 2008; Discamps et al., 2011; Delagnes and Rendu, 2011; Discamps et al., 2011; Guérin et al., 2012). While species abundance data at archaeological sites has a lot to do with climate fluctuations, it is important to recognize that Neandertals through time were sharing the landscape with the community of animals in the species list presented in Table 1.1.

One faunal pattern that is often overlooked (although see Marean, 2007) is that differences in the type of site can lead to large changes in species composition: larger animals (e.g., *Equus*, *Bison*) are found in higher abundances at open air sites (e.g., La Micoque, Mauran) and rock shelters (e.g., Abri Suard, Artenac, Jonzac, Saint-Césaire, La Quina) than in cave sites, where cervids dominate assemblages (see Delagnes and Rendu, 2011 for species abundance data from each of these sites). This pattern is likely the result of Neandertal and modern human hunting behaviors and transport patterns (Bunn, 1988; O'Connell et al., 1988, 1990; Chase, 1989; Jelinek et al., 1989; Hoffecker et al., 1991; Gaudzinski, 2000; Marean, 2007; Schoville and Otárola-Castillo, in prep).

As is the case with the hominin and animal fossil remains, lithic material from southwestern France has also played an influential role in the development of modern archaeological method and theory. The classic Neandertal tool industry, the Mousterian (dated between 300-30 ka), was first described and named from the site of Le Moustier in Southwestern France. Variability within this industry (observed at archaeological assemblages from France and elsewhere, including stone tools from Pech de l'Azé) inspired the Bordes, Binford and Mellars debates that took place in the 1960s and 1970s (see Bordes, 1961, 1973; Mellars, 1965, 1970, 1973; Binford and Binford, 1966; Bordes and de Sonneville-Bordes, 1970; Binford, 1973, Dibble, 1991). More recently, material from the site of Grotte des Fées de Châtelperron (located in central France) has been the topic of heated scientific arguments (see Gravina et al., 2005; Zilhao et al., 2006; Mellars et al., 2007). In these exchanges, archaeologists wrestled with ideas about whether or not it is possible to identify cultural groups, group activities, and cultural interactions and/or replacements using evidence from lithic material. These debates set the tone for current archaeological research which largely emphasizes transdisciplinary and often experimental approaches for understanding patterns observed in the archaeological record.

*TABLE 1.1. Species list compiled from multiple archaeological sites in southern France (see text for list of sites)**

Scientific Name	**Common Name**	**Environmental Association**
Mammuthus primigenius	Mammoth	Steppe and Tundra vegetation
Coelodonta antiquitatis	Woolly rhinoceros	Steppe and Tundra vegetation
Rangifer tarandus	Reindeer	Steppe and Tundra vegetation
Megaloceros giganteus	Giant deer	Steppe and Tundra vegatation
Alopex lagopus	Arctic fox	Steppe and Tundra vegatation
Ursus spelaeus	Cave bear	Steppe and Tundra vegatation
Ursus arctos	Brown bear	Ubiquitous taxa
Vulpes vulpes	Red fox	Ubiquitous taxa
Cervus elaphus	Red deer	Ubiquitous taxa
Canis lupus	Wolf	Ubiquitous taxa
Capra ibex	Ibex	Upland, mountain
Rupicapra rupicapra	Chamoix	Upland, mountain
Marmota sp.	Marmot	Upland, mountain
Erinsceus europaeus	Hedgehog	Temperate, woodlands
Sus scrofa	Boar	Temperate, woodlands
Capreolus capreolus	Roe deer	Temperate, woodlands
Castor fiber	Beaver	Temperate, woodlands, river
Meles meles	Badger	Temperate, woodlands
Mustela putorius	Pole cat	Temperate, woodlands
Lynx lynx	Lynx	Temperate, woodlands
Equus caballus	Horse	Continental, Steppe
Equus ferus	Horse	Continental, Steppe
Equus hydruntius	Wild ass	Continental, Steppe
Saiga tatarica	Saiga antelope	Continental, Steppe
Crocuta crocuta	Hyaena	Continental, Steppe
Crocuta spelaea	Cave hyaena	Continental, Steppe
Panthera leo	Lion	Continental, Steppe
Panthera leo spelaea	Cave lion	Continental, Steppe
Dama dama	Fallow deer	Continental, Steppe
Bison priscus	European Bison	Continental, Steppe
Bos primigenius	Aurochs	Continental, Steppe

* Laquay, 1981; Delpech, 1983, 1996, 2007; Grayson and Delpech, 1994, 2003; Gardeisen, 1999; Boyle, 2000; Stewart et al., 2004; Rendu, 2010; Delagnes and Rendu, 2011; Discamps et al., 2011.

Fig.1.1. Map of France showing the location of Roc de Marsal and Pech de l'Azé IV.

Among the well know Neandertal sites (e.g. La Ferrassie, Grotte de Combe-Grenal, La Chapelle-aux-Saints, La Quina, Grotte XVI) of southwestern France are Pech de l'Azé IV (Pech IV) and Roc de Marsal (RDM) (Fig. 1.1). Excavation of these cave sites began in the 1950's and since that time, an abundance of lithic and faunal material has been unearthed from each site. For this dissertation, detailed zooarchaeological analyses were completed on faunal material excavated from Pech IV and RDM. The location, ecological context and the excavation history of each site are detailed below.

Location of archaeological sites

Pech IV and RDM are located approximately 200 km east of the Bay of Biscay (Atlantic Ocean), 140 km to the west, and 88km south of the Massif Central, and 260 km north of the Pyrénées Mountains (Fig.1.1). The cave site of Pech IV and RDM are located in caves within limestone cliffs that have been carved out over time by the meandering Dordogne and Vézère rivers and their tributaries. The Dordogne river originates on the highest mountain (Puy de Sancy) in the Massif Central at an elevation of 1,720 m. The river flows west across southwestern France, meeting up with the Vézère River near the town of Le Bugue (close to the location of RDM) before continuing west and eventually emptying into the Gironde estuary, which flows into the Atlantic Ocean (see Travade et al., 1998; Wilson, 1998; Semhi et al., 2000; Schäfer et al., 2002). The Vézère River also originates in the Massif central at an elevation of 970 m. It flows southwest from the mountains emptying into the Dordogne River (Wilson, 1998; Semhi et al., 2000). The greater Dordogne Valley region is defined as encompassing the Garonne, Dordogne, Vézère, Isle, and Dronne river valleys (Jones, 2007), and this region occupies the eastern edge of a large sedimentary basin, known as the Aquitaine Basin (the area of the Aquitaine Basin is 66,000 km^2). The Dordogne River region is characterized by narrow valleys with shear limestone cliffs that rise to a maximum height of approximately 600 meters above the valley floor ending in plateaus at the top (Jones, 2007). Within this region, Pech IV and RDM exist in the richly vegetated sub-region know as the Black Perigord. This area takes its name from the dark forests populated by oak, chestnut and pine trees that dominate the landscape today.

Paleoecological reconstructions of western Europe

In recent years, there has been an emphasis on modeling the global climate of the Pleistocene using ice, speleothem, marine and continental sediment core data, coleopteran (beetle) assemblages, and pollen preserved in fossil assemblages (De Beaulieu and Reille, 1984; Guiot et al., 1987, 1989, 1993; Guiot, 1990; Harrison, 1995; Ponel, 1995; Van Andel and Tzedakis, 1996; Coope, 2002; Van Andel, 2002; Alfano et al., 2003; Sánchez-Goñi and Harrison, 2010; Boch et al., 2011). It is now widely recognized that the later Pleistocene, particularly of Western Europe, was characterized by punctuated warm and cold oscillations caused by Heinrich events and Dansgaard-Oeschger events (D-O events) (d'Errico and Sánchez-Goñi, 2003; Finlayson et al., 2003, 2004; Boch et al., 2011).

Heinrich events occur when large icebergs float into the North Atlantic Ocean and melt (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001; Seidov and

Maslin, 2001). This melting releases large amounts of fresh water into the circulation system making the surface waters less dense (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001). Ocean circulation in the Atlantic relies on warm equatorial water moving north, cooling, and becoming more dense, and more saline due to evaporation (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001). As the water moves northward, it eventually becomes so dense and salty that it submerges to the ocean floor, pushing the water in front of it forward (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001; Seidov and Maslin, 2001). If glaciers melt into the North Atlantic, decreasing the salinity of the surface water, then the water no longer submerges (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001; Seidov and Maslin, 2001). This stops the water on the ocean floor from being pushed northward and stops warm equatorial water from moving north, because it can no longer occupy the former position of the submerged water (Heinrich, 1988; Bond et al., 1992; Ruddiman, 2001; Seidov and Maslin, 2001). Thus, during Heinrich events, stagnant cold water sits off the coast of Western Europe, causing drastic cooling.

Dansgaard-Oeschger events are defined as cycles of rapid climatic warming followed by more gradual cooling (Sánchez-Goñi and Harrison, 2010; Boch et al., 2011). These cycles occur during global glacial periods at intervals that range between 2000 to 7000 years (Ruddiman, 2001; Muscheler, 2006). The onsets of these cycles are abrupt, causing temperatures to increase as much as 8-16°C in time periods that range from a few years up to 200 years (Sánchez-Goñi and Harrison, 2010; Boch et al., 2011). The subsequent cooling events can take up to 2000 years (Sánchez-Goñi and Harrison, 2010). These events are recognized by deposits of dust and differing oxygen isotopes in the Greenland ice cores and in speleothems recovered from the Alps (Ruddiman, 2001; Muscheler, 2006; Boch et al., 2011). Heinrich events are sometimes associated with D-O events, but not always (Sánchez-Goñi and Harrison, 2010).

Paleoecological reconstructions for northern France

During most stable warm phases in Europe, summer and winter temperatures have been reconstructed as only a few degrees cooler than temperatures today: during warm climate oscillations temperatures averaged 3° C in the winter and 19° C in the summer (Barron et al., 2004; Huntley and Allen, 2004; Coope, 2002). Biomes in the Pleistocene were different from biomes observed today, thus the term “parkland” biome has been created to refer to the unique combination of plants that occurred in the past (Williams et al., 2001). During warm climatic oscillations, open parkland environments have been reconstructed for northern France, and compared to modern Europe, appears to have had a high frequency of boreal conifers like *Pinus* (pine), *Picea* (spruce) and *Betula* (birch) (Huntley and Allen, 2004; de Beaulieu and Reille, 1992; Gruger, 1989). Such paleoecological reconstructions can help guide the choice of appropriate modern analogues (among modern human hunter-gatherers) for inferring aspects of Neandertal subsistence and mobility. Hunter-gatherer groups (e.g., Naskapi, Montagnais, Eastern Cree, and the Attikamek Native Americans) that occupy forested environments and who hunt multiple species of non-migratory large herbivores, generally reside within the forest throughout the year, moving residential camps over a linear yearly distance of 150-500 km/year (Speck and Eisley, 1942; Custer and Stewart, 1990:317).

During brief interstadials (warm phases, within glacial cycles), northwestern France was an open, treeless environment that was dominated by grasses (*Poaceae*), sedges and (*Cyperaceae*) and shrubs (*Salix*, *Betula* and *Juniperus*) (de Beaulieu and Reille, 1992; Fletcher et al., 2010). A lack of pollen found in sediments deposited during full glacial cycles suggests that northern France was non-vegetated during these time periods (Fletcher et al., 2010). Thus, climatic reconstructions indicate that areas north of Pech IV and RDM appear have to been dramatically affected by climate changes. If northern France became non-vegetated, it may have been uninhabitable. However, if an open tundra environment existed, it may have been similar to environments inhabited by the Nunamuit Inuit or some groups of the Montagnais and Chipewyan Native Americans. These groups focused on migratory *Rangifer* and tended to be highly mobile themselves, with some groups moving 50 times per year, over an average distance of 1800-3600 km/year (Speck and Eiseley, 1942; Kelly, 1983). These modern hunter gatherer groups may be a good analogue for Neandertal groups inhabiting tundra environments, especially since *Rangifer* were often hunted by Neandertals.

Paleoecological reconstructions of southwestern France

In southwestern France, open boreal and temperate forest appear to have been present during interglacial cycles (Fletcher et al., 2010), with vegetation dominated by *Pinus* (pine) and *Picea* (spruce) (Barron et al., 2004; Huntley and

Allen, 2004; de Beaulieu and Reille, 1992; Gruger, 1989). During cooler time periods and interstadials, the northern limit of temperate forests was positioned at 45°N latitude (Fletcher et al., 2010). The Dordogne Valley of France (and Pech IV and RDM) is located just south of the 45th parallel, and is thus located in an area that could sustain forests even during cooler time periods. Between 74–59 ka, pollen data suggest an expansion of conifers in this area (Van Andel and Tzedakis, 1996). During this time, mean annual temperatures ranged between approximately -4 – 6°C, which is 12 – 13° lower than current temperature ranges for southwestern France (9 – 19° C) (Van Andel and Tzedakis, 1996). An increase in global ice sheets during this time caused a decrease in precipitation: average precipitation rate for southwestern France is estimated to have been between 220-370 mm/year, which is 650–800 mm less than current rates (mean 1020 mm/year) (Pons et al., 1992; Van Andel and Tzedakis, 1996). During the stable warm phase of MIS 3 (59–45 ka), the snow fall for mid- to northern France is estimated to have been about 70 cm/year with two to six months of snowy ground cover (Barron et al., 2004; Huntley and Allen, 2004). Temperature estimates are reconstructed as -4 – 0° C in the winter and 12–18° C in the summer (Barron et al., 2004). Once again, if the paleoenvironmental reconstruction described here is used to help guide the choice of appropriate modern hunter-gatherer analogues for Neandertals groups living in environments described above, it would appear that the Naskapi, Montagnais, Eastern Cree, and the Attikamek Native Americans groups are most appropriate since they also inhabit boreal forests and hunt multiple herbivore species.

In later time periods, (37–16 ka), the environment in Europe shifted toward colder temperatures. At that time, central and southern France became temperate grassland, with steppe tundra/warm step occurring in some regions (Barron et al., 2004; Huntley and Allen, 2004). Temperature estimates for France during this cooler period are on average -5 ° C not exceeding 15° C in winter months; summer months are estimated to have been on average 8° C (Guiot et al. 1989; Ponel, 1995; Van Andel and Tzedakis, 1996; Alfano et al, 2002; Barron et al., 2004). Snow most likely accumulated throughout Europe during the last glacial maximum, but no more than 20 cm of snow would have accumulated at any one time in areas south of 55° N latitude (Barron et al., 2004). Precipitation appears to have decreased as the climate cooled, due to a reduction in global ocean and sea water, caused by the buildup of glaciers and sea ice, which reduced the evaporation of water into the atmosphere (Barron et al., 2004; Huntley and Allen, 2004). In France, during the last glacial maximum snow most likely covered the ground for two to three months of the year (Barron et al., 2004). Environmental reconstructions for this colder time period seem most similar to environments inhabited by the Nunamuit Inuit and some groups of the Montagnais and Chipewyan Native Americans. Furthermore, these Native American groups have hunting economies dependent upon migratory *Rangifer*.

Paleoecological reconstructions of southern France

Paleoenvironmental reconstruction of southern France (north of the Pyrénées) have found that during the warm phase at the beginning of MIS 3, environments were characterized by open deciduous woodlands with *Quercus* (oak), *Ulmus* (elm), and *Fagus* (beech) trees (Huntley and Allen, 2004; de Beaulieu and Reille, 1992; Gruger, 1989). Snow fall in this area would have been minimal (<20 cm) with no long term accumulation (Huntley and Allen, 2004). However, during glacial cycles, this region became arid and sparsely vegetated (Bruxelles and Jerry, 2011). Pollen records from sites close to the Mediterranean sea and from the central Pyrénées show a dominance of *Artemisia*, which suggests that this region was a steppe or semi-desert environment (Jalut et al., 1992). In fact, the Landes de Gascogne, an area bordering the Atlantic Ocean, (west of Pech IV and RDM) became a sandy desert populated by sand dunes (Bertran et al., 2009). As was the case with northern France, environments in southern France appear to have been drastically affected by warm and cold climate oscillations. While environments in the Dordogne Valley changed during climatic oscillations, the effect of these shifts appears to have been more muted than in surrounding areas.

Excavation history of the archaeological sites

Pech de l'Azé IV. In 1952, Françoise Bordes discovered a collapsed cave site about 50 meters above a dry valley floor located approximately two kilometers from the Dordogne River. 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 square meters. This massive project exposed a three meter 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 by Harold Dibble, Alain Turq, Shannon McPherron and their team 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. He excavated in one meter squares with stratigraphic subdivisions within each unit corresponding to the natural geological contours and features as he observed them. Many of the lithic and faunal remains recovered from the site were point-provenienced and Bordes kept detailed field notes throughout the excavation. Interestingly, when searching through the back dirt generated by Bordes' excavation, Dibble et al. (2005) found very few artifacts, and a majority of pieces recovered from the dirt were less than 5 mm in size, providing evidence that most of the material excavated from the site by Bordes were retained.

Excavated material from Pech IV was housed at the Institut de Préhistoire et de Géologie Quaternaire at the University of Bordeaux I, but was moved to the Musée National de Préhistoire in Les Eyzies in 2007. During Bordes' excavation, fragments deemed large enough (no actual size was specified) by excavators were piece plotted and assigned a number, which was written on each specimen. Tooth fragments and epiphyseal ends were preferentially plotted and assigned numbers;

however, this bias can be corrected since small finds were retained. The piece-plotted and numbered material was then stored in bags organized by square. Specimens that were not large enough were placed in small finds bags with the elevations from which they were found written on the bag. During Dibble et al.'s (2005) analysis of excavated material from the site, a database was created using Bordes' field notes, which lists all stratigraphic levels and units from the site, along with the minimum and maximum elevation coordinates of each. Thus, this database allowed all bone fragments, even small finds, to be assigned to stratigraphic level. Dibble et al.'s (2005) analysis demonstrated that many of the biases introduced into the archaeological material during the original excavation and curation process where correctable. It was also determined that stratigraphic layers identified by Bordes aligned well with layers identified in the recent excavation of the site (Fig. 1.2). It should be noted that the faunal material analyzed for this study come from Bordes' original excavations; therefore, because stratigraphic layers from both Bordes' excavation and Dibble and coworkers' excavation align, Bordes' original level designations will be used throughout the paper (Specifically Level YZ, in lieu of Dibble et al.'s Level 8 and Level I2, in lieu of Dibble et al.'s, Level 4).

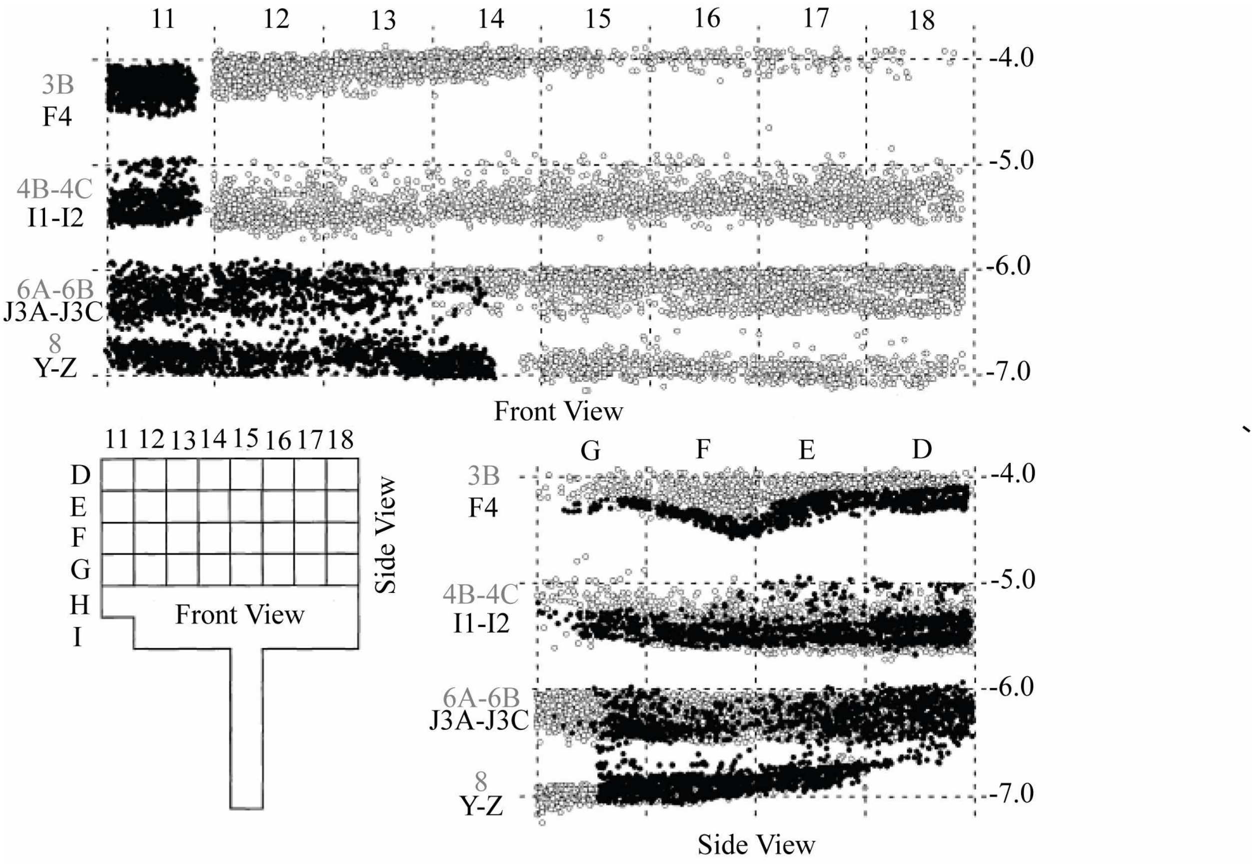

Fig. 1.2. Front and side view of artifacts recovered from Bordes' excavation (black) and Dibble's excavations (gray) from Pech IV, demonstrating that stratigraphic layers from both excavations align (modified from Dibble et al. 2005).

Recent excavations of Pech IV allowed stratigraphic layers from the site to be dated using thermoluminescence (TL). The lowest layer of the cave site (Level YZ, see Fig. 1.3) has been dated to 95.5 ±4.9 ka, which places it within the warm interglacial cycle of MIS 5c (Fig. 1.4) (Winograd et al., 1997; Johnsen et al., 2001; van Andel., 2004; Gibbard and Van Kolfschoten, 2005; McPherron et al. 2012).

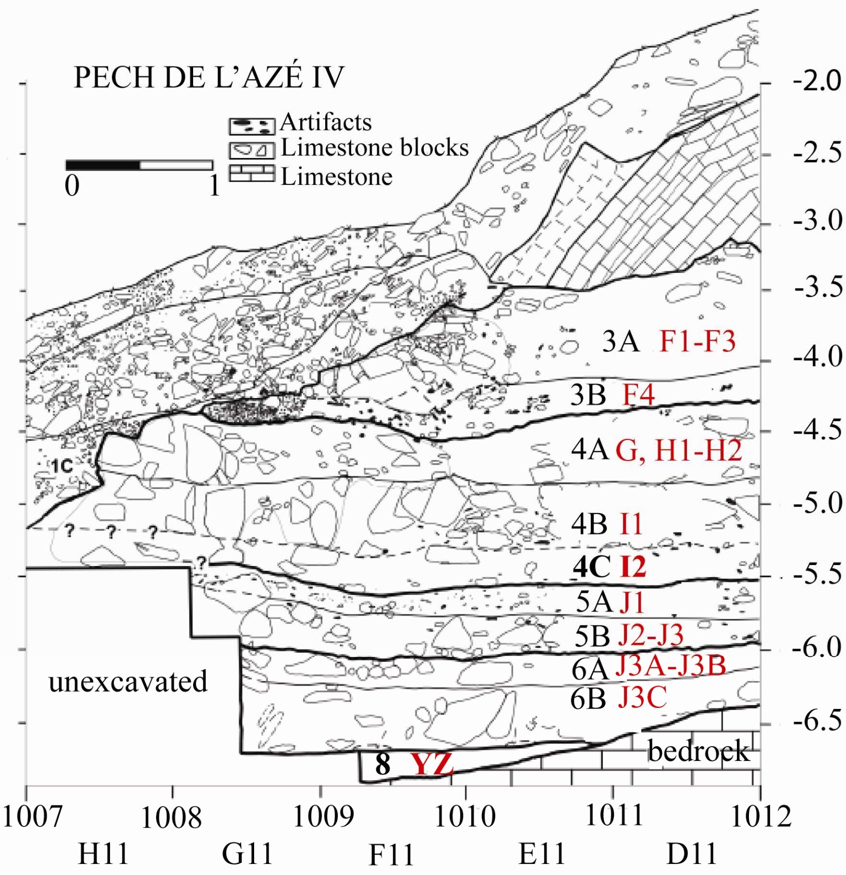

Fig. 1.3. Stratigraphic section of the west profile of Pech IV modified from Dibble et al. (2009). Stratigraphic layers identified by Dibble and coworkers are in black and those identified by Bordes are in red. Numbers H11-D11 identify the one-meter-by-one-meter excavation squares illustrated in this figure.

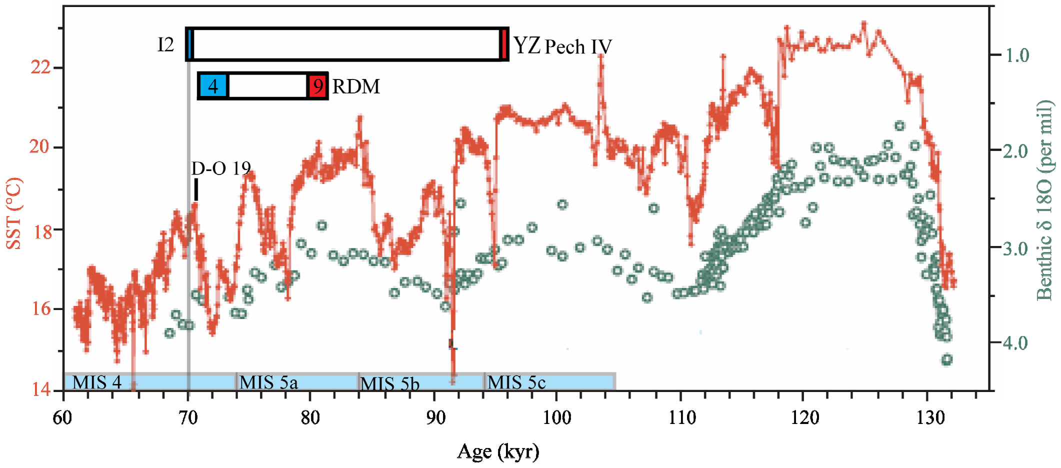

Fig. 1.4. Stratigraphic layers from Pech IV and RDM mapped temporally along with benthic δ^{18}O and sea surface temperatures (SST). This figure has been modified from Lehman et al. (2002). Dansgaard-Oeschger (D-O) event 19 is shown (Boch et al., 2011).

Faunal analysis of layer YZ revealed that *Cervus elaphus* were most abundant at the site followed by *Capreolus capreolus* and horse (*Equus caballus*) (Laquay, 1981; Dibble et al., 2009). A few specimens of pig (S*us scrofa*), beaver (*Castor fiber*) and *Rangifer tarandus* were also found in this level (Laquay, 1981; Dibble et al., 2009). As described in Dibble et al. (2009), examination of the lithics from Level YZ suggests that tools were not intensively utilized, as demonstrated by a high blank-to-core ratio (32.1), and a low retouched-tool-to-unretouched-flake ratio (0.07). In addition, lithic material from YZ is characterized by a high Levallois component and an abundance of scrapers (single, double and convergent scrapers) along with some Asinipodian tools (Dibble et al., 2009; Sandgathe et al., 2011). The Asinipodian industry includes very small (< 30 mm) prepared cores (Levallois cores, and Kombewa cores), truncated-faceted pieces, small flakes that appear to have two “interior” surfaces, and an absence of retouched tools (Dibble and McPherron, 2006). Overall, the tools from this layer are characterized as “Typical” Mousterian tools, an industry that is composed of 25-55% scrapers (Bordes, 1968; Richter et al., 2012). Interestingly, YZ contains well-preserved ash lenses (Fig. 1.5) along with burnt bones and lithics.

Fig. 1.5. Charcoal and ash lenses from Level YZ at Pech IV. Photo from Sandgathe et al. (2011).

The extent of bone burning will be one of the subjects covered in this paper; however, a study conducted by Dibble et al. (2009) from recent excavations of Level YZ found that 54% of osseous material showed signs of burning. Analysis of the ash lenses, viewed cross-sectionally and from above, suggest that hearths were built on the surface of the cave frequently, so that overtime the lenses from multiple fires merged, blending into each other (Sandgathe et al., 2011). Charcoal collected from YZ revealed that oak

(*Quercus*), birch (*Betula*), hornbeam (*Carpinus*), and elm (*Ulmus*) were present (Dibble et al., 2009). These finding confirm paleoenvironmental reconstructions which suggest that during this time, deciduous forests existed across France (Van Andel and Tzedakis, 1996). The ash layers still preserve calcareous ash crystals. Evidence of randomly distributed artifact orientations, a low percentage of lithic edge damage, and a low frequency of dry bone breaks demonstrates that very few changes have occurred within YZ through post-depositional processes (Dibble et al., 2009). Evidence of deciduous trees, thermoluminescence dates corresponding to MIS 5c, and a dominance of *Cervus elaphus* strongly support the idea that YZ was deposited during a warm interglacial phase. Thus, the temporal placement of this layer along with its excellent preservation has made layer YZ an excellent candidate for further faunal analysis.

For the purposes of this project, it was important to compare faunal material that was deposited during a warm interglacial cycle to fauna accumulated during a colder time period. Two thermoluminescence dates (68.5±6.6, 71.8± 6.7 ka) have been obtained from Level I2 at Pech IV (for the stratigraphic position of this layer see Fig. 1.3), and these provide an average age of 70 ka (McPherron et al., 2012; Richter et al., 2012). A date of 70 ka places Level I2 squarely within MIS 4, and more specifically within D-O event 19 (Boch et al., 2011). Based on speleothem data from the Alps, this D-O event appears to have lasted 950 years, (Boch et al., 2011). The rapid warming phase of D-O 19 has been dated to 71.69 ± 0.22 ka, which was followed by a dramatic cooling trend. If the TL date from Level I2 of 71.8± 6.7 ka is correct, it is possible this level was deposited during the rapid warming phase of D-O 19; however, the second TL date and the error ranges around each date make it most likely that Level I2 was deposited during the colder phase of D-O 19. Additionally, though it is possible that Level I2 may not have been deposited during the coldest time period within MIS 4, Level I2 was deposited during a colder time period than Level YZ. In fact, it has been shown that sea surface temperatures (SST) were considerably colder at 70 ka than at 95 ka (Lehman et al., 2002) (Fig. 1.4).

Faunal material from I2 is well preserved. Laquay's (1981) faunal analysis of this layer found that *Rangifer* were most abundant followed by *Bos/Bison*, and *Equus*. The dominance of these three species supports the idea that Level I2 was deposited during a cold time period. However, it should be noted that *Cervus* and *Capreolus* were also identified in this level, but at a much lower abundances (Richter et al., 2012). Lithics from layer I2 are dominated by scrapers, including some reduced convergent and transverse forms (McPherron and Dibble, 1999). Again in this layer, tools do not appear to have been utilized intensively, as the blank-to-core ratio is high and the tool-to-flake ratio is low (McPherron and Dibble, 1999). Tools from this level are most closely characterized as belonging to the Quina Mousterian (Richter et al., 2012). This industry is characterized by a high percentage of scrapers (50-80%), which includes simple thick scrapers, convex scrapers, scrapers with scalariform retouch, and transverse scrapers (Bordes, 1968). No hearth lenses have been found in this level and there is very little evidence of bone burning. However, the extent of bone burning is further investigated and documented in this study. The excellent preservation of fauna from I2 and its placement within the long cold glacial cycle of MIS 4 have made this level ideal for additional faunal analysis.

Roc de Marsal. Roc de Marsal (RDM) is a cave site located on a steep cliff face 80 meters above a valley floor. The plain below the cliff is traversed by a small tributary of the Vézère River. The site was originally 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; Skinner, 1997). The remains of the child were originally thought to have been intentionally buried (Bordes and Lefille, 1962), and this interpretation has been included in literature pertaining to Middle Paleolithic burials (e.g., Chase and Dibble, 1987; Smirnov, 1989; Riel-Salvatore and Clark, 2001). However, this conclusion has been challenged (Couchoud, 2003; Sandgathe et al., 2011). In a report on the geological formation of the cave, Isabelle Couchoud (2003) cites evidence for diffuse water runoff within the cave, including areas close to where the child was found. This water runoff created natural pits in the sediments, leaving open the possibility that the child was placed in a natural pit. A team of scientists including Harold Dibble reopened excavations of the site in 2004 with an eye toward reexamining this question along with the goal of excavating and analyzing the site using current archaeological techniques. A recent publication from this excavation provides a detailed examination of the natural pits found in RDM, which the authors describe as having formed when the cave was developing. This new analysis supports the conclusion that the Neandertal child was not intentionally buried (Sandgathe et al., 2011).

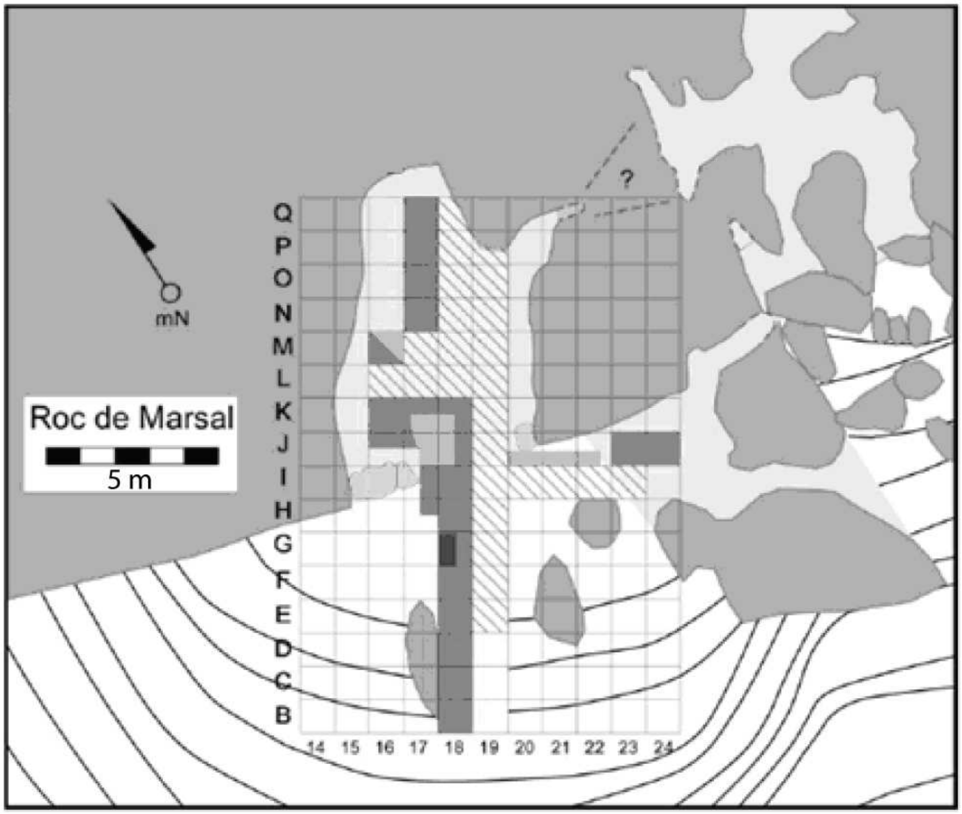

Fig. 1.6. Plan of RDM showing the excavation undertaken during the 2004-2009 field seasons (light and dark grey), as well as the excavations undertaken by LaFille from 1954-1971 (grey stripes). The one-meter-by-one-meter excavation units are shown. Each unit is assigned a letter and a number. This figure is from the 2009 Roc de Marsal site report (Turq et al., 2009).

Excavations at RDM run by Harold Dibble and his team were methodologically rigorous. A depiction of the older excavation undertaken by Lafille and the 2004-2009 excavation can be seen in Figure 1.6. Descriptions of Dibble’s excavation and curation techniques have been well published (see Dibble et al., 2005; 2007; McPherron et al., 2005). All excavated material greater than

25mm in size were piece-provenienced using a total station. Each artifact was then assigned a unique Unit-ID number, which reflects the excavation square in which the artifact was recovered. Material smaller than 25mm were screened and placed in small-finds bags, with a label identifying the square and level (with XYZ coordinates) from which it came. The faunal remains analyzed in this study come from Dibble's excavations of the site.

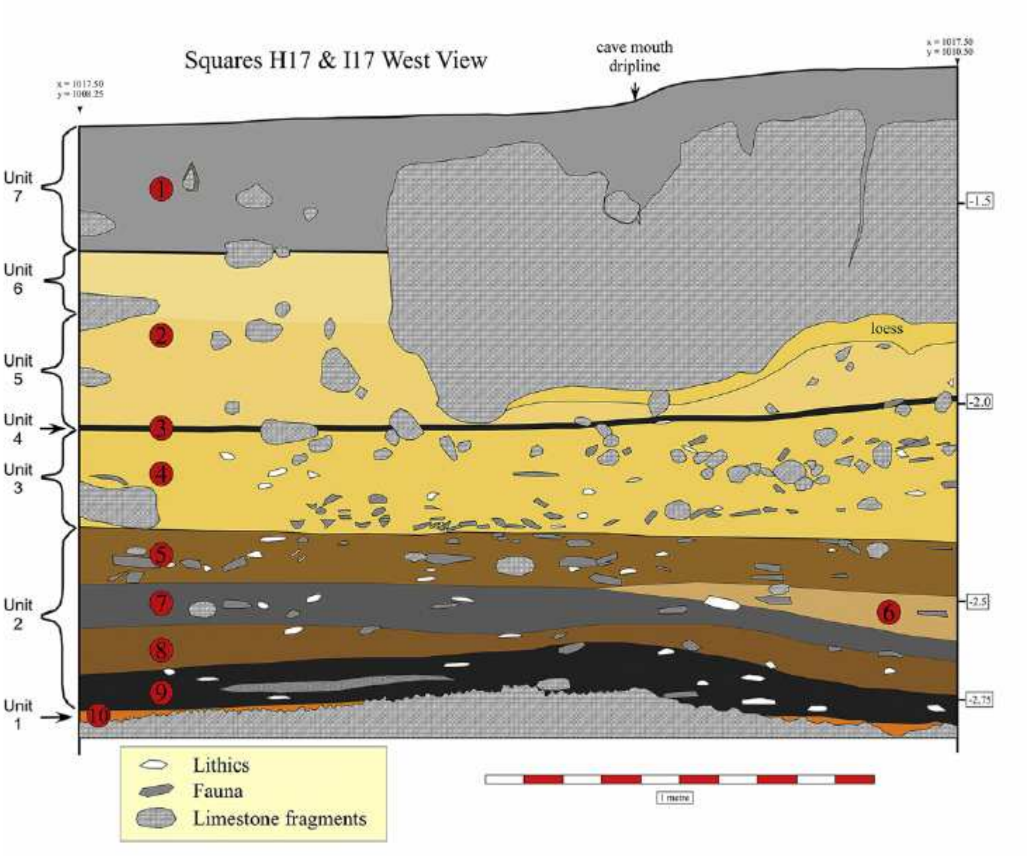

Fig. 1.7. Stratigraphic section from squares H17 and I17 at Roc de Marsal. Level designations are shown in red. This figure is modified from Guérin et al. (2012).

Recently, dates have been reported for RDM (Sandgathe et al., 2011). 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 (located toward the base of the stratigraphic levels; Fig.1.7), and provide an average age of 81.8 ka (Sandgathe et al., 2011). This places Level 9 within the warm interglacial of MIS 5a (Genty et al., 2003, 2010; Dorale et al., 2010), and in line with the MIS 5a "highstand event" that occurred from 84-80 ka, in which the sea level rose one meter above levels observed today (Dorale et al., 2010). It should be noted that the ages listed above are in disagreement with age estimates recently published by Guérin et al. (2012). In their study, Guérin et al. (2012) published a series of nine TL age estimates that provide an average age of 63.6 ka (Guérin et al., 2012) for Level 9. According to Greenland ice core records (NGRIP), the dates obtained by this study may place the deposition of Level 9 during D-O 18, a rapid warming event within MIS 4 (Boch et al., 2011). The rapid warming phase of this event has been dated to 64.17 ka and the interstadial lasted until 63.81 ka (Boch et al., 2011). Thus, regardless of which age estimates are used, the deposition of Level 9 appears to have occurred during a warm climatic phase. A pilot study for this dissertation found that *Cervus* was the most dominate taxa at the site, *Rangifer*, *Bos/Bison*, *Capreolus* and *Equus* were also present in this layer, but at lower abundances (Fig. 1.8). These results are in agreement with a taxonomic analysis conducted by Maryléne Patou-Mathis for fauna excavated from the same stratigraphic level at RDM by LaFille (in Sandgathe, et al. 2007; Guérin et al., 2012). Thus, results from these faunal analyses further indicate that Level 9 was deposited during a warmer time period. The dates reported by Sandgathe et al. (2011) are used in Figure 1.4.

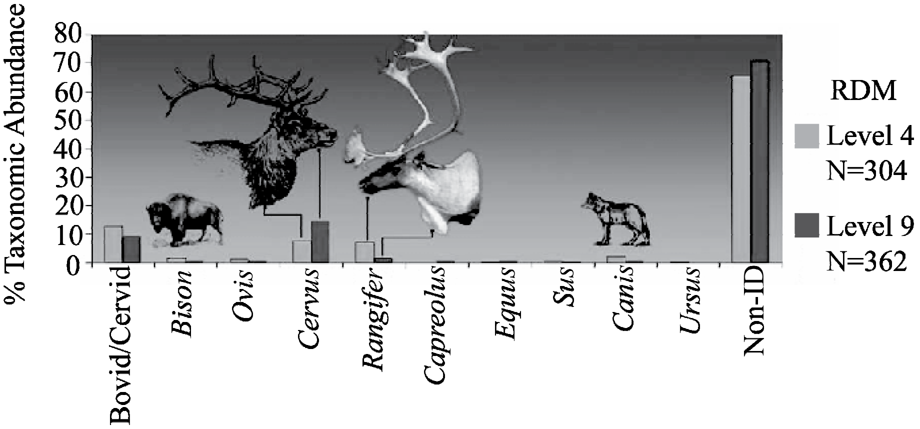

Fig. 1.8. Number of identifiable specimens determined from a study conducted by me in 2007 of layers 4 and 9 from Roc de Marsal (RDM).

The coassociation of *Cervus*, *Rangifer,* and *Capreolus* is not uncommon for sites in the Dordogne valley (see Table 1.1, the description of fauna found at Pech IV, and Delpech, 1983; Grayson and Delpech, 2003; Discamps et al., 2011). However, even among recently published papers, the presence of these species together is noted as unusual. In a recent paper on RDM, Guérin et al., (2012) state the following:

> For Layers 9-4 the ungulate remains pattern is complex, since *Rangifer tarandus* remains are found in association with abundant *Cervus elaphus* (red deer) and *Capreolus capreolus* (roe deer) remains—taxa that are generally indicative of more temperate conditions.

As will be discussed later in this dissertation, *Rangifer* exist today in boreal forest and tundra ecosystems. Given the paleoenvironmental reconstructions of southwestern France, it appears that this area remained forested even during colder time periods. Thus, it should not be surprising that *Rangifer* maintained a consistent presence throughout the Pleistocene. King and Graham, (1981) noted that species with differing ecological needs can coexist, but in different ecological contexts one species may thrive while the other struggles, thus causing relative species abundances to change. King and Graham (1981) thus recommend using species abundance data to reconstruct paleoenvironment. 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 along with the dominance of *Cervus* support the finding that Level 9 was deposited during an interglacial cycle. Interestingly, hearth lenses occur in this layer (Fig. 9) along with burned faunal and lithic remains. The extent of burned bones is further examined in the current study.

Fig. 1.9. Ash and charcoal lenses from Level 9 at RDM. Photo modified from Sandgathe et al., (2011).

Age estimates have also been obtained for the base of Level 4 at RDM as Electron Spin Resonance places this layer between 80-72 ka (Sandgathe et al., 2011). These dates correspond to the start of MIS 4, which begins at approximately 74 ka, and is generally characterized as a long cold MIS stage (Johnsen et al., 2001). Once again, recently published age estimates by Guérin et al. (2012) are in disagreement with dates published by Sandgathe et al. (2011). In the Guérin et al. (2011) study, two TL age estimates (45.4 ± 3.5 ka and 61 ± 6.8 ka) were obtained for Level 4 at RDM (Guérin et al., 2012). These dates correspond to the end of MIS 4 and to middle of MIS 3 respectively (Fig. 1.4; Johnsen et al., 2001; Van Andel et al., 2004; Genty et al., 2003, 2010). The date of 61 ka places this layer within Heinrich event 6 (Gentry, 2010), which has been labeled the first glacial maximum (Van Andel et al., 2004). The date of 45 ka places this level within the long cold decline of D-O event number 12 (Gentry, 2010). Thus, the time period in which Layer 4 was deposited appears to have been fairly cold, globally based on either set of dates. However, for this dissertation, the dates provided by Sandgathe et al (2011) are used in Figure 1.4. Artifacts are abundant in this level. The lithic material is dominated by scrapers, including Quina scrapers (Sandgathe et al., 2008). Faunal remains excavated from the site are dominated by *Rangifer*, but also include *Bos/Bison*, *Equus*, *Cervus* and a small sample of *Capreolus* (Fig. 1.8; Sandgathe et al., 2011; Guérin et al., 2012). Microfauna from the site include the water vole *(Arvicola terrestris*), common vole *(Microtus arvalis*), narrow-headed vole (*Microtus gregalis*), snow vole (*Chionomys nivalis*), and the tundra vole (*Microtus malei*)

(Sandgathe et al., 2011). Thus, faunal analyses do confirm that this level was deposited during a glacial cycle. No hearth lenses have been found in Layer 4 and burnt bones and lithics are rare. The abundance of faunal material recovered from this layer and dates that align it with MIS 4-3 have made it highly useful for the current study.

Ecological and migratory history of mammals

In order to understand Neandertal behavior and local ecology, it is critical to reconstruct the behaviors of their prey, including whether herbivores were long distance round trip migrants or whether they stayed within smaller ranges. Generally, populations of woodland ungulates are less mobile than tundra and grassland ungulates because food resources are distributed in patches that are geographically closer together in woodland environments than in open tundra and grassland ecosystems (Skogland, 1984; Senft et al., 1987; Tyler and Oritsland, 1989; Johnson et al., 2001, 2002a, 2002b). It has also been observed that modern humans and carnivores that hunt migratory species are more mobile and live at lower population densities than hunter-gatherers and carnivores that hunt non-migratory species (Moran, 1981; Winterhalder, 1981; Mills and Shenk, 1992; Wiessner, 1996; Ballard et al., 1997; Heinsohn, 1997; Kormondy and Brown, 1998). For example, Sharp (1977) reported that the Chipewyan hunter-gatherers, who specialized on migratory tundra *Rangifer*, chose dwelling locations on the basis of *Rangifer*. That is, Chipewyan camps only lasted as long as *Rangifer* were in the region; once the *Rangifer* left, the people split into smaller bands and dispersed. Oswalt (1966:27) gives a very similar description of Chipewyan movement patterns, writing that, “settlements in which these Indians lived ranged from an individual family dwelling in total isolation from others to clusters of as many as seventy separate households. The size of any community was a function of the time of the year and the availability of food resources.” In additional studies, as many as 800-1000 Chipewyans have been reported as coming together for communal hunts during *Rangifer* migrations (Smith, 1978). In general, Native Americans that depended on migratory *Rangifer* for a majority of their food were found to be highly mobile throughout the year (Speck and Eiseley, 1942, Oswalt, 1966; Burch, 1972; Smith, 1978; Burch, Kelly, 1983; Custer and Stewart, 1990). The Nunamuit, for example, moved residential camps 10 times per year, over an average total distance of 724.7 km/year. Similarly, members of the Montagnais, who inhabited the northern tundra environments of Quebec, moved residential camps 50 times per year, over an average distance of 1800-3600 km/year (Speck and Eiseley, 1942; Kelly, 1983). In general the mobility pattern described here is known as logistical mobility (as defined by Binford, 1980), which is characterized by groups of hunter-gatherers that travel to collect resources, eventually taking them back to a residential base. One important component of this mobility pattern for hunter-gatherers is that it allows different groups (family groups, hunting groups, etc.) to be in contact with each other year round in a collective effort to track the movements of migratory species across the landscape. For example Smith (1978:83), who studied the Chipewyans states the following:

> For the more normal pattern of movement, the Caribou Eater hunting groups were strategically situated in a long front, with relatively shallow depth, near treeline, from a point west of the Hudson Bay to the Great Slave Lake [~1000 km]. There they overlapped with their northern

> branch, the Yellowknives…They were thus potentially in contact with all the constituent herds of the Kaminuriak, Beverly and Bathurst populations of caribou. The hunting groups may be viewed as strategically situated reconnaissance patrols for collecting information on caribou movements and intentions…. The information network allowed Chipewyans to know of caribou abundance or scarcity.

One important strategy employed by hunter-gatherers who practice logistical mobility is that they store food resources. Binford (1978) reported that Nunamuit hunters would butcher a *Rangifer* carcass, place some of the meat on a sled to take back to camp, while some meat was cached to be retrieved later. Often caches of meat were marked by placing the head of the deer with the antlers positioned up, over the meat, so that the hunter could find the location again later. Binford (1978) also found that the Nunamuit often dry meat on drying racks to preserve it over time. Evidence for meat preservation and storage is lacking in the archaeological record of Neandertals. It has been suggested that Neandertals dried meat in order to preserve it (Sørensen, 2009), but drying racks made out of wood or antlers are not likely to preserve. The use of food caches marked by deer skulls and antlers are also not likely to survive. It is therefore possible that food storage in the form of dried meat was a behavioral adaptation used by Neandertals, but as of yet there is no record of it. Nevertheless, if Neandertals were living in open tundra environments with hunting economies dependent on migratory *Rangifer*, the Chipewyan, Nunamuit and Montagnais appear to be good modern analogues.

On the other hand, if Neandertals inhabited boreal forest environments, with hunting economies focused on multiple species of herbivores, then different modern hunter-gatherer analogues need to be found. Studies of hunter-gatherer groups that lived in boreal forest environments located in northeastern North

America (e.g., the Naskapi, Montagnais, Eastern Cree, and the Attikamek) have reported that these groups were generalized foragers who occasionally hunted woodland *Rangifer*, but also hunted a broad range of species, especially other cervids (e.g., moose: *Alces alces*) (Speck and Eisley, 1942; Custer and Stewart, 1990). Speck and Eisley (1942) described the mobility patterns of these boreal forest Native American groups as less mobile than groups living on the barren grounds. In general hunter-gatherers in these boreal forest environments practiced residential mobility (as defined by Binford, 1980), moving camps within the boreal forest to places where resources were available. Ethnographic studies revealed that these groups traversed an average of 285 km/year, with a maximum distance of 500km/year and minimum distance of 150km/year (Custer and Stewart, 1990:317). Additional reports of boreal forest hunter-gatherers include Northern Athapaskan groups, who lived on the Upper Tanana River in southeastern Alaska. For half of the year, these groups also focused on hunting large terrestrial ungulates within the forest. These animals were viewed as stable and evenly spaced food resources by ethnographers (Heffley, 1981).

> The basic exploitive unit … was the two-family hunting group (8-20 people). When the available resources were moose, sheep, and small animals these smaller groups scattered into the forest… (Heffley, 1981:141).

These groups were recorded as changing their location of their camps five times during the winter and if food was not available, they would sometimes move daily within the forest (Heffley, 1981).

The pattern that hunters who focus on migratory prey have larger hunting ranges (and therefore longer movements) than hunters who focus on non-migratory prey, appears to be an ecologically driven pattern that applies to hunters in general (humans and nonhumans alike). Carnivores, such as wolves (*Canis lupus*) and mountain lions (*Puma concolor*) that focus on migratory prey also have larger hunting ranges and smaller populations than conspecifics that hunt sedentary prey (Pierce et al. 1999; Fuller, 2004). For example Fuller (2004:46) reports that, "for wolves that depend only on these [migratory] caribou for food, the best survival strategy is to move with the caribou when they can, and when they can't (during the denning season) they make many long trips to hunt caribou." Conversely, Fuller (2004:46) states that, "Prey that have small home ranges themselves will seem relatively sedentary to wolves, and a wolf pack's territory might consistently contain the amount of prey required for wolves to persist." In this last case, wolves hunt within their home range. It is interesting that wolves can move with a migrating herd for some time, while modern humans do not; however, it is not likely that Neandertals could follow migratory herds closely either. Migrating *Rangifer* move on average 25-30 km/day (Kelsall, 1968). As Burch (1972:345) points out,

> No hunting band, with women, children, and aged, could hope to follow them for even a day or two when they are migrating unless the animals belong to one of the smaller, more sedentary herds which move "vertically" into mountain areas rather than horizontally in their annual tundra-forest movement. Even if adult male hunters in superior physical condition could keep up with the migrating animals for a while, they would not have time to butcher the meat, and unprocessed carcasses would be scattered thinly over a wide area in a very short time. The energy expenditure would be so great, and the net production so low, as to be disastrous for people who tried it.

Importantly, studies have found that due to their larger body mass, Neandertals likely had high basal metabolic rates and would have needed to consume more calories/day than modern humans (Froehle and Churchill, 2009). Thus, it is likely that Neandertal groups who hunted migratory animals would have had mobility patterns that allowed them to intercept migration routes as modern hunter-gatherer groups have been observed to do. This type of hunting behavior may have required Neandertals to move more than 1000 km/year. On the other hand, if they hunted non-migratory herds, Neandertals likely would have hunted within the home range of the caribou. If this is the case, it is possible that Neandertal hunting ranges were akin to those observed among Native American groups from the northeastern United States, roaming 150-500 km/year. Either way, the studies presented here demonstrate that prey migration patterns are likely to have had a profound influence on Neandertal ecology, and understanding the migratory behaviors of Neandertal prey in the Dordogne region of France will have important implications for reconstructing the movement patterns and group sizes of these hominins.

Migration analyses of herds in the French Paleolithic

The dominant view among researchers focused on the Paleolithic hunting economies of southwestern France is that European Pleistocene ungulates, particularly *Rangifer*, were migratory in the sense that they undertook long distance round trip migrations (Burch, 1972; Sturdy, 1975; Bahn, 1977; Gordon, 1988; Straus, 1997; Morin, 2004; Britton et al., 2011; Delagnes and Rendu, 2011). For example, it has been proposed that *Rangifer* spent their winters in southwestern France and northern Spain, but during the summer they would move north to areas where tundra existed (e.g., Scandinavia (~3216 km) or Switzerland (635 km), or up into the mountains close to glaciers (e.g., the Massif Central (~88–140 km) or Pyrénées (260 km)), or that they would make seasonal movements between the Massif Central and the Bay of Biscay (~300 km) (Arbos, 1932; Bahn, 1977; Dibble and Rolland, 1992; Mellars, 1985; Gordon, 1988; Straus, 1997). The bulk of the archaeological evidence supporting the hypothesis that *Rangifer* in southern France were migratory has come from seasonality studies based on the eruption, wear and cementum growth on herbivore teeth and antler growth patterns (Bahn, 1977; Delpech, 1983; Gordon, 1988; Burke, 1995; Enloe and David, 1997; Burke and Pike-Tay, 1997). For example, the lack of adult male antlers, but the presence of antlers from females and fawns, suggests a winter occupation while the presence of attached antlers on both male and female *Rangifer*, suggests a spring to fall occupation (Bouchud, 1954, 1966; Delpech, 1983; Pike-Tay, 1991; Burke and Pike-Tay, 1997. Recently, Britton et al. (2011) conducted a radiogenic strontium isotopic study of *Rangifer* and *Bison* teeth from the site of Jonzac (also known as Chez-Pinaud), located in the Charente-Maritime region of southwestern France, and also concluded that *Rangifer* from that site were likely migratory. However, analyses of antler growth patterns, cementum growth, tooth wear and faunal-based paleoecological studies have also been used to argue that *Rangifer* in this region were not migrating long distances (< 80-100 km; see Bouchud, 1966; Mellars, 1985; Burk, 1995). Accordingly, it has been suggested that at least some groups of *Rangifer* were present year round (Lartet and Christy 1875; Bouchud, 1966, Delpech, 1983; White, 1985; Pike-Tay, 1991).

The issue of whether or not mammals were undertaking long distance migrations is important for reconstructing the movements of Neandertals (Binford, 1973; Bahn, 1977; Spiess, 1979; Gordon, 1988). Ideas about hunter-gatherer mobility in the European Paleolithic have been driven by studies of *Rangifer* archaeological remains and based on ethnographic research of hunter-gatherers who specialized on migratory *Rangifer* herds (Spiess, 1979; Mellars, 1985; Burke and Pike-Tay, 1997). However, the remains of other species of animals (e.g., *Bison*, *Equus*, *and Cervus*) are abundant in Paleolithic archaeological sites and the behaviors of these species should be considered as well when reconstructing the behaviors of their hunters (Spiess, 1979; Mellars, 1985, Dibble and Rolland, 1992; Burk, 1995; Burke and Pike-Tay, 1997). In a broad analysis including stone stool reduction, faunal remains and paleoclimatic reconstructions, Dibble and Roland (1992) suggested that during cold glacial cycles when *Rangifer* dominated faunal assemblages Neandertals may have had long winter occupations in southwestern France, moving little during the winter months. During interglacial cycles when *Bison*, *Cervus* and *Equus* dominated archaeological sites, Neandertals may have been more mobile: occupying sites for short periods of time. Other researchers have pointed out that the abundance of animal species present during the Middle and Upper Paleolithic of southwestern France may have created a stable and predictable supply of food year-round, possibly leading to less mobile hunter-gatherer groups (Spiess, 1979; Mellars, 1985). Burke and Pike-Tay (1997) have suggested that if seasonality data on *Cervus*, *Rangifer* and *Equus* remains from Late Upper Paleolithic sites in southwestern France are compared to each other, the data indicate an annual hunting range of only 40-50 km within the northeastern portion of the Aquitaine Basin. Recent studies have found that *Bison* excavated from Pleistocene archaeological sites in France and southeastern Ukraine were non-migratory (Britton et al., 2011; Julien et al., 2012). Thus, if Neandertals from Pech IV and RDM had access to reliable terrestrial resources year round, this may indicate that they were living in small groups that practiced residential mobility, moving camps within the Dordogne Valley to places where resources were available similar to hunter-gatherers groups living in boreal forests (Speck and Eiseley, 1942; Smith, 1983; Dods, 1998; Binford, 2001).

The reconstructions of Pleistocene *Rangifer* in southwestern France as highly migratory may be reasonable (at least given tundra *Rangifer* as a comparative model). However, in order to understand Neandertals better, it is necessary to further test these hypotheses and to determine as precisely as possible the geographical locations to which *Rangifer* and other large herbivores were moving.

Historical documentation of the movement patterns of *Rangifer, Bison, Cervus*, and *Equus*

Recently, ecologists have emphasized that the word migration is used to describe many types of movement patterns including round trip travel, one-way movements, altitudinal shifts, and nomadism, in which an animal does not follow a predictable route, but forages opportunistically (Dingle and Drake, 2007).

Ultimately migratory behaviors are a response to ecological stimuli, and thus groups within one taxon can exhibit different behaviors (Dingle and Drake, 2007). Long distance round trip migratory behavior in large ungulates has been shown to be selectively advantageous to 1) enhance temporary access to high quality food resources in areas that cannot be inhabited year round, and 2) to reduce risk of predation in open environments where animals are easily visible (Fryxell and Sinclair, 1988; Tyler and Oritsland, 1989). Insects also drive movement patterns in large ungulates (Downes et al., 1986; Russell et al., 1993; Grayson and Delpech, 2005). Barren ground *Rangifer* and *Bison* that live in productively poor ecosystems (e.g., some grassland environments) migrate over vast distances seasonally. The average round trip migration distance measured among three different herds of barren ground *Rangifer* is 1673±491 km, with the longest distance measured at 2500 km (Bergerud, 1974; Brown et al., 1986; Berger, 2004). Similarly, *Bison* that occupy habitats that are low in productivity have large home ranges: 712 km^2-1240 km^2 (Hanson, 1984; Reynolds et al., 2003; Berger, 2004). *Bison* that inhabited the Canadian Plains are thought to have undertaken long distance migrations that were greater than 300 km in length (Morgan, 1980; Chisholm et al., 1985). However, many groups of woodland *Rangifer*, woodland *Bison*, European *Bison* and even American *Bison* that inhabited tall grass prairies have been described as non-migratory (Stardom, 1975; Shoesmith and Storey, 1977; Helle, 1979; Fuller and Keith, 1981; Darby and Pruitt, 1984; Edmonds and Bloomfield, 1984; Hanson, 1984; Senft, 1987; Tyler and Oritsland, 1989; Krasinska and Krasinski, 1995; Krasinska et al., 2000;

Berger, 2004; Widga et al., 2010; Julien et al., 2012). For example, the Svalbard *Rangifer* of Norway are largely sedentary (Tyler and Oritsland, 1989), while *Rangifer* from southeastern Manitoba are reported as non-migratory—roaming within ranges that vary from 100-180 km^2 in the spring, 175-190 km^2 in the summer, 115 km^2 in the fall and 90-140 km^2 in the winter (Darby and Pruitt, 1984). Similarly, *Bison* that have inhabited productively rich environments such as the American *Bison* that inhabited the tall grass prairie roamed within a 50 km radius (Widga et al., 2010), and European *Bison* that live in the forests of Bialowieza are non-migratory (Krasinska and Krasinski, 1995; Krasinska et al., 2000). Thus, diversity has been observed in the movement patterns exhibited among different groups of *Rangifer* and *Bison*, and this variation can be related to differences in habitat.

Woodland *Rangifer* live throughout Canada (e.g., north-central British Columbia, northwestern Quebec, Labrador, Ontario, northeastern Alberta), and in the northwestern United States (e.g., Idaho, Montana and Washington) (Evans, 1960; Layser, 1974; Brown et al., 1986; Stuart-Smith et al., 1997; Johnson et al., 2001; Johnson et al., 2002b). Woodland *Rangifer* are present in the Norwegian arctic archipelago of Svalbard and in Finland (Tyler and Oritsland, 1989; Kojola et al., 2004). In North America, woodland *Bison* historically inhabited much of the same habitats as woodland *Rangifer* with species ranges extending from northwestern Canada into eastern Alaska (Reynolds et al., 2003). In Europe, the woodland bison (*Bison bison bonasus*), [thought to be closely related to the North American woodland bison (*Bison bison athabascae)* and to the now extinct species *(Bison priscus)*] inhabited forests in northern, eastern, and western Europe (Pucek et al., 2004, Julien et al., 2012). The environments inhabited by woodland *Bison* and woodland *Rangifer* are composed of mosaic habitats of pine and spruce woodlands with feather mosses and lichens, shrub/sedge and forb-dominated wetlands, river and lake environments, alpine shrublands and alpine grasslands (Johnson et al., 2002b). In general, the mobility patterns of *Rangifer* and *Bison* appear to be regulated by the temporal and spatial variability of high quality resources, particularly lichen, sedges and grasses (Johnson et al., 2001; Johnson et al., 2002a; Tyler and Oritsland, 1989; Larter and Gates, 1991). The fact that most populations of woodland *Rangifer* and *Bison* are less mobile than individuals that live in more open environments is most likely because food resources are distributed in patches that are geographically closer together in the mosaic woodland, boreal and alpine forest environments than in the open tundra and grassland ecosystems (Johnson et al., 2001; Johnson et al., 2002a; Tyler and Oritsland, 1989). Also, the tree cover in woodland environments may offer some protection from predators, insects and snow cover (Johnson et al., 2001; Johnson et al., 2002a; Tyler and Oritsland, 1989).

To better understand the diversity of prey animals available to Neandertals in the Dordogne Valley over time, two additional species found at Neandertal sites in high abundance are analyzed in this study: *Equus caballus* and *Cervus elaphus.* Analysis of the movement patterns of horses found at Pech IV and RDM are largely exploratory, as not much is known about how these animals would have behaved in the past. Several subspecies of *Equus caballus* have been identified from Pleistocene sites in France (e.g., *Equus caballus gallicus*, *Equus caballus germanicus*) (see Delpech, 1983). These subspecies are closely related to *Equus przewalski* (also sometimes referred to as *Equus caballus przewalski* or *Equus ferus przewalski)*, a species which is now extinct in the wild, but lived on the steppes of central Asia, Russia, Mongolia and China until the early 1900's (George and Ryder, 1986; Groves, 1994; Wakefield et al., 2002; Burke et al., 2003; Jenkins and Ashley, 2003). A woodland subspecies of the Przewalski horse (*Equus przewalski silvaticus)* is also known to have inhabited forests in the Republic of Belarus, Lithuania, Poland and Germany until the early 1800's (Pruski, 1959; Groves, 1994). To date the best information available about the mobility patterns of *Equus* in the past come from a radiogenic strontium isotope study conducted by Hoppe and Koch (2007), who sampled three equid teeth from the late Pleistocene of Florida. They found that the mobility patterns among these equids varied: samples from two teeth indicated long distance movements greater than 150 km and one tooth indicated movements within a local range. Because of the dearth of knowledge about the movement behaviors of wild equids, the radiogenic strontium isotope analysis conducted here will help clarify how this species behaved in the Pleistocene of southwestern France, as well as adding to information about the availability of Neandertal prey at the sites of RDM and Pech IV.

Although not much is known about the behavior of wild equids, a significant amount of research has been conducted on the movement patterns of *Cervus elaphus* (Georgii, 1980, 1983; Pike-Tay, 1991; Albon and Langvatn, 1992; Peek, 2003; Steele, 2004). *Cervus* populations are widely distributed with extant populations ranging throughout western North America, northern Africa, and from Western Europe to Siberia (Mahmut et al., 2002; Peek, 2003). Many *Cervus* populations are known to move from lower altitudes in the winter to higher altitudes in the summer (Albon and Langvatn, 1992). This seasonal altitudinal shift prolongs access to high quality food resources (Albon and Langvatn, 1992). However, as is the case with the other large herbivores studied here, a great deal of variability has been observed in *Cervus* movement patterns (Georgii 1980, 1983; Albon and Langvatn, 1992; Schmidt, 1993; Peek, 2003, Steele, 2004), with some groups (including populations in the Alps) undertaking long distance round trip migrations, while other groups are non-migratory (Georgii 1980, 1983; Peek, 2003). Once again, this variability in migratory behavior and home range size appears to be the product of the availability of high quality resources, difficulty of travel, cover quality and the presence of insects (Brazda, 1953; Peek, 2003).

This extensive knowledge about the environments in which modern populations live, and the movement behaviors undertaken by herds living in different types of environments, can be used to help form expectations about how populations of animals would have behaved in the past. Despite the fact that the more common view within European Paleolithic archaeology has been that Pleistocene *Rangifer* were migratory, much of the ecological literature has concluded that during the Pleistocene much of southwestern Europe, acted as a refugium for trees (e.g., spruce, pine, oak, elm, beech), faunal species and hominids (de Beaulieu and Reille, 1992; Barron et al., 2004; Huntley and Allen, 2004; Gamble et al., 2004) during cold climatic oscillations (Although see, Bruxelles and Jarry, 2011). As mentioned previously, reconstructed temperature ranges for southern France between 74-59 ka appear to have been similar to temperatures observed in modern boreal forests, inhabited by woodland species today (e.g., mean annual temperatures during the Pleistocene southwestern France = - 4 - 6 °C; mean annual temperatures in modern boreal forests = -5 - 5°C (Whittaker, 1976; Barron et al., 2004). If these temperature reconstructions are accurate, then mammals living in these environments may have behaved more like extant woodland-dwelling ungulates in undertaking localized non-migratory movements within the Aquitaine Basin (Lartet, 1875; Bouchud, 1966, Delpech, 1983; White, 1985; Pike-Tay, 1991). If this is true, it is possible that the Neandertals that hunted these populations may have stayed within the Aquitaine Basin themselves: ranging within the region, but not moving far beyond. Further isotope-based mammal migration analyses will help to answer this question. Given the known climatic instability of the late Pleistocene it is important to note that modern studies have demonstrated that in certain circumstances, individual *Rangifer* and/or herds of *Rangifer* can change their migratory behavior. For example in Canada, woodland *Rangifer* of the Caniapiscau herd have been observed to join the George River herd, migrating as far as 520 km with that herd before returning to their regular calving grounds (Brown et al., 1986). In some cases, range expansion by woodland *Rangifer* has been observed in times of above average snowfall (Brown et al., 1986). Thus, if global cold climate changes extended to local Neandertal habitats, causing boreal forests to give way to more open environments, then the migration patterns of prey species should have changed, requiring Neandertals to intercept migratory herds.

Radiogenic strontium isotopic mobility studies

Radiogenic strontium isotopic studies have been used to track mobility patterns in modern and archaeological animal and human populations (e.g., Ericson, 1985; Price et al., 1994; Hoppe et al., 1999; Knudson et al., 2004; Britton et al., 2011; Scharlotta, 2011) including fossil hominids (Richards et al., 2008; Copeland et al., 2010). To "ground-truth" the method for such uses in fossil *Rangifer*, Britton and colleagues (2009) analyzed radiogenic strontium isotope ratios from the teeth of extant caribou belonging to the Western Arctic Herd in Alaska for which movement patterns are known. Results from their analysis showed that the ratios found in the second and third molars of each deer broadly matched the geological ratios throughout the migration route demonstrating that this is an effective method for tracking caribou migrations. As summarized in Price et al. (2002), radiogenic strontium isotope ratios are useful for tracking migrations because the bedrock of a particular geological region has a characteristic isotopic signature. Older rocks (e.g., granites) tend to have higher values (0.710-0.740), and younger rocks (e.g., sedimentary rocks such as limestone) tend to have lower values (0.707-0.709) (Bentley, 2006). Thus, the radiogenic strontium isotope values found in old versus young rocks are distinct. The radiogenic strontium isotope values present in bedrock is eroded by water, carried into water systems and taken up by plants, which are ingested by herbivores. The strontium is incorporated into herbivore teeth as a substitute for calcium; consequently, the $^{87}Sr/^{86}Sr$ value in an herbivore's teeth is generally indicative of where the animal was as its dentition developed. Thus, studying radiogenic strontium ratios from distinct enamel layers, developed over multiple seasons, can determine if an animal was migrating. If the $^{87}Sr/^{86}Sr$ values within one region are distinct from the values in adjacent areas, then the radiogenic strontium isotope value found in enamel layers of migrating herbivores that forage across regional boundaries will be distinct from the ratios found in resident populations. Conducting a radiogenic strontium isotope analysis to reconstruct the migratory behaviors of herbivores from France is promising, because the interior basins of France (Paris and Aquitaine Basins) are composed of young sedimentary rocks (Wilson, 1998); thus, herbivores foraging within this area would have picked up low radiogenic strontium isotope values in their teeth. In contrast, the mountains that create the borders of France are composed of older granitic rocks (Wilson, 1998), and herbivores foraging in the mountains would have picked up higher radiogenic strontium isotope values in their teeth. Pech IV and RDM exist within the sedimentary Aquitaine Basin. If herbivores from both cave sites were non-migratory, the radiogenic strontium isotope values sampled throughout their teeth should have consistently low values that reflect values found in the basin. As discussed previously, the dominate view within Paleolithic archaeology of France is that Pleistocene mammals were migratory, and all reconstructed movement patterns for *Rangifer* suggest that they moved from sedimentary basins into granitic mountain ranges (Arbos,1932; Bahn, 1977;

Dibble and Rolland, 1992; Mellars, 1985; Gordon, 1988; Straus, 1997). If herbivores from Pech IV and RDM undertook long distance round trip migrations moving from sedimentary basins into older mountain ranges, and returning to the sedimentary basin, the radiogenic strontium isotope values in their teeth should change from lower values to higher values to lower values over the course of dental development.

Hypotheses and predictions

As detailed above, stratigraphic layers from Pech IV and RDM are ideal for testing whether cold climates stressed Neandertal populations, because they occur toward the end of the Pleistocene era, a time characterized by climatic instability, but before modern humans entered Europe; thus, competition with other hominins is removed as a confounding factor.

Specific prediction for zooarchaeological analyses. If Neandertal populations underwent stress during cold-climate periods, then faunal material processed during cold phases should reflect intensified butchering strategies (see analytical methods for specifics).

Possible outcomes for zooarchaeological analyses. If bone processing behaviors are consistent throughout warm and cold climatic phases, then zooarchaeological evidence will not detect changes in the stress level of Neandertals induced by climate. This result will have two implications:

1) The climate change was not extreme in the Dordogne Valley. This outcome will be secondarily tested though analysis of the migration behaviors of herbivores excavated from Pech IV and RDM.

2) Neandertal behavior was not flexible enough to change with changing climates. If Neandertals were in fact stressed during cold climate phases, but unable to change their subsistence behaviors, then this lack of flexibility maybe one of the reasons they could not survive.

Zooarchaeological and taxonomic analyses can provide information on Neandertal behavior (i.e., hunting preferences, transport behaviors, butchering strategies). However, testing the assumption that the Dordogne Valley was affected by global climate change requires an independent assessment of the ecology of the Dordogne. As discussed above, isotope analysis can trace the mobility patterns of fossil mammals, and the migratory behaviors of mammals can be tied to an animal's adaptation to an environment.

Specific Prediction for radiogenic strontium isotope analyses. If global climate instability extended to the Dordogne Valley, causing periods of extreme cold, then the migratory behaviors of ungulates in the region should change from being non- migratory in warmer periods to migratory in colder periods.

Possible outcomes for radiogenic strontium isotope analyses. Further interpretive implications are listed as bulleted points below each specific outcome:

1) If migratory behaviors change between stratigraphic layers deposited in warm and cold climates, this would demonstrate that local environmental changes were severe enough to induce behavioral changes in the mammals living in the valley.

- Similarly, if zooarchaeological analysis reveals that bone processing behaviors also change between warm and cold layers, this would further indicate that local environmental changes caused Neandertals to react to them. This outcome would be consistent with the hypothesis that climatic factors played a role in Neandertal extinction by reducing the carrying capacity of the local environment, causing herbivores to undertake long distance migrations, and thereby forcing Neandertals to intercept migratory herds.
- If the bone processing behaviors of Neandertals did not change between warm and cold layers despite changes in mammal migration patterns, this may indicate that Neandertals were able to cope with changes without altering their behavior, or that Neandertal behavior was not flexible enough to cope with the changing climate and migration patterns.

2) If mammals in both warm and cold layers behaved like woodland species (i.e., only migrating over short distances (as demonstrated by low variation in the radiogenic strontium isotope values found in enamel samples taken from individual herbivore teeth) this would suggest that local climates in the Dordogne were not greatly affected by global climate changes. This outcome would provide evidence that the Dordogne Valley was a stable refuge in the Pleistocene and may explain the long survival of Neandertals in this region of France.

- If it is found that Neandertal behavior still changed between layers despite the lack of behavioral change in their prey, this may indicate that Neandertal behavior was simply changing over time for reasons other than shifts in animal movement patterns. Alternatively, it may indicate that the local climate did not change enough to affect the behavior of mammals in the valley, but colder temperatures still placed stress on Neandertals. It is also possible that ecological and geographical barriers prevented mammals in the valley from changing migratory behaviors in cold climates. The inability of herbivores to forage for resources outside of the Dordogne Valley may have placed nutritional stress on herbivores resulting in a population reduction that in turn placed stress on the Neandertals.
- If Neandertal behavior did not change between warm and cold layers, this would confirm results from the migration study that climates did not change enough to have caused behavioral changes in Neandertals or mammal populations.

3) If the herbivores analyzed here in both warm and cold layers were migratory over long distances, traveling over mountain ranges between European countries, this would provide evidence that the local environment of the Dordogne Valley was more open with nutrients poorer in quality and quantity, and thus less sheltered than modern woodland and boreal forest ecosystems. Such an environment is unlikely to have been a refugium and would have been more affected by global climate changes.

- If Neandertal bone processing behaviors changed even though mammal migration patterns did not, this may still support the notion that cold climates stressed the hominin populations.
- If Neandertal behaviors did not change between warm and cold layers, this might suggest that they were not stressed by climatic changes—possibly in part because the behavior of their prey remained constant.

CHAPTER 2: METHODS AND MATERIALS

ZOOARCHAEOLOGICAL METHODS

Sites

The sites of Roc de Marsal and Pech IV provide effective case studies for testing hypotheses regarding climate-induced ecological stress on Neandertals. These caves have been well dated and it has been demonstrated that one level from each cave (Pech IV Level I2 and RDM Level 4) was deposited during a cold phase within Marine Isotope Stage (MIS) 4, and one level from each cave (Pech IV Level YZ, and RDM Level 8) was deposited during a warmer climatic phase. These dates make an analysis of Neandertal subsistence behaviors across time and global temperature oscillations possible. Faunal material excavated from all four levels was studied at the Musée National de Préhistoire in Les Eyzies, France, where the Pech IV collection is currently housed. The RDM collection is housed in the town of Carsac (~30 km from the museum), but this material was transported to the museum for analysis.

Sample selection

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 YZ n = 4847) including an abundance of cervid and bovid/cervid remains. For this reason analyzing all bone fragments from all four levels was not feasible. Instead, bone fragments from both levels at each site were selected at random from all excavation squares. In the end, of the archaeological material excavated at RDM data were collected on 2068 bone fragments from the cold Level 4 (~10% of the total sample) and 1922 bone fragments from the warm Level 9 (> 50%). At Pech IV, data were collected on 910 bone fragments from the cold Level I2 (>10% of the total sample) and 727 bone fragments from warm level YZ (>15%). Selecting fauna for analysis from the RDM collection was greatly simplified by the systematic way in which the collection has been curated and stored. As mentioned in the background section, all specimens from this collection have been individually bagged with each specimen's Unit-ID number written on the bag.

Faunal material from Bordes' excavation of Pech IV was not as organized as the collection from RDM. Basic information about Bordes' curation techniques was provided in the background section; however, I will briefly describe my role in the organization of the assemblage. When I first began to work with faunal material from Bordes' excavation in 2005, part of it was housed at the Institut de Préhistoire et de Géologie Quaternaire at the Université de Bordeaux I, while the small finds bags were housed in an off campus storage facility. At that time, most of the collection was organized into bags by square. Specimen numbers were written on each bone, so the task was to identify bone fragments that belonged to levels I2 and YZ. This was done by pulling individual bone fragments out and matching their specimen number to their excavation level using the database created by Harold Dibble, Shannon McPherron, Alain Turq and their team (see background section). Over a three week period in 2005, a portion of the assemblage was organized in this way. During this organization process, I discovered that another portion of the assemblage was already organized into boxes by square, level and taxon. These specimens had been organized by Guy Laquay who had analyzed the material in 1981. While, this organization scheme only applied to a subset of the collection, it did help to isolate some of the cervids for analysis. In 2007, all of the material from Bordes' excavation (including the small-finds bags) was moved to the Musée National de Préhistoire in Les Eyzies. The organization of bone fragments into levels was greatly facilitated by the move, and this organizational work continued over a period of a month and a half in 2007, and again for a month in 2010. It is important to note, that as mentioned in the background section, small finds from Bordes' excavation were not given specimen numbers. However, small-finds bags did contain tags indicating the elevation from which the bone fragments were excavated. These elevations could then be matched to the minimum and maximum level elevations. Thus, specimens (mostly shaft fragments) that were thought to be too small or unidentifiable were organized into the same assemblage by level as the numbered specimens and were thus sampled for analysis in the same way. Numbers were also assigned to each unnumbered specimen. Time did not permit the full reorganization of this collection, but as of March 2011, several thousand bone fragments had been sorted by level.

Taxonomic assessment

The goal of the zooarchaeological component of this study was to collect taphonomic, taxonomic and behavioral information from skeletal elements of artiodactyls in the size 2 (21-113 kg), and 3 (114-340 kg) body size range (following Bunn, 1988) that were excavated from levels I2 and YZ at Pech IV and 4 and 9 and RDM. Artiodactyls within this body size range from the Pleistocene of southwestern France are largely dominated by *Cervus*, *Rangifer*, and *Capreolus* (see Kurtén, 1968; Delpech, 1983; Laquay, 1981; Dibble et al., 2009). Thus, identifications of fragments were 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). Importantly, the museum in Les Eyzies has a mammalian osteological reference collection including full skeletons of all three cervids, as well as other size 2/3 ruminants (e.g. sheep *Ovis,* goat *Rupicapra,* musk ox *Ovibos*), which were utilized for taxonomic identification. The purpose of focusing on small to medium artiodactyls, and three species of deer specifically through time and temperature changes, was done to control for two variables. First, it has been observed that animals that vary significantly in overall size and anatomy are butchered differently (White, 1954; Binford, 1978; O'Connell et al., 1990; Lyman, 1992, 1995; Monahan, 1998); therefore, restricting analysis to morphologically similar animals helps to control for these factors. Second, because this is a study investigating 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 that has been well studied (see Bunn et al., 1988; O'Connell et al., 1988, 1990; Lyman, 1995; Monahan, 1998; Hill and

Hurtado, 1996) and continues to be studied (Schoville and Otarola-Castillo, in prep). 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 and O'Connell et al., 1988, Monahan, 1998). It has also been reported that among the Evenki, all skeletal elements of *Rangifer* are transported to a central place for processing, although the Evenki did use sleds and domesticated *Rangifer* to help with transport (Abe, 2005). 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, from Nowak and Wilson, 1999), *Rangifer tarandus* (91-169 kg, from Miller, 2003); *Capreolus capreolus* (15-50Kg, from Nowak and Wilson, 1999).

Even though this analysis was structured so that only animals with a high likelihood of transport were chosen, skeletal element transport analyses (see below) were performed in order to understand which elements from these animals were transported most often. The main hypothesis tested in the zooarchaeological analysis of this dissertation is that cold climate oscillations caused nutritional stress in Neandertals. However, no specific predictions have been made for how climate would have impacted the transport strategies of Neandertals. To date, no skeletal element transport studies have compared transport decisions made by hunter-gatherers in cold versus warm environments. Perhaps this study will be helpful in determining if predictable transport differences existed between glacial and interglacial climatic oscillations in the European Paleolithic. Although no specific predictions have been made, it is still relevant to analyze skeletal element representation at Pech IV and RDM simply to assess which elements were being transported more often, and to determine if transport decisions made by Neandertals match decisions made by modern hunter-gatherers (see Binford, 1978; Faith and Gordon, 2007). In his pivotal 1978 study, Binford calculated the meat, marrow and bones grease associated with each skeletal element, and he recorded which skeletal elements were chosen by the Nunamiut Inuit for transport. The data collected in this analysis allowed Binford (1978) to establish basic transport strategies, which are referred to as utility indices. These indices reflect the bulk, unbiased, and gourmet transport strategies. More recently Faith and Gordon (2007) have added the unconstrained transport strategy to this list. Each of these strategies is described in the following section.

Skeletal element analysis

In addition to the taxonomic and size identification procedures described above, several more methods were used to analyze faunal fragments from both caves. Data generated by these methods were entered into Microsoft Access, Bone Entry GIS and Bone Sorter (following Marean et al., 2001; Abe et al., 2002). First, all fragments were identified as specifically as possible to skeletal element, and element side. Long bone shaft fragments were of particular interest in this analysis because dense cortical bone is more resistant to taphonomic destruction and carnivore modification than epiphyseal ends and bones of the post-cranial axial skeleton, which have lower density and contain more bone grease (see Marean and Spencer, 1991; Marean et al., 1992; Marean and Frey, 1997; Marean and Kim, 1998; Marean 1998; Lam et al., 1999; Marean and Cleghorn, 2003; Pickering et al., 2003; Cleghorn and Marean, 2004, 2007; although see Stiner, 2004). Due to their higher probability of preservation, limb bone shaft fragments maybe more indicative of the original number of skeletal elements transported to a cave site (see Cleghorn and Marean, 2004, 2007; Marean and Frey, 1997; Lam et al., 1999; Marean and Cleghorn, 2003, 2007; Pickering et al., 2003; Faith and Gordon, 2007; Yravedra and Dominguez-Rodrigo, 2008). These elements have been dubbed the high survival set (see Marean and Cleghorn, 2003), which includes: crania, mandibles, humeri, radioulnae, metacarpals, femora, tibiae and metatarsals. The high survival set can be used in calculations of minimum number of skeletal elements (MNE) and individuals (MNI). When bone fragments of skeletal elements from the high survival set are used in calculations of MNE, taphonomic factors that affect bone representations, such as density mediated destruction, and carnivore consumption of epiphyseal ends may be controlled.

During analysis, the presence and completeness of diagnostic landmarks on each skeletal fragment was also recorded (e.g. greater trochanter 10% present). Teeth were identified as specifically as possible to their anatomical position and taxon. The age of specimens was noted when possible by coding elements as fused or unfused and noting the wear pattern on teeth. Bone and tooth fragments that were identifiable to skeletal element and side were then drawn onto a bone template in ArcView GIS 3.3 (see Marean et al., 2001; Abe et al., 2002). Drawing fragments into GIS allowed the MNE and MNI to be calculated by overlapping all fragments drawn onto a template and counting the number of times fragments overlapped. It also provided a record of the shape and placement of each fragment. The use of ArcView GIS for calculating MNE will be discussed in detail in a section entitled "Zooarchaeological data presentation."

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 the number of times the element appears in the complete skeleton of an animal (See Binford, 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 (see Binford, 1978). It should be noted that for cranial and mandibular remains the MNE and %MAU were calculated both with identifiable teeth included and without identifiable teeth include. Providing both values make the data broadly comparable for researchers who choose to include or not include dentition in their calculations. However, in this dissertation the %MAU was calculated with identifiable teeth included, and these % MAU values were used in analyses of skeletal element abundances in order to estimate the number of cranial remains and mandibles that were transported in each archaeological level. Once calculated, the %MAU was plotted for each high survival skeletal element to visually determine the transport patterns utilized at each site. The %MAU was also 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 (Metcalfe and Jones, 1988). Plotting the %MAU versus the SFUI for each archaeological level allowed 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 bones are transported except those of the lowest utility; 2) the gourmet strategy, where only the highest quality bones are transported; and 3) the unbiased strategy, where bones 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 skeletons are transported, thus all bones are transported equally.

In an effort to come to a more detailed understanding of how Neandertals were prioritizing which skeletal elements to transport to a cave site, an analysis was done comparing the %MAU with the standardized marrow index created by Binford (1978:27). The marrow index is a numerical representation of the grease value (fat quality, marrow quantity) and the efficiency of accessing and processing the grease (ml of grease processed/min work) for the skeletal element in question. In Binford's study, the marrow quantity was calculated by measuring the marrow cavity volume of each bone (Binford, 1978: 24). Fat quality was calculated based on the percentage of oleic acid (unsaturated fat) in the marrow of each bone (Binford, 1978: 24).   The efficiency of processing bone marrow was based on marrow extraction experiments that correlated marrow cavity volume data with the amount of time it took to extract the marrow (Binford, 1978:26). Through a series of conversations with the Nunamiut Binford learned that fat quality was the most important variable used when ranking the relative values of different skeletal elements for marrow utility. Thus, in the creation of his marrow index, Binford increased the mathematical weight of fat quality over efficiency. However, Binford remarked that the ease with which marrow was extracted did play a role in the decision-making processes about which bones to save and which to discard for marrow processing. For example, he states, “In addition, experience with the Eskimo led me to believe that their decision making regarding abandonment or retention of parts for the extraction of marrow was related to their experience with the ease of extraction (Binford, 1978:25).” This last statement suggests that marrow utility and ease of access can affect hunter-gatherer decisions about which bones to discard and which to keep. It is possible that these decisions influence the choice of which skeletal elements to transport for processing. For this reason it is important to compare skeletal element representation data at Pech IV and RDM to indexes of marrow utility to understand if skeletal elements with high marrow utility are well represented at each site. In this study, the marrow index values provided by Binford for proximal and distal portions of all high survival elements were summed to create a whole bone standardized marrow index. The bone with the highest value was used as the standard for a normed scale: each skeletal element’s whole bone marrow index value was divided by the highest index value found in the sample and multiplied by 100.

Binford's marrow index calculations have been criticized by Jones and Metcalfe (1988) for being overly complicated. They suggest that marrow cavity volume is sufficient for understanding how Nunamiut rank different skeletal elements for marrow utility. Jones and Metcalfe (1988) found a strong correlation between the actual skeletal elements used by Nunamiut in marrow processing and marrow cavity volume (r_s=0.93). However, Morin analyzed the data presented by both Binford (1978) and Jones and Metcalfe (1988) and found that when square-root transformed marrow cavity volumes were plotted against bones that were actually used by the Nunamiut during marrow processing, two linear relationships emerge (Morin, 2007:73). In this analysis Morin found that metapodials, radioulna, carpals and tarsals were selected more often than would be predicted based on marrow cavity volume alone. However, these skeletal elements are high in oleic acid. Morin (2007:77) therefore put forward the unsaturated marrow index (UMI), which takes into account the marrow cavity volume of each skeletal element and the proportion of unsaturated fat present in the marrow (data presented in Binford, 1978: 24). This index has been argued to be more productive than simply analyzing bones based on their fat quantity (marrow cavity volume), because hunter-gatherers appear to have a preference for marrow with high proportions of unsaturated fat (Stefansson, 1921; Wilson, 1924; Binford, 1978; Morin, 2007). Thus, in addition to utilizing Binford's marrow index, % MAU data from Pech IV and RDM were compared to the UMI to determine if Neandertals were preferentially transporting bones that were high in overall marrow content and high in unsaturated fat.

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 bulk, gourmet, unconstrained, and unbiased 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: $\text{evenness} = -\Sigma\, p_i \ln p_i / \ln S$, 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 (rho) 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 (rho) 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, the calculation of both evenness and rho helps to determine the following: 1) if Neandertals were transporting skeletal elements in direct relationship to their utility (unbiased strategy); 2) if Neandertals were transporting all skeletal elements except for those with the lowest utility (bulk strategy); 3) if Neandertals were transporting elements of the highest utility (gourmet strategy), or 4) if Neandertals were transporting all skeletal elements (unconstrained strategy).

Analysis of nutrient extraction behaviors

A suite of techniques have been used to observe and quantify processes of intentional bone breakage (caused by either hominids or carnivores) and non-intentional bone breakage (caused by taphonomic processes). These methods were developed by Villa and Mahieu (1991), who defined a set of criteria that can be used 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 unintentionally broken while in a dry state (non-nutritive). Such unintentional 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 (following Villa and Mahieu, 1991). The method aims 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 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. For example, based on actualistic experiments in which skeletal elements were broken for only marrow extraction, the expected frequency of elements with fresh-bone breaks is 85± 3% (Blumenschine 1988; Capaldo 1998, 1995; Marean et al. 2000); under stressful conditions, the intensity of fragmentation is expected to be higher (Marean et al. 2000; Outram 2001, 1999). During this portion of the analysis, the maximum length and breadth of all bone fragments were measured to provide an estimate of fragment size (for more on this, see section below regarding the statistical analysis of the data).

Surface modification analysis

The last set of techniques used to analyze faunal remains involves detailed observations of bone surfaces. Surface modification analysis (analysis of cut, percussion, tooth marks, etc.) enables the intensity 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 (see Binford, 1981, 1988; Brain, 1981; Potts and Shipman, 1981; Shipman, 1981; Blumenschine and Selvaggio, 1988;

Blumenschine, 1995; Blumenschine et al., 1996; Pickering et al., 2004; Marean et al., 2004; Dominguez-Rodrigo and Barba, 2006; Pickering and Egeland, 2006). It has been shown (Blumenschine et al., 1996) through a series of 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 (Dominguez-Rodrigo and Barba, 2006), trampling marks vs. butchering marks (Olsen and Shipman, 1988; Fiorillo, 1989; Dominguez-Rodrigo et al., 2009), and to distinguish tooth marks created by different carnivores (Dominguez-Rodrigo and Piqueras, 2003; Pickering et al., 2004). The criteria outlined in each of these studies were utilized to examine each fragment from Pech IV and RDM, including non-identifiable fragments from size 1, 2 and 3 mammals using incident lighting and a 45x binocular microscope. Every surface modification mark observed on a bone fragment was then drawn onto the image of that fragment within ArcView GIS. The surface modification marks were labeled with the specimen number of the fragment allowing for the number of marks per fragment to be quantified. As with the analysis of bone breakage, these data were then compared to baseline values established from actualistic experiments (e.g. Blumenschine 1988; Capaldo 1998, 1995; Marean et al. 2000).

Indicators of ecological and nutritional stress using surface modification

Researchers interested in the subsistence behaviors of Neandertals have typically focused on the patterns, placement and frequency of cut marks and percussion marks on faunal remains to infer butchering practices (e.g., Binford, 1981, 1985; Stiner, 1991, 1994; Mellars, 1996; Chase, 1994, 1989; Chase et al., 1994; Grayson and Delpech, 1994, 1998, 2003; Marean 1998; Marean and Kim, 1998; Marean and Assefa, 1999; Boyle, 2000; Burke, 2000; Conard and Prindiville, 2000; Gaudzinski, 2000; Patou-Mathis, 2000; Costamagno, 2006). The frequency with which surface modification marks are found on archaeological faunal bone fragments and their linkage to butchering strategies has led researchers to address whether such marks can be used to infer the level of stress (in this case nutritional stress) experienced by hominids (Egeland, 2003; Marean, 2005; Egeland and Byerly, 2005; Costamagno, 2006; Pickering and Egeland, 2006). As discussed above, for taphonomic reasons all of the studies just listed focused on high-survival long bones. Observations from ethnographic studies (Jenness, 1959; Oswalt, 1966; Hearne, 1968; Binford, 1978; Bunn et al., 1988; O'Connell et al., 1988; Monahan, 1998; Nilssen, 2000) and archaeological finds (Outram, 1999, 2001; Bar-Oz and Munro, 2007) have revealed that under stress hunter-gatherers will fully processes epiphyseal ends and extract all marrow in order to access stores of fat and calcium. Furthermore, all meat will be cut from bones (Binford, 1978, 1981; Nilssen, 2000; Marean, 2005). Therefore it is likely that an abundance of cut and percussion marks on long bones, including evidence of heavy processing of epiphyseal ends (Binford, 1978; Outram, 1999, 2001, Marean, 2005) could provide a strong signal of nutritional stress. It should be mentioned here that because epiphyseal ends are subject to taphonomic processes that tend to remove them from the archaeological record (see taxonomic methods above for a review) an abundance of epiphyseal ends are not expected to be found. However, of those remaining, it is expected they should show signs of percussion marks if hominids were processing them for nutrient extraction (Marean, 2005). In addition, evidence of surface modification marks on bones with low nutritional value (i.e., low meat and marrow yields) such as the phalanges of medium-to-large ungulates may also provide evidence of intensive bone processing by hominids (Bar-Oz and Munro, 2007; Jin and Mills, 2011).

The full suite of analyses described above are necessary for investigating butchering intensity in the archaeological record (e.g., investigation of cut marks, percussion marks, and evidence of heavy processing of epiphyseal ends and on low marrow-yield bones). It has been observed that in isolation each of these analyses will not indicate stress. For example, Jin and Mills (2011) have recently pointed out that hunter-gatherers will sometimes preferentially crack open the phalanges of artiodactyls and consume the marrow. Thus, modification marks on phalanges themselves are not necessarily indicative of stress, but evidence of heavy processing of all long bones including phalanges does suggest effort was put into extracting all calories from a carcass. Similarly, it has been pointed out that surface modification marks are accidental by-products of butchering behavior—that is, the goal of the butcher is not to create a cut or percussion mark (Pickering and Egeland, 2003; Lyman, 2005). Experimental data have revealed that a one-to-one correlation does not exist between the number of cutting strokes taken by a butcher and the number of cut marks left on a bone (Egeland, 2003), nor between the number of impact events taken to break a bone open for the extraction of marrow and the number of percussion marks (Pickering and

Egeland, 2006). Therefore, cut marks and percussion marks analysis of long bones in isolation from other zooarchaeological measures may not be indicative of stress. However, an abundance of surface modification marks on high-survival marrow-yielding long bones coupled with evidence of percussion marks on low marrow-yielding phalanges and percussion marks on epiphyseal ends can be taken as evidence of intense butchering behaviors likely to occur in times of stress (Outram, 1999, 2001; Egeland, 2003; Marean, 2005; Egeland and Byerly, 2005; Costamagno, 2006; Pickering and Egeland, 2006; Bar-Oz and Munro, 2007; Jin and Mills, 2011).

All inclusive analysis of the intensity of butchering

As discussed in the last section, inferring the intensity of butchering in the archaeological record has been a contentious issue. Thus, in this analysis the intensity of butchering (the proxy for stress) was measured using a suite of characteristics incorporating evidence from all zooarchaeological methods described above including 1) the frequency of nutritive-bone breaks on all skeletal elements 2) the relative frequencies of epiphyses compared to mid shafts, controlled by other density-mediated destruction processes (i.e., carnivore ravaging) (Marean 2005, 1991; Outram 2001, 1999); and 3) the frequency and distribution of cut marks (Binford 1981, 1978; Nilssen 2000) and percussion marks (Pickering and Egeland 2006) on all long bones including low marrow-yielding phalanges and epiphyseal ends. In addition to these measures of nutrient extraction, the MNE of high survival elements (Marean and Cleghorn 2003) was compared from all levels to see if elements were transported equally (Faith, 2007;

Faith and Gordon, 2007), or if they were transported based on their associated meat marrow and bone grease (Binford, 1978; Metcalfe and Jones 1988; Morin, 2007). Skeletal element abundance analyses are used here to help determine Neandertal transport strategies.

Bone burning

Another type of bone surface analysis involves recording evidence of bone burning. Recording the color of burned bones has been found to be an effective method for documenting the extent of bone burning in the archaeological record (Buikstra and Swegle, 1989; Stiner et al. 1995). In fact, Buikstra and Swegle (1989) note that, “for bone that shows incomplete combustion of organic materials (smoked), color patterning is the best indicator of pre-incineration conditions.” Stiner et al.’s (1995) experimental tests helped to define a set of criteria for coding the extent of burning on bone fragments (e.g., 0 = not burned (cream/tan), 3= fully carbonized (black), 6= fully calcined (completely white)). These criteria were used in this study. It should be noted the evidence for the use of fire has already been studied at RDM and Pech IV. An interesting pattern has been found at these sites. Hearth lenses and burned bone fragments are present at these two cave sites in levels deposited during warm climate phases, but evidence for fire is lacking in layers deposited during glacial cycles (Sandgathe et al., 2011). Because this pattern has already been documented, predictions were not made in this dissertation for how burning behavior should have changed during warm and cold climatic oscillations. Instead the goal of this analysis was to provide more evidence for the use of fire at RDM and Pech IV, and to further investigate whether the burning behavior at these sites match behaviors documented in experimental analyses. For example, research by Costamagno et al. (2009) has shown that different burning behaviors leave different signatures in the archaeological record. These burning behaviors include 1) accidental burning, caused by natural fires or by dropping bones close to a hearth, 2) use of bones as fuel, a pattern focused on epiphyseal ends, and 3) bones burned for both cleaning and for use as fuel for fires, a pattern where shafts and epiphyseal fragments are burned. The frequency of burned bone fragments, carbonized fragments, and spongy bone fragments associated with each of the bone burning behaviors described above will be discussed in the discussion section.

Zooarchaeological data presentation

Often in the literature, the abundance of species, skeletal elements, post-depositional bone breakage, hominid induced bone breakage, and surface modification marks (cut, percussion, tooth marks, etc.) are represented by the Number of Identifiable Specimens (NISP). Presenting data in this way allows other analysts to see the basic characteristics of a faunal assemblage and enables them to manipulate the data as they choose before any quantitative transformations have been done (see Grayson and Frey, 2004; Thompson, 2008); thus, data from the current study are presented in this way as well. However, NISP counts can be greatly inflated by extensive bone breakage (Abe et al., 2002; Grayson and Frey, 2004; Otarola-Castillo, 2010). It has been argued that NISP values of assemblages from different layers, sites or even different areas of the same site, may not be comparable if behavioral and taphonomic processes that result in bone breakage were not equally applied to all faunal material analyzed (Abe et al., 2002). The ArcView GIS program (developed in the early 2000s and run on windows XP) helps to get around this issue. This program allows bone fragments drawn onto the same template (e.g. same skeletal element and side) to be virtually overlapped (see description in Abe et al., 2002). GIS will graphically show where fragments overlap each other and will assign different colors to different numbers of overlaps (e.g. 0 overlaps=light blue, 1 overlap = medium blue, 2 overlaps =dark blue, etc.). The highest number of overlaps for a given skeletal element is equal to the minimum number of elements (MNE). Mapping bone fragments onto a bone template also allows the total surface area of bone analyzed to be calculated. Surface area is calculated by the number of pixels that compose a bone template. Bone templates have been created for a number of taxa so that analysts can map bone fragments onto templates for the specific animal being analyzed. What makes this approach even more useful is that each specimen drawn onto the GIS template is connected to a database where all zooarchaeological information describing that fragment is stored. Therefore, MNE analyses can be tailored to the specific question being asked. For example, in this study it was possible to find the MNE for left tibiae of size 2/3 bovid/cervids from level I2 at Pech IV. The data generated by this query as well as many similar queries will be presented in the results section. As mentioned above, once the MNE is found, other derived measures can be calculated, such as the minimum animal unit (MAU): the number of times the element appears in the body (See Binford, 1984; Grayson, 1984). The calculation of the minimum number of individuals can also be calculated by finding the highest number of overlaps among all skeletal elements from particular taxon or group (e.g. size 2/3 bovid/cervids) excavated from a specific site and level (Abe et al., 2002).

The ArcView GIS program was not only established to map bone fragments and calculate MNE and MNI. It was also designed to aid in surface modification analysis. The program allows all surface modification marks to be mapped onto bone templates and allows the number of marks to be standardized by the total surface area of bone analyzed (see Abe et al., 2002). The procedures for this analysis are as follows: 1) all surface modification marks are drawn on bone templates; 2) the placement of surface modification marks and the frequency with which they occur in different portions (proximal epiphysis, proximal shaft, etc.) of skeletal elements are calculated; 3) the percentage of bone surface area recorded per anatomical region (e.g. proximal epiphysis, proximal shaft, etc.) are determined; 4) the corrected number of cut marks (CNC) is calculated by dividing the number of cut marks per anatomical region by the percentage of bone surface area recorded for the same anatomical region; 5) the CNC is then divided by the total CNC for the whole bone and multiplied by 100. These procedures are outlined in Abe et al. (2002), however for step 3 above it is important to understand that the GIS method calculates the surface area of all fragments drawn on to a template, which means that in areas where multiple fragments overlap, the surface area represented will be greater than 100%.

In addition to allowing the number of modification marks be standardized by total surface area analyzed, one of the major benefits to using the ArcView

GIS program for modification analysis is that it creates a visual representation of the anatomical position of each mark. Images of the placement of cut marks on bones can then be compared to ethnographic studies that detail the pattern of surface modification marks created by modern butchers (Nilssen, 2000). For example, Nilssen has documented the frequency and placement of cut marks created on bones by filleting, and filleting plus disarticulating meat and bones. With the aid of ArcView GIS surface modification, marks from RDM and Pech IV were compared to Nilssen's data.

Zooarchaeological statistical analysis

As discussed above, there are many benefits to using ArcView GIS for zooarchaeological analysis. However, one drawback of the GIS method is that it does not allow surface modification marks to be included in analyses when they are observed on unidentifiable fragments because these fragments cannot be mapped onto a specific bone element or side. Likewise, because unidentifiable bone fragments cannot be mapped the amount of surface area that was analyzed from those bone fragments cannot be quantified. As described in the introduction, the goal of this analysis is to understand if cold climates stressed Neandertal populations by determining if butchering intensity changed between warm and cold climatic cycles. Therefore, in this study it was critical to analyze surface modification marks preserved on all specimens and to quantify the total surface area analyzed for all fragments.

Following the recommendation of Jungers et al. (1995), who evaluated a number of techniques to account for size correction in morphometric analyses, a size proxy for each fragment was calculated as the geometric mean of the maximum length and width measurements. The geometric mean is calculated as the square root of the product of length and width. Therefore, butchering intensity was quantified in this study for all identifiable and unidentifiable marrow yielding long bone fragments including the metapodials (high survival long bones, following Marean and Cleghorn, 2003) and the phalanges (Bar-Oz and Munro, 2007) of animals in the size 2/3 body size category by using the fragment size proxy to correct the per fragment count of modification marks for comparison between sites and climatic conditions.

A generalized linear model was applied to test the hypotheses that butchering intensity varies significantly by 1) site (i.e., Pech IV and RDM) and 2) climatic conditions (i.e., warm vs. cold). The generalized linear model (e.g., Meyers et al., 2010) 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. 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. Because surface modification marks comprise count data (and for some fragments counts of zero), the model assumed a Poisson distribution (Zar, 1999), which is beneficially applied to ranges of values that include small numbers (Whitaker, 1914). 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, thus allowing the statistical evaluation of the following question: for each site, is the mean number of modification marks per bone fragment (i.e., butchering intensity) greater in the cold-climate layers than it is in the corresponding site's warm-climate layers? Possible alternative outcomes are 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 (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 layer of the other (an interaction effect). Significant effects were considered at an alpha level of < 0.05. All statistical analyses were conducted using Statistica 7. 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.

In another analysis, cut mark count data obtained from the ArcView GIS corrections were used in conjunction with chi-square goodness of fit tests and actualistic data from animal-butchery experiments in an effort to infer butchery patterns based on the frequency of cut marks on different parts of long bones. As mentioned above, ArcView GIS was used to record the placement of all cut marks on size 2/3 bovid/cervid skeletal elements, and then to calculate the frequency with which cut marks were found on specific anatomical regions of long bones (e.g., proximal epiphysis, etc). Once the frequency of cut marks per long bone anatomical region was known, this information was then compared to experimental data reported by Nilssen (2000). In his study, Nilssen observed, filmed, and recorded the location of cut marks produced by modern butchers, who were butchering large and small bovids at Merriman in central South Africa. Nilssen's study documented the frequency and placement of cut marks produced by different butchering behaviors. For example, he recorded the number of cut marks produced while removing all flesh from skeletal elements, which he called "filleting", and the number of marks created by removing all flesh and disarticulating attached elements, which he referred to as "filleting and disarticulating". To date, this study is unique in providing expected frequencies of cut marks produced on distinct anatomical portions of all skeletal elements (e.g., on long bones distinct anatomical portions include the proximal epiphysis, proximal shaft, mid shaft, etc.). Archaeological samples can be compared to these actualistic data in an effort to infer different butchering strategies. Thus, for this analysis, calculated frequencies of cut marks in all long bone anatomical regions from RDM and Pech IV were used as observed values in the randomized chi-square goodness of fit test, with expected values coming from Nilssen (2000). It then randomly drew 1000 samples from a population with the expected frequencies and calculated the chi-square statistic for each sample drawn. The exact p-value for the test was determined as the proportion of those randomized samples with a chi-square value greater than or equal to the chi-square score calculated from the observed data. Statistical significance was assumed at the 0.05 level. P-values less than 0.05 indicate that butchering patterns at RDM and Pech IV are significantly different from the pattern reported by Nilssen (2000), while p-values greater than 0.05 indicate that the butchering patterns at RDM and Pech IV match the butchery pattern in question.

Methods for the paleomobility analysis using radiogenic strontium isotopes

To track the paleomobility patterns of Pleistocene herbivores excavated from levels deposited during glacial and interglacial cycles at Pech IV and RDM, data were collected on archaeological *Rangifer*, *Cervus*, *Bison*, *Equus* and rodent (*Microtus arvalis*) teeth. In addition to these tooth samples, wine, soil, water and snail shells *(Helix aspersa*) were also collected throughout France to identify distinct isotopic regions, and to establish where herbivores may have been living and/or migrating during tooth development. Collection of these context samples, followed standard protocols for developing baseline datasets for strontium (see Evans and Tatham, 2004; Bentley, 2006). Fortunately, the geology of France is complex and characterized by basins (Aquitaine and Paris basins) composed of young sediments and uplifted areas composed of older granites. The presence of these distinctive regions increases the likelihood that mammal migration patterns can be tracked across the landscape.

Radiogenic strontium isotope sample preparation

Radiogenic strontium isotope sample preparation took place in the Archaeological Chemistry Laboratory (ACL) at Arizona State University (ASU) and in the Facility for Isotope Research and Student Training (FIRST) at the State University of New York at Stony Brook (SBU). The separation of the strontium from the sample matrix (which followed procedures described by Horwitz et al., 1992), was conducted in the Metal-Free Clean Laboratory at ASU (W. M. Keck Foundation Laboratory for Environmental Biogeochemistry) and at SBU (in the class 100 HEPA filtered FIRST lab in the Department of Geosciences).

The bulk linear-sampling technique, in which horizontal lines are drilled into each tooth mesial/distally to form enamel powder, has been recommended for studies of herbivore migrations (Scharlotta et al., 2011), and this technique was used here. There are two main reasons why this technique is recommended. The first is that it is now known that the process of tooth formation involves a series of steps before maturation. During this time the enamel matrix is an open system and mixing or averaging of chemicals in the enamel matrix can occur (Fincham et al., 1999; Balasse, 2003; Bentley, 2006; Montgomery et al., 2010; Scharlotta et al., 2011). However, while the overall maturation process of a tooth takes time (weeks to months depending on the species) an overall linear trend exists in the mineralization process which progresses from the tip of the crown to the cingulum, therefore sequentially sampling a tooth from tip to cingulum can determine if an animal was moving across geological boundaries with distinct radiogenic ratios. Secondly, enamel formation is accomplished through the incorporation of different minerals that are available within an animal’s body, which are derived from the diet the animal is consuming. Each of the minerals used in enamel formation is available within the body for a particular period of time, which is known as the "residence time" (Scharlotta et al., 2011). Within herbivore teeth the effect of the residence time is that an abrupt signal may not be seen as an herbivore moves from one radiogenically distinct region to another—instead a more gradual change in $^{87}Sr/^{86}Sr$ values is found (Montgomery et al. 2007, Scharlotta et al., 2011). The residence time of different minerals and the mineralization time of enamel are important factors to consider especially when using microsampling techniques such as laser ablation, which seek to determine isotopic values from closely spaced enamel crystals. Such microsampling techniques are highly sensitive to residence-time and mineralization-time effects, and thus may cause problems for inferring the migration of animals in which the teeth develop rapidly. Thus, the bulk linear-sampling technique is appropriate for the study conducted here.

Radiogenic strontium isotope sample selection

Archaeological samples included first, second and third molars of *Rangifer, Cervus, Equus, Bison* and rodents (with the exception of specimen K17-1418 which is the mandibular fourth premolar of a horse). Studies of dental development and eruption in the large herbivore species just listed demonstrate that these teeth develop over the first few years of life in these animals (see Table 2.1); thus, linearly-sampling layers of enamel from each tooth has the potential to track the movement behaviors of each specimen over the course of tooth development. Because the enamel of many of these teeth mineralizes during the first year of life, it is important to note that weaning does not influence $^{87}Sr/^{86}Sr$ values (Bentley, 2006).

TABLE 2.1. Tooth crown formation and eruption in large herbivores.

Taxon	**Reference**	**Tooth**	**Formation**	**Eruption**
Rangifer	Spiess, 1979; Hillson, 2005; Kelly, 2007; Britton et al., 2011	M1	*in utero* to several months	3-5 months
		M2	3-9 months	10-15 months
		M3	9-18 months	15-29 months
Cervus	Brown and Chapman, 1991; Hillson, 2005	M1	*in utero* to 4 months	3-5 months
		M2	3-9 months	10-15 months
		M3	9-18 months	15-29 months
Equus	Levine, 1982; Hoppe et al., 2004; Hillson, 2005; Kelly, 2007	M1	*in utero* to 1.5 months	7-12 months
		M2	5.5-8.5 months	16-24 months
		M3	18-24 months	2.5-5 years
		P4	16-22 months	3-5 years
Bison	Gadbury et al., 2000; Britton et al., 2011; Kelly, 2007	M1	*in utero* to several months	9-12 months
		M2	birth to 13 months	18 months
		M3	9-24 months	2.25-2.5 years

Ideally, strontium isotope analyses would be conducted on individual mandibles or maxillae with all molars present (see Britton et al., 2011). However, it is often difficult to find well preserved and associated dentitions in archaeological assemblages. In this study, two partial mandibles were found from RDM Level 4 with mostly complete premolar and molar dentitions: specimens J17-2266 (*Bison*), and J18-1379 (*Rangifer*). In these specimens, isotope samples were taken from all available molars (see Fig. 2.1). In addition to these specimens, a *Cervus* mandible (F17-2485) was recovered from Pech IV Level YZ that contained the second and third molars, and these teeth were sampled.

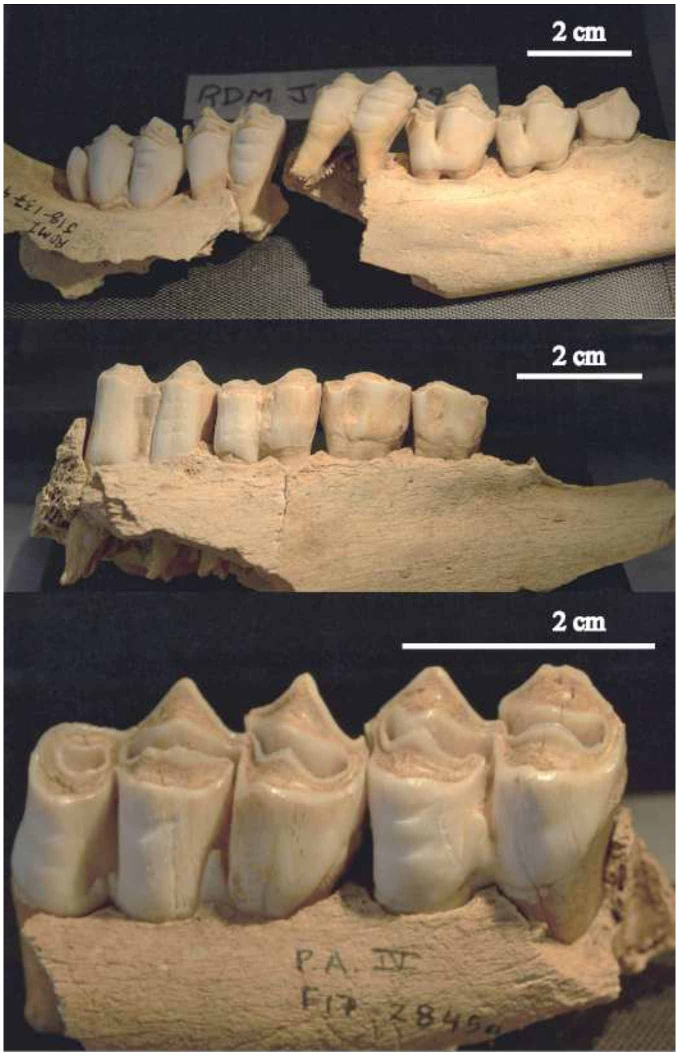

Fig. 2.1. The buccal view of mandibular dentition from a *Rangifer* (top, specimen RDM J18-1379), a *Bison* (middle, specimen RDM J17-2266) and a *Cervus* (bottom, Pech F17-2845). Photographs taken by Jamie Hodgkins and Jennifer Everhart at the State University of New York at Stony Brook.

In order to track the movement patterns of multiple species from different archaeological layers, it was also necessary to analyze single unassociated teeth. Teeth were chosen that appeared to be well preserved, displaying few cracks in the enamel, and with as little discoloration as possible. Teeth were also chosen based on the extent of wear. Teeth categorized as having no wear to early-wear were prioritized; however, these teeth were uncommon and nearly half of the specimens sampled were categorized as mid-wear, which means that strontium accumulated in these teeth during the first few months of development could not be sampled. In the end, a total of 14 specimens were sampled from RDM. From Level 4, these specimens included one *Bison* (partial mandible with dentition), one *Rangifer* (partial mandible with dentition), one *Cervus* and one *Equus* excavated from the middle (one meter by one meter) excavation squares in the cave (Fig. 1.6: J17, J18, K17, J16, K16). For Level 9, these specimens included two *Cervus* and one rodent, excavated from the front and middle excavation squares (Fig. 1.6: G18, F18, K17). Tooth specimens were particularly rare and poorly preserved in Level 9; thus, in an attempt to better understand the movement behaviors undertaken by herbivores during warm climate cycles, teeth excavated from Level 8 at RDM were also analyzed. Electron spin resonance age estimates from RDM indicate that Level 8 is older than 80 ka, and thus was deposited during the MIS 5a-c interstadial (Sandgathe et al., 2011). Specimens analyzed from this layer included: two *Rangifer*, one *Cervus*, one *Equus*, and one rodent excavated from squares located in the middle and front of the cave (K18, K17, and G18). At Pech IV a total of ten specimens were sampled. From Level I2, these specimens included: four *Rangifer*, two *Bison* and one *Equus*, which were excavated from units distributed throughout the cave (Fig. 1.2: D11, C13, E11, D14, F16, D17). Specimens from Level YZ included: two *Cervus* (one partial mandible with dentition) and one *Equus*. These specimens were excavated from a unit located in the front of the cave and from units located towards the right side of the cave (F16, F17, and M15). While every project would benefit from an analysis that includes a large sample of individuals, there are several reasons to believe that the 21 ungulates sampled here will provide useful information about the mobility patterns used by large herbivores over time in southwestern France. First, the specimens included in this project come from well-dated archaeological layers, and within each of those layers the specimens selected were the best preserved of their kind. Second, the species represented in this analysis are known to have different ecological niches. Including each species in this analysis helps to highlight the mobility patterns of each of these animals, which is useful for paleoecological interpretations of the Dordogne Valley through time and also for inferring the subsistence behaviors of the Neandertals. Finally, *Rangifer*, *Cervus*, *Bison* and *Equus* are the four most abundantly represented large herbivore species recovered not only at Pech IV and RDM, but also at most cave sites throughout Europe; thus, the information garnered from this isotope analysis is broadly relevant to Paleolithic archaeologists.

Radiogenic strontium isotope sample processing

The processing of archaeological tooth samples followed procedures outlined in Knudson and Price (2007). All teeth (including rodent teeth) and modern snail shells were mechanically cleaned using a Dremel Minimite-750 cordless drill with a tungsten carbide bur (Dremel engraving cutters number 106). These samples were then rinsed with high purity deionized water (Millipore 18.2 megaohms) and submerged in an ultrasonic bath of Millipore water for 30 minutes. Due to the potential for diagenesis (chemical, physical or biological alterations of skeletal and dental remains after death), the Dremel drill and cleaned carbide burs were used to remove the outer enamel surface of each tooth (Lambert et al., 1989; Hoppe et al. 2003; Budd et al., 2000). For snail shell samples, each shell was drilled in half and both the outer and inner surface of the shell were removed. Shells and rodent teeth were then placed in 10 ml of 0.8 M acetic acid for five to twenty minutes to remove organics, secondary carbonates and soluble apatites (Sillen, 1989; Lee-Thorp and van der Merwe, 1987; Sillen and Sealy, 1995; Koch et al., 1997), and then rinsed with Millipore water. Once the teeth of large herbivores were mechanically cleaned, sampling began by drilling horizontal lines into each tooth to form 4-6 mg of enamel powder (Fig. 2.2). Layers were drilled sequentially down the tooth, with the first layer drilled close to the occlusal surface and the last layer close to the cingulum of the tooth. After each line of enamel was drilled the tooth was again placed in an ultrasonic bath of Millipore water for 10 minutes so that all powder adhering to the tooth was removed before the next sample was taken. The resulting enamel powder from each layer was then analyzed under a light microscope to ensure that no dentin was included in the sample.

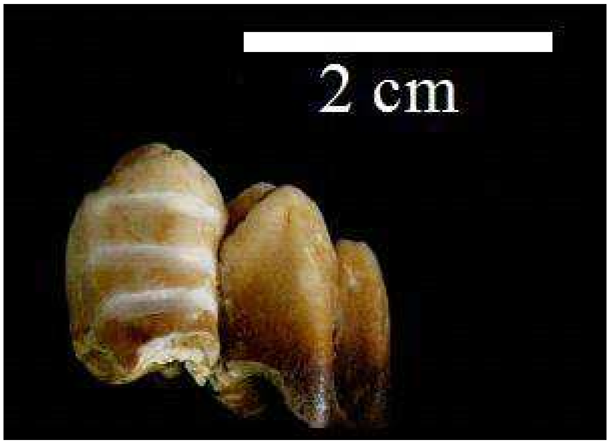

Fig. 2.2. Photograph of horizontal layers drilled sequentially from just below the cusp to the cingulum on the left mandibular third molar of a *Rangifer* (Specimen G18-1882 from RDM Level 8). Photograph taken by Jamie Hodgkins at Arizona State University.

Sampling snail shell and rodent teeth began by placing the mechanically and chemically cleaned specimens into crucibles in a furnace at 800°C for 14 hours and then collecting the ashed samples. Repeated weak acid washes have been found to effectively remove organics, secondary carbonates and soluble apatities, which have the potential to alter values obtained in radiogenic strontium isotope analysis (Sillen, 1989; Lee-Thorp and van der Merwe, 1987; Sillen and Sealy, 1995; Koch et al., 1997). In fact, diagenetic apatite has been found to be highly soluble on specimens excavated from areas with carbonate rich rocks (Sillen and Sealy, 1995). Thus, weak acid washes can be effective at removing diagenetic apatite on fossil material found in limestone cave sites (Sillen and Sealy, 1995). Thus, all tooth and snail shell samples were then placed in an acid washed 1.5 mL centrifuge tubes with 0.5 mL of twice distilled 5M nitric acid.

Soil samples were processed by first grinding each sample in a mortar and pestle. Once ground, 4.0 grams of each sample were then ashed in a furnace at 800°C for 14 hours. After ashing, 100 mg of each sample were reground in a mortar and pestle and placed in 15 mL centrifuge tubes and dissolved in 5.0 mL of twice distilled 5M nitric acid and 1.0 mL of hydrofluoric acid. Once all tooth, shell and soil samples were fully dissolved, they were placed on a hot plate at 50°-60° C until evaporated. Twice distilled 3M nitric acid (250 μL) was then added to each sample. At this point, the water and wine were also processed by pipetting 20 mL of each water sample and 2mL of each wine sample into acid washed 20 mL Teflon beakers. Once samples were placed in the beakers, 500 μL of twice distilled 5 M nitric acid was added to each wine sample. These samples were then also placed on a hot plate at 50°-60° C until evaporated and then brought up in 250 μL of twice distilled 3M nitric acid. Following procedures by Horowitz et al., (1992) acid washed columns were prepared by adding 30-50μL of EiChrom SrSpec ion-exchange resin to the tip (100-150 μL in diameter) of each column. Once in the column, resin was washed with 1000 μL of twice distilled 3M nitric acid followed by three washes of 1000 μL of Millipore water. The resin was then conditioned with 500 μL of twice distilled 3M nitric acid. Next, the dissolved samples were loaded into columns, washed with 500 μL of twice distilled 3M nitric acid and eluted with 500 μL of Millipore water.

All samples were analyzed in a Thermo-Finnigan Neptune multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) at the W.M. Keck Foundation Laboratory for Environmental Biogeochemistry. Sample concentrations ranged between 3.5 and 158 ppb Sr with a median concentration of 22 ppb and an average concentration of 28.7 ppb. Internal and external standards with varying concentrations were run during the analysis demonstrating that for samples with elemental strontium concentrations above 5 ppb the error of ^{87}Sr/^{86}Sr values was less than 0.00004. None of the samples included in this analysis had concentrations less than 5 ppb. The value and standard deviation of the international strontium isotope standard NIST SRM 987 was determined over the course of analysis (long-term ^{87}Sr/^{86}Sr value= 0.710265 ± 0.000014, 2σ, n=18, 1 SE = 0.000002). This value shows strong accuracy and precision when compared to analyses of the SRM-987 using a thermal ionization mass spectrometer (TIMS, ^{87}Sr/^{86}Sr=0.710263±0.000016, 2σ; Stein et al., 1997) and using a MC-ICP-MS (^{87}Sr/^{86}Sr=0.710251 ± 0.000006, 2σ; Balcaen et al.,2005).

Sample processing for major, minor, and trace elemental concentrations

To determine if the teeth analyzed in this study have been diagenetically contaminated over time, major, minor and trace element analysis was run on a sub-set of herbivore teeth from each site. All archaeological materials are subject to diagenetic processes, but these processes are not uniform over space or time, and therefore specimens buried in different locations within the same site may undergo different chemical, physical or biological changes. Therefore, a minimum of one specimen from all archaeological levels analyzed in this study (RDM Levels 4, 8 and 9 and Pech IV Levels I2 and YZ) was selected for major, minor and trace elemental concentration analysis. An attempt was also made to select specimens from multiple excavation units within each level. The selected individuals therefore serve as proxies of contamination for other specimens excavated from those same levels and units. In addition, from RDM one specimen from Level 4 (K17-1338, deposited during a glacial cycle) and one specimen from Level 8 (K17-2382, deposited during an interglacial) were selected to have both the enamel and the dentin analyzed for trace elements. This analysis was done to determine the level of contamination that occurred in the more porous dentin portions of specimens as compared to the level of contamination that may have occurred in the enamel. Enamel has been shown to be more resistant to diagenetic contamination than dentin (see Price et al., 1992; Budd et al, 2000; Bentley, 2006). Compared to dentin or bone, the structure of enamel is denser, harder and more inert, with a smaller amount of pore space (see Price et al., 1992; Kohn et al., 1999; Budd et al, 2000; Bentley, 2006). The fact that enamel has little pore space is significant, because this compact structure makes it less vulnerable to pore-filling by secondary minerals (Bently, 2006). Dentin however is vulnerable to diagenetic contamination because it contains large poor spaces (Kohn et al., 1999). After burial, if ground water or water dripping from cave ceilings penetrate dentin or bone specimens, minerals from these sources can be incorporated into the pore spaces of these samples masking or replacing the original strontium that was placed in the tooth or bone biologically during the animals life (Price et al., 1992; Kohn et al., 1999; Budd et al, 2000; Bentley, 2006). Analyzing dentin for signs of contamination provides a proxy for the level of diagenetic activity that has taken place within the cave. If it is found that all biogenic strontium has been replaced by diagenetic strontium in dentin samples, this indicates that diagenetic activity has been strong at that locality. In this case, extensive efforts should be made to clean enamel samples, as cleaning with weak acids has been shown to effectively remove secondary minerals from enamel (Hoppe et al., 2003). For the purposes of this dissertation, analyzing dentin and enamel from two specimens in different archaeological levels at RDM will indicate if differential levels of contamination occurred between levels deposited in warm and cold climatic cycles.

Procedures for processing tooth samples for major, minor and trace element analysis are outlined in Knudson and Price (2007). Sample collection for trace elements involved drilling 3mg of enamel powder or dentin power from each tooth. The enamel or dentin powder was then placed in a 15 mL centrifuge tube and 960 μL of twice distilled 5M nitric acid was then added to each tube along with 14 mL of Millipore water. All samples were then analyzed using a Thermo Electron X-Series (with collision cell technology) Quadrupole Inductively Coupled Plasma Mass Spectrometer (Q-ICP-MS). A series of solutions with known concentrations (an internal standard CUE-0001, a llama bone and an external standard NIST-1400, a cow bone) were measured repeatedly at regular intervals throughout the analysis. The measurements obtained from these standards were used for calibration of analytical sensitivities and to correct for drift, so that the Q-ICP-MS was optimized for major, minor and trace element analysis. The value and standard deviation of the international standard NIST-1400 was determined over the course of analysis. The average calcium-to-phosphorus ratios calculated from the Q-ICP-MS at the Keck lab were 2.10±0.06

(2σ, n= 9). This value shows strong accuracy and precision when compared to the certified calcium and phosphorus values published by the National Institute of Standards and technology (Ca/P=2.13±0.03, 2σ).

CHAPTER 3: ZOOARCHAEOLOGY RESULTS

Taphonomy and post-depositional destruction

One of the first steps in a zooarchaeological analysis is to determine the level of post-depositional destruction that has occurred in a site over time. Destructive processes can delete or alter information in the archaeological record. For example, post-depositional destruction can increase the fragmentation of specimens, impeding specimen identification, and removing cut marks and percussion marks on fragments. Thus, it is important to try to measure how intensively archaeological remains have been altered since the time of burial. Non-nutritive bone breakage 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. The frequency and 95% confidence intervals with which these types of breakage patterns occur on bones modified by hominids only, carnivores only, and both hominids and carnivores have been determined (see Marean et al., 2000). Data from Pech IV and RDM were compared to these expected frequencies (Table 3.1, Fig. 3.1,). Results from this analysis show that the frequencies of non-nutritive bone breakage are lower in all archaeological levels than frequencies of transverse outline and right angle breaks that occur when humans and/or carnivores are actively removing nutrients from long bones. Thus, post-depositional processes do not appear to have greatly affected bones in any of the levels analyzed.

TABLE 3.1. Number of identifiable 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) (Villa and Mahieu, 1991).

Nutritive Bone Breaks				
Level	**Oblique**	**Curved**		**Total Long Bone Ends**
RDM 4	2000	1977		2160
RDM 9	837	837		910
Pech IV I2	603	600		728
Pech IV YZ	477	477		568

NISP Non-Nutrative Bone Breaks				
Level	**Right**	**Transverse**	**Unbroken**	**Total Long Bone Ends**
RDM 4	29	45	11	2160
RDM 9	20	24	6	910
Pech IV I2	24	27	17	728
Pech IV YZ	23	23	8	568

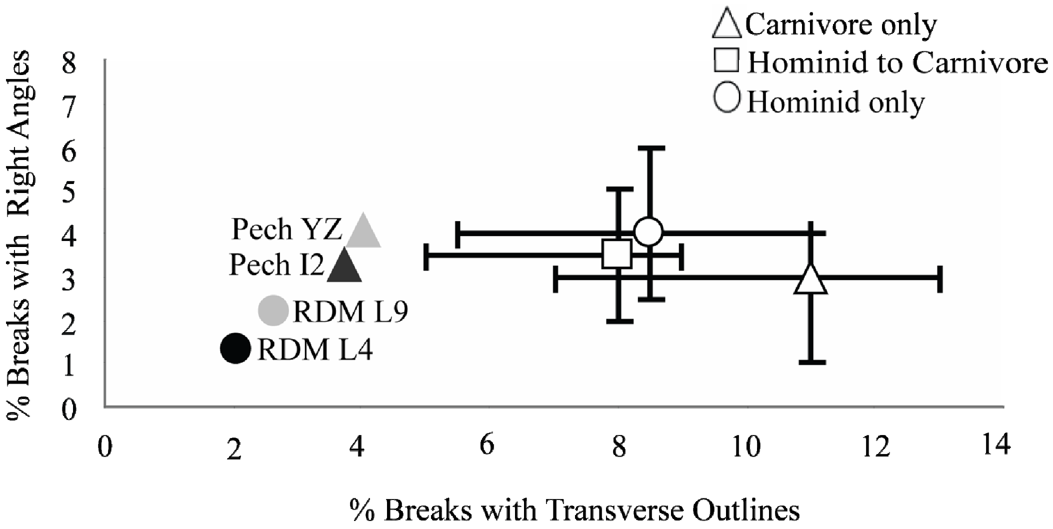

Fig. 3.1. The frequency of non-nutritive bone breaks recorded on all size 2/3 long bone fragments from Roc de Marsal and Pech IV. Data are compared to experimental and naturalistic assemblages were nutrients were extracted by hominids only, hominids then modified by carnivores, and carnivores only (Marean et al., 2000).

Taphonomy and bone modification

Throughout the Pleistocene both hominids and carnivores inhabited the Dordogne Valley and made frequent use of cave sites. It is therefore pertinent to understand the primary agents of bone breakage for each archaeological level analyzed at Pech IV and RDM. Table 3.1 shows the frequency of nutritive bone breaks in each archaeological level analyzed, these frequencies have been plotted against expected frequencies (fig. 3.2) based on experimental and naturalistic assemblages (Blumenschine, 1988; Marean and Spencer, 1991; Marean et al., 2000; 2004; Capaldo, 1995). The assemblages listed as carnivore only, hominid to carnivore, and hominid only indicate the end-members of the accumulating processes for large mammals in caves. “Carnivore Only” includes experiments in which carnivores (in this case, hyenas) were fully responsible for breaking bones, and “Hominid Only” refers to experiments for which humans were fully responsible for breaking bones. “Hominid to Carnivore” is a situation where humans broke the bones first and then carnivores were allowed to feed on them. The frequency of nutritive bone breaks from Levels I2 and YZ at Pech IV fall just outside the lower 95% confidence interval for assemblages modified by hominids only. However, nutritive bone breaks are so common on long bones from RDM that Levels 4 and 9 fit within the upper 95% confidence intervals for bones where marrow was extracted by both hominids and carnivores. Thus, it is not clear from this analysis alone if carnivores played an active role in extracting nutrients from specimens at RDM.

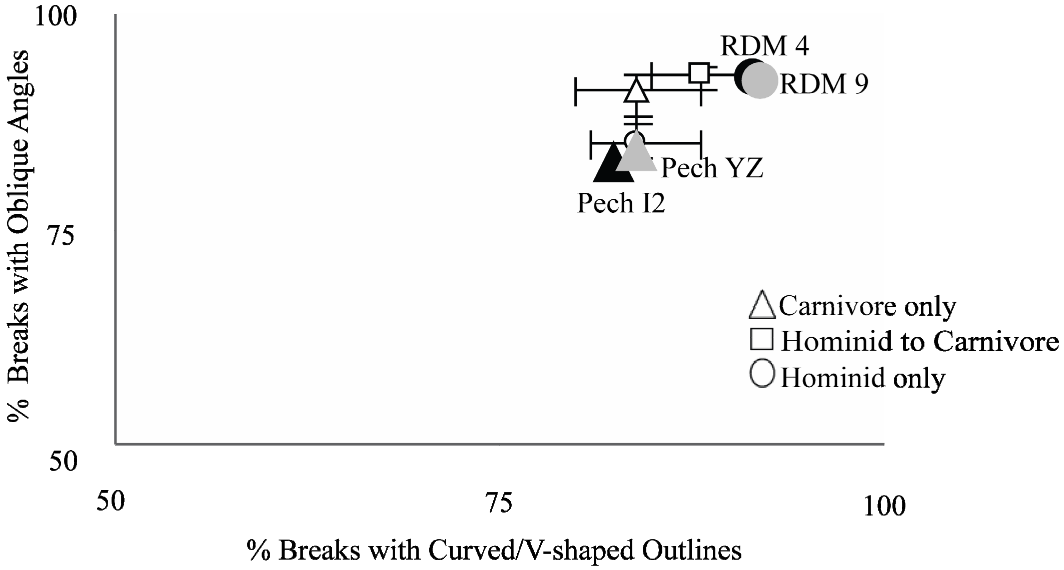

Fig. 3.2. The frequency of nutritive bone breaks recorded on all size 2/3 long bone fragments from Roc de Marsal and Pech IV. Data are compared to experimental and naturalistic assemblages where nutrients were extracted by hominids only, hominids then modified by carnivores, and carnivores only (Marean et al., 2000).

To further investigate the possibility that carnivores were agents of bone modification at both archaeological sites, the abundance of shaft fragments and epiphyseal ends were analyzed. Table 3.2 provides the raw data for the frequency of epiphyseal fragments and shaft fragments from each level. Figure 3.3 then shows the frequency of shaft fragments and epiphyseal fragments plotted against expected frequencies based on experimental and naturalistic assemblages of bones modified by carnivores only, hominids only, and both carnivores and hominids (Blumenschine, 1988; Marean and Spencer, 1991; Marean et al., 2000; 2004; Capaldo, 1995). Despite the variation in agent, it is evident that each of these major bone accumulators produced similar types of assemblages in which shafts far outnumber epiphyses. Data from Pech IV and RDM also show very high frequencies for shaft fragments and very low frequencies of epiphyseal ends. In fact, the frequency of epiphyseal fragments at each site is so low that they compare most closely with actualistic and naturalistic studies in which carnivores were the sole agent of bone destruction (see Fig. 3.3). This leaves open the possibility that carnivores were the major agents responsible for extracting nutrients from skeletal material through time at Pech IV and RDM, but as will be shown through an analysis of tooth mark frequencies, this line of evidence is not sufficient to draw this conclusion.

TABLE 3.2. Raw data on the number of marrow yielding long bone shaft fragments (including the proximal and middle phalanges) and epiphyseal ends from Pech IV and RDM.

Level	Long Bone Shaft Fragments	Long Bone Epiphyses
RDM L4	1080	24
RDM L9	455	13
Pech IV I2	364	30
Pech IV YZ	284	24

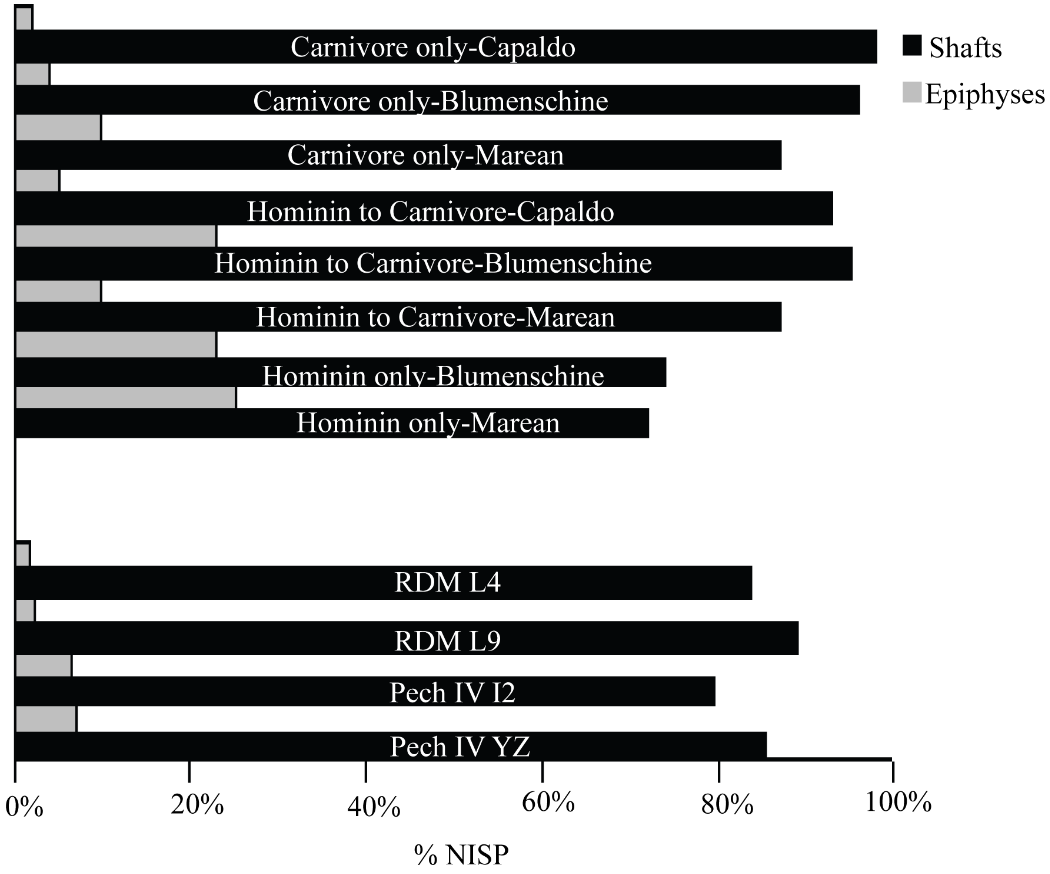

Fig. 3.3. The frequency of long bone shaft fragments from size 2/3 bovid/cervids at Pech IV and RDM compared to actualistic data (Blumenschine, 1988; Marean and Spencer, 1991; Marean et al., 2000; 2004; Capaldo, 1995).

In a final effort to better understand the role that carnivores played at Pech IV and RDM an analysis of surface modification was undertaken that focused on the percentage of percussion marks versus the percentage of tooth marks found on bone fragments. Once again, the data collected in this study were compared to data from actualistic and naturalistic studies where humans, carnivores and both humans and carnivores extracted nutrients from long bones (Blumenschine, 1995, 1988; Capaldo, 1997, 1995; Marean and Spencer, 1991; Marean et al., 2000, 1992; Marean and Bertino, 1994). These studies allowed expected values with 95% confidence intervals to be established for the frequency of tooth marks and percussion marks created when carnivores, humans and both carnivores and humans attempt to extract nutrients from bones (data are summarized in Marean et al., 2000). At Pech IV and RDM virtually no tooth marks were observed on bone fragments (Table 3.3, Fig. 3.4). To be exact, from RDM tooth marks were found 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 YZ. Therefore, the results from this analysis reveal that carnivores did not actively modify the vast majority of bones at RDM or Pech IV. In light of this information and results from the breakage analysis (showing high frequencies of nutritive bone breaks on specimens from RDM), it would appear that Neandertals themselves put considerable effort into extracting marrow and bone grease from long bones at that site. 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. A discussion of possible reasons why carnivores did not actively modify bones at Pech IV and RDM is provided in the zooarchaeological discussion section.

Results from this analysis of taphonomy and surface modification show that archaeological assemblages at Pech IV and RDM are anthropogenic in origin and that little post-depositional destruction has occurred in each level under analysis. These results demonstrate that corrections for post-depositional damage or the effects of carnivore modification are unnecessary in the analyses that follow.

*TABLE 3.3. Raw data for the number of skeletal elements with at least one percussion mark (PM) or one tooth mark (TM).**

Element	**RDM L4 PM**	**RDM L9 PM**	**Pech I2 PM**	**Pech YZ PM**	**RDM L4 TM**	**RDM L9 TM**	**Pech I2 TM**	**Pech YZ 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

*Note no bones were observed with both PM and TM.

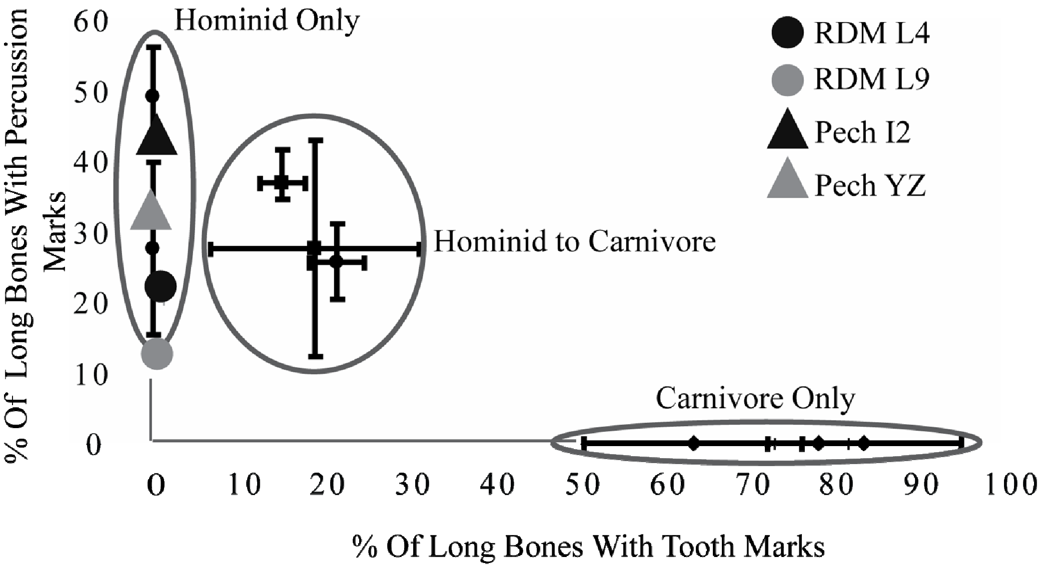

Fig. 3.4. The percentage of long bone shafts with percussion marks versus the percentage with tooth marks. Data are compared to experimental and naturalistic assemblages broken by hominids only, hominids then modified by carnivores, and carnivores only (Blumenschine, 1995, 1988; Capaldo, 1997, 1995; Marean and Spencer, 1991; Marean et al., 2000, 1992; Marean and Bertino, 1994). The ellipses are used for emphasis, but have no statistical meaning.

Taxonomic representation

As discussed in the introduction and methods, data were collected on bovid/cervids that ranged in body size between 21–340kg. Table 3.4 shows the number of bone fragments identified as specifically as possible to taxonomic group. Throughout this analysis the term “size 2/3 bovid/cervids” is used to indicate bone fragments identified to the following groups: nonidentifiable size 2/3 bovid/cervid, size 2/3 cervid, *Capreolus capreolus*, *Cervus elaphus*, and *Rangifer tarandus*. Some fragments belonging to larger species (e.g., *Equus*, *Bison*) were randomly drawn from levels 4 and 9 at RDM and I2 and YZ at Pech IV. These specimens have been listed as “other taxa” in Table 3.4. Data were collected on these specimens, but for the purposes here, bones from these larger animals were not analyzed.

TABLE 3.4. Number of dental and skeletal remains identified to each taxonomic group.

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

The taxonomic analysis of size 2/3 bovid cervids clearly shows that *Rangifer* were more abundant in levels deposited during glacial cycles, while (within a site) *Cervus* and *Capreolus* were more abundant in layers deposited during interglacials (Fig. 3.5).

However, it is important to note that each species of deer, including *Rangifer*, were present in every level analyzed (Table 3.4). In fact, *Cervus* are well represented in all levels. The ecological factors that may have allowed all species to remain in the Dordogne over time will be elaborated on in the discussion chapter.

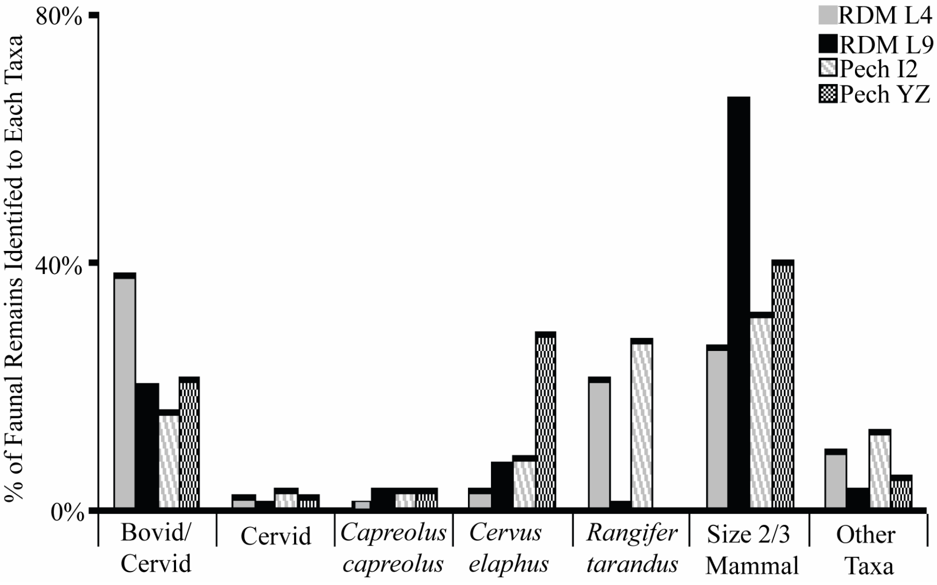

Fig. 3.5. Percentage of faunal remains identified to each taxonomic grouping from Levels 4 and 9 at RDM and Levels I2 and YZ at Pech IV.

Skeletal element representation

The use of ArcView GIS to draw all identifiable bone fragments onto bone templates has allowed the minimum number of elements (MNE) and the minimum number of individual (MNI) deer analyzed to be calculated (Table 3.5 provides MNI calculations). An example of a template map (*Rangifer* cranial remains) is provided in Fig. 3.6 with additional templates for other elements provided in Appendix A.

TABLE 3.5. Minimum number of individuals calculated from Arc View GIS for each species of cervid analyzed from RDM and Pech IV.

Taxon	RDM L4	RDM L9	Pech IV I2	Pech IV YZ
Rangifer tarandus	11	2	9	0
Cervus elaphus	3	4	4	10
Capreolus capreolus	1	3	2	1

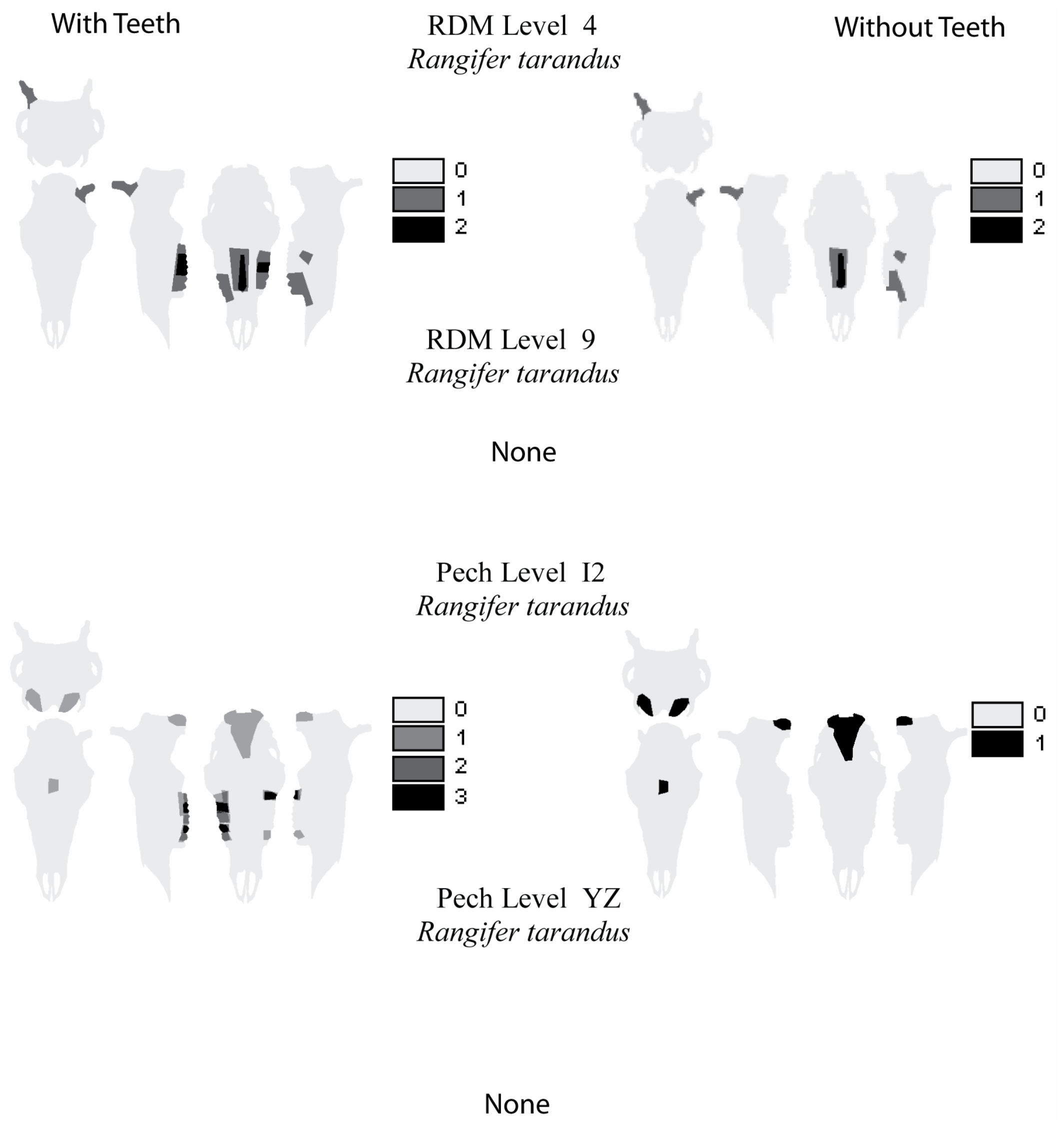

Fig. 3.6. Cranial remains of *Rangifer* analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. Each fragment was drawn into ArcView GIS where it was then mapped onto the same template and fragment overlaps were used to identify elements from different individuals. The darkest areas on the 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 out of all bones analyzed of a particular species.

At RDM Level 4 =cold, Level 9 = warm
At Pech Level I2=cold, Level YZ =warm

For simplicity, in Tables 3.6a-d 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. Tables 3.6a-d present results of the percent minimum animal units (%MAU) both with and without teeth for comparative purposes (see Binford, 1984; Grayson, 1984), along with the evenness index and Spearman's rho for all levels analyzed (see Faith and Gordan, 2007). Table 3.7 shows the minimum number of size 2/3 bovid/cervids identified (NISP) to each skeletal element. Analysis of the %MAU of high survival elements shows that the abundance of each element remained fairly consistent over time, which suggests Neandertals used similar transport strategies through time and across sites (Fig. 3.7).

TABLE 3.6a: 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.

Element	**MNE L**	**With Teeth**	**MNE R**	**With Teeth**	**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 3.6b. 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.

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					

* Note 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 3.6c. 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.

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					

* Note 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 3.6d. 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 YZ.

Element	MNE L	With Teeth	MNE R	With Teeth	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					

* Note 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 3.7. Number of specimens identified to specific skeletal elements for size 2/3 bovid/cervids. *Note this table does not include fragments that could not be identified to a specific element.*

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

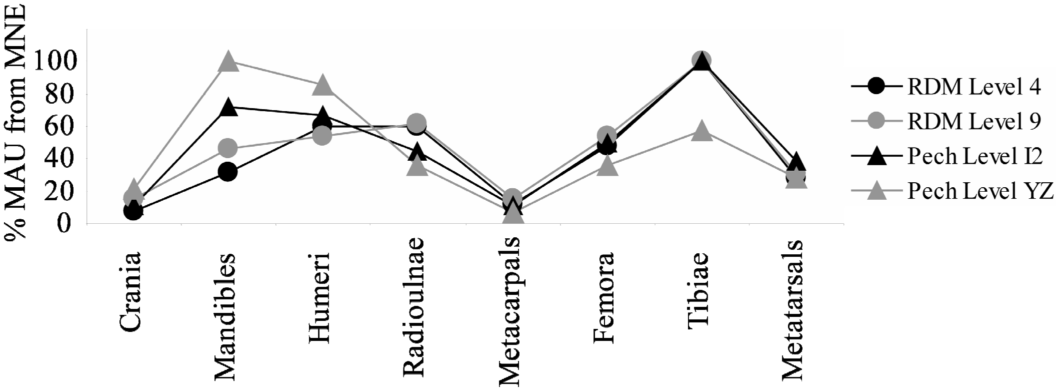

Fig. 3.7. The abundance of high survival skeletal elements including teeth analyzed from Levels 4 and 9 at Roc de Marsal and I2 and YZ at Pech IV.

When the %MAU of each high survival element is plotted against the standard food utility index (SFUI), which is a measure of the amount of nutrients (e.g., meat, marrow, and bone grease) associated with different body parts (see Metcalfe and Jones, 1988), the resulting plot aligns most closely (although not perfectly) with Binford's bulk transport strategy (Fig. 3.8). This strategy is characterized by the transport of all high utility (i.e., high nutritional value) elements, with elements of lower nutritional value left behind (Binford, 1978). The main difference between Binford's proposed utility strategies and skeletal representation at Pech and RDM is that in all levels femora are not as well represented as would be predicted by the bulk transport strategy. Binford calculates the femur as the bone with the highest utility (SFUI=100, also see Metcalfe and Jones, 1988). It is also interesting to note that transport strategies utilized in level YZ at Pech IV, while broadly similar to transport strategies utilized in all other levels, did have a higher frequency of mandibles and a lower frequency of tibiae than observed in other levels (Fig. 3.7). This transport pattern appears to favor elements that are of moderate utility (Fig. 3.8).

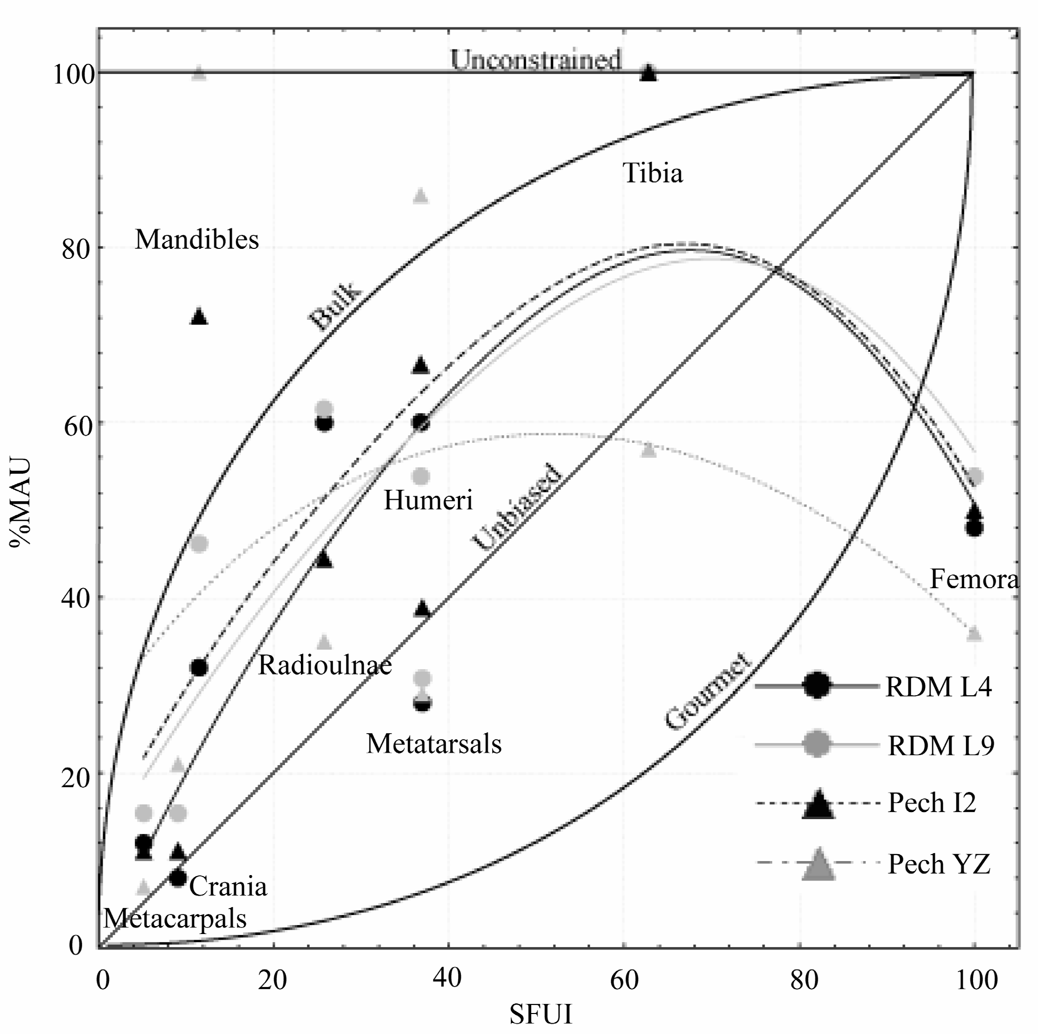

Fig. 3.8. The relationship between the relative abundance of high survival skeletal elements and their Standardized Food Utility Index (SFUI) for levels 4 and 9 at Roc de Marsal and I2 and YZ at Pech IV. A distance-weighted least squares curve was fitted to the data points from each level. Utility curves proposed by Binford (1978) are plotted with the data for comparison.

This study is particularly focused on understanding how Neandertals were utilizing all nutrients, including within bone nutrients, available in the bodies of size 2/3 bovid/cervids. Therefore, two analyses were conducted that investigated the relationship between the relative abundance of high survival skeletal elements at the site (%MAU) and the utility of the marrow in the bones. The first analysis looked at the relationship between the %MAU and the standard marrow index, which was created by Binford (1978: 27) as a measure of the grease volume and the efficiency (ml/min work) of processing the grease from each bone (Fig. 3.9). As mentioned in the methods section, the standard marrow index has been calculated for whole bones in this analysis (see Table 3.8). The benefit of Binford's standard marrow index is that he included mandibles in his calculations. Mandibles were found in high frequency at Pech IV and RDM, especially in level YZ at Pech IV where mandibles have the highest %MAU.

Results from an analysis of the relationship between the %MAU and the whole bone standard marrow index show that a strong relationship does not exist between the bones recovered from the site and marrow utility. In fact, Figure 3.9 suggests that bones of moderate marrow utility were favored. One factor driving this pattern in all levels was a lack of metatarsals. A negative (reverse) utility curve was observed for Levels at Pech IV. However, the abundance of mandibles in levels at Pech IV, particularly in Level YZ drove this reverse utility curve.

TABLE 3.8. Indices and values used as measures of marrow utility in long bones.

Skeletal Element	**Whole Bone Standardized Marrow Index**	**Standardized UMI**	**Proportion of Unsaturated Fatty Acids**
Mandible	3.16	N/A	N/A
Humerus	31.92	44.62	0.6007
Radioulna	60.39	51.47	0.7313
Metacarpal	70.85	38.36	0.932
Femur	45.63	66.54	0.6546
Tibia	75.21	100.00	0.7986
Metatarsal	100.00	91.00	0.9123

The whole bone standardized marrow index was calculated from Binford (1978:27). The standardized unsaturated marrow index (UMI) was calculated from Morin (2007:77). The proportion of unsaturated fatty acids values come from Meng et al. (1969:189) and from Morin (2007:77).

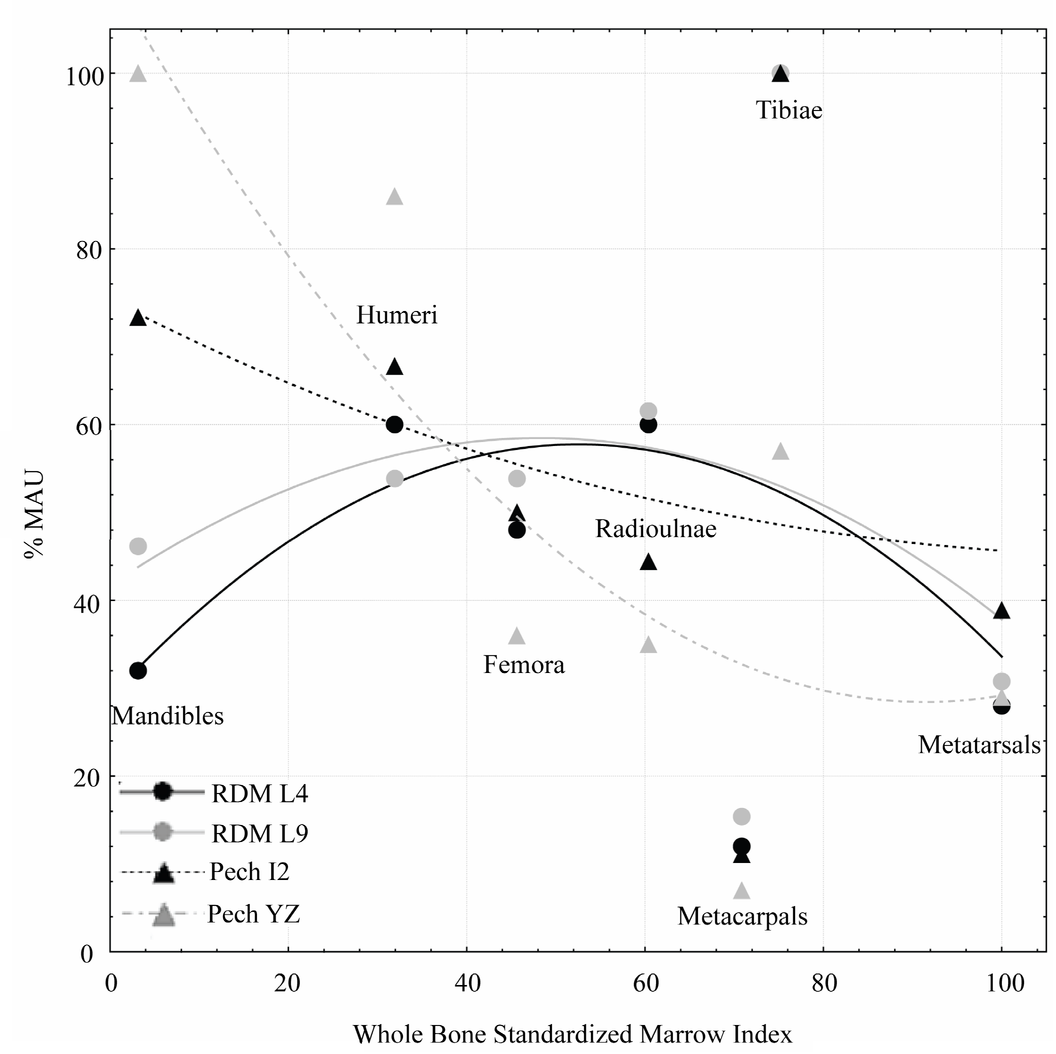

Fig. 3.9. The relationship between the relative abundance of high survival skeletal elements and their whole bone standard marrow index (Binford, 1978: 27) for levels 4 and 9 at Roc de Marsal and I2 and YZ at Pech IV. A distance weighted least squares curve was fitted to the data points from each level.

The second analysis looked that the relationship between the %MAU and the unsaturated marrow index (UMI) created by Morin (2007), which is a measure of the marrow-cavity volume and the proportion of unsaturated fat within the marrow of long bones (Fig. 3.10 and Table 3.8). Unfortunately, Morin did not calculate the UMI for mandibles, so these were left out of this analysis. Results from a comparison of the %MAU and the UMI show that for Levels 4 and 9 at RDM and I2 at Pech IV, no correlation exists between the skeletal elements represented at the site and marrow utility as measured by the standardized UMI. This lack of correlation is further demonstrated by the Spearman's rho values which are not significant (Fig. 3.11). While not statistically significant, a slight positive trend is observed in the data for Levels 4, 9, and I2. This trend is driven by the abundance of tibiae at each site. However, there is a significant negative correlation between the %MAU and the standardized UMI for level YZ at Pech IV. This indicates that bones with a higher proportion of unsaturated fat are not well represented within this level. This pattern appears to be driven by a lack of tibiae, metatarsals, femora, and radioulnae. Interestingly, level YZ is one of two levels analyzed in this study where there is evidence of bone fragments having been burned. Whether bones were burned as fuel in this level is an issue that will be elaborated on in the zooarchaeological discussion section.

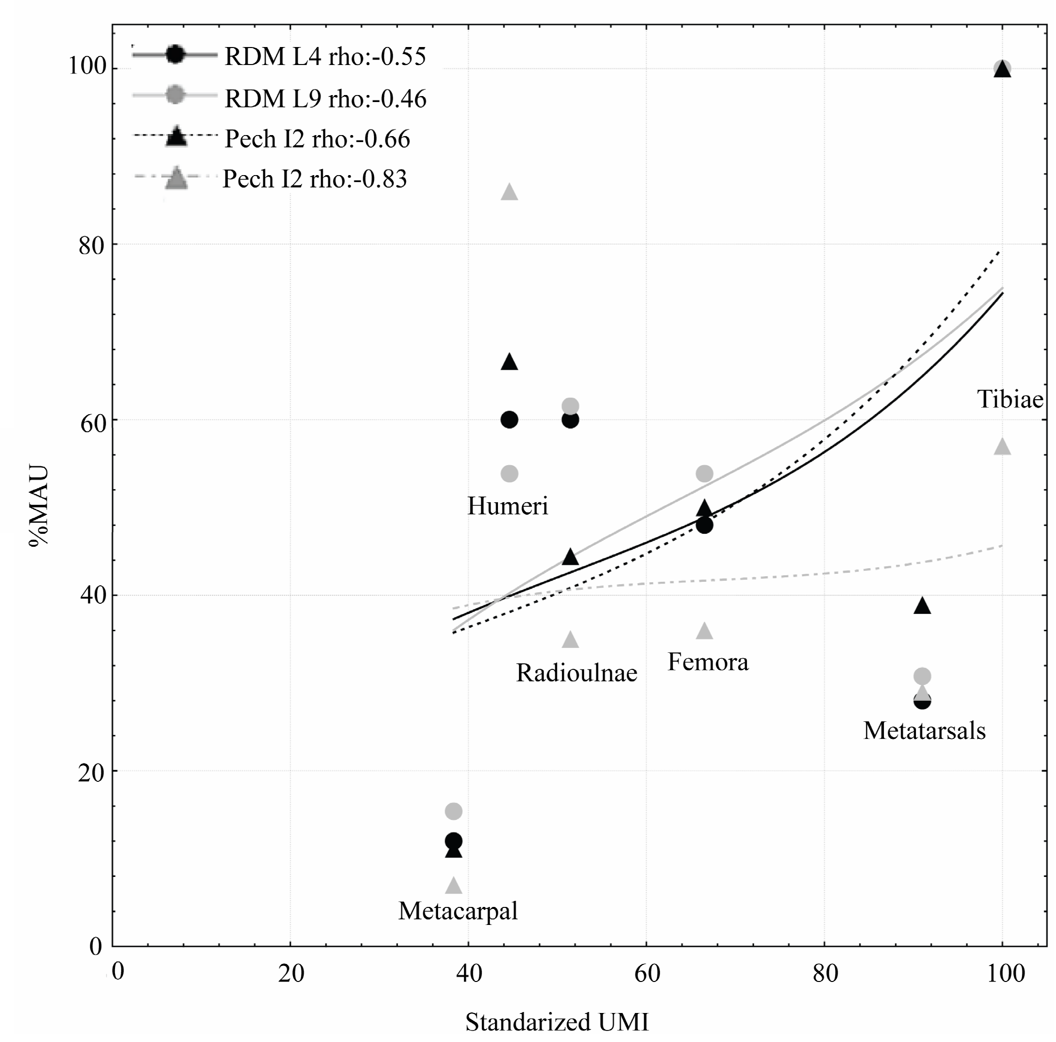

Fig. 3.10. The relationship between the relative abundance of high survival skeletal elements and their standardized unsaturated marrow index (Morin, 2007:77) for levels 4 and 9 at Roc de Marsal and I2 and YZ at Pech IV. A distance weighted least squares curve was fitted to the data points from each level.

When evenness and Spearman’s rho values were calculated for each of the high survival skeletal elements from Pech IV and RDM and compared to experimental 95% confidence intervals established by Faith and Gordon (2007) for the gourmet, unbiased, bulk and unconstrained transport strategies, levels 4 and 9 at RDM and I2 at Pech IV align most closely with Binford’s bulk strategy (Fig. 3.11). However, the Spearman’s rho and evenness values calculated from Level YZ at Pech IV do not align with any of Binford’s transport strategies. They appear most similar to the unconstrained strategy proposed by Faith and Gordon (2007). Interestingly, the evenness calculated for Level YZ (E=90) is very similar to the evenness calculated for Level I2 at Pech IV (E=0.91) and Levels 4 (E=0.92) and 9 (E=0.92) at RDM, suggesting that the overall proportion of skeletal elements represented at all sites is quite similar. However, the relationship between the specific skeletal elements represented (%MAU) and the utility of those bones (SFUI) differs greatly, as reflected by the Spearman’s rho values (Level 4 Spearman’s rho= 0.63, Level 9 Spearman’s rho= 0.67, Level I2 Spearman’s rho=0.056, Level YZ Spearman’s rho=0.14). As mentioned above, this difference is caused by a high abundance of mandibles and a lower abundance of tibiae in Level YZ: a transport strategy that appears to favor bones of moderate utility. Possible reasons for differences observed in skeletal element abundances in Level YZ will be discussed further in the zooarchaeological discussion section.

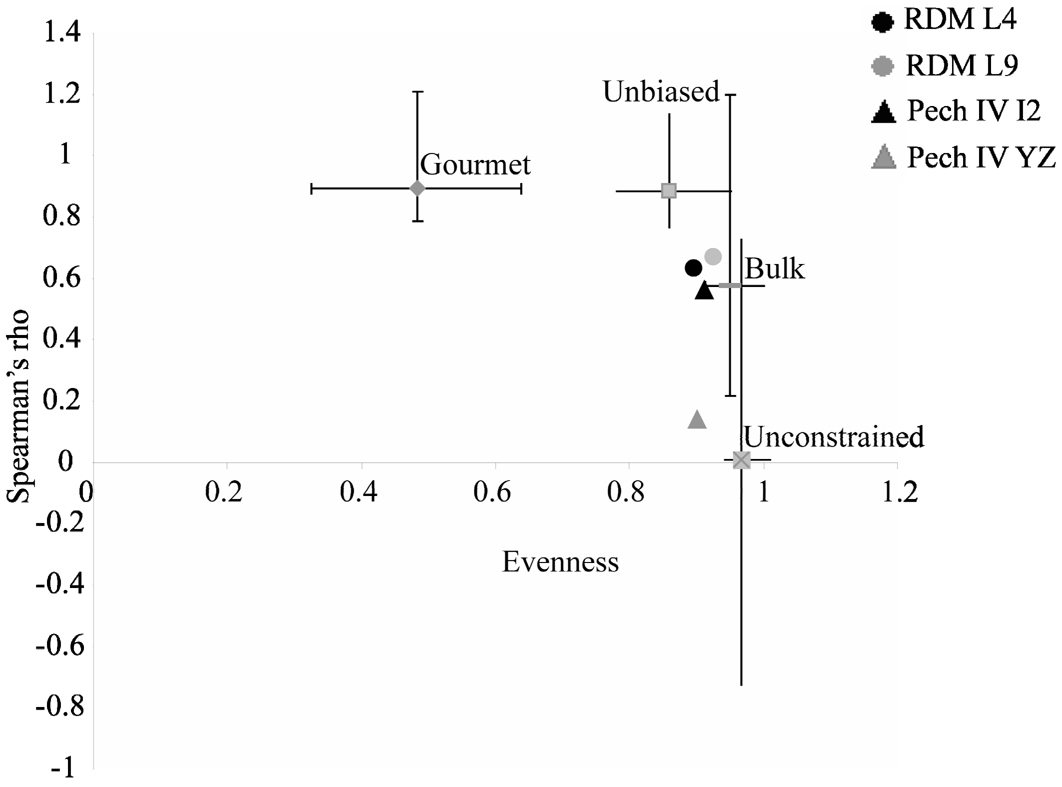

Fig. 3.11. The Spearman's rank correlation (rho) between % Minimum Animal Units and Standard Food Utility Index and the evenness values of high survival skeletal elements at Roc de Marsal and Pech IV. These data are plotted against the expected values for assemblages with a sample size of 50 that were accumulated using the gourmet, unbiased, bulk and unconstrained transport strategies (from Faith and Gordon, 2007).

Bone surface modification by hominids

It is important to reiterate that the results above demonstrate that carnivores did not heavily modify bones at Pech IV and RDM. In addition, post-depositional processes like trampling and sediment compaction are not responsible for the vast majority of bone breakage at these sites. Thus, these taphonomic processes do not have to be controlled for when further analyzing hominid-derived surface modification marks preserved and recorded on bone fragments. It is also important to note that results from the analyses above have shown that epiphyseal ends are poorly represented in all levels analyzed. In addition, a majority of long bones from each site show signs of nutritive bone breakage. These findings suggest that bones from every level did undergo a considerable degree of processing by Neandertals. The next set of analyses will hone in on the intensity of bone processing at each site by focusing on the number of percussion marks and cut marks recorded on each bone fragment along with the frequency of cortical bone fragments to spongy bone fragments preserved in small finds bags from each site.

Table 3.9a and 3.9b show the raw values of the number of bones that preserve a minimum of one cut mark or percussion mark, as well as the total count of all cut and percussion marks on each fragment.

*TABLE 3.9a. Raw data from Roc de Marsal on the number of size 2/3 bovid/cervid specimens with a minimum of one cut mark (CM) and percussion mark (PM), and the cut mark and percussion mark count per bone.**

	RDM L4					**RDM L9**				
Skeletal Element	**NISP**	**N With CM**	**Total N of CM**	**N With PM**	**Total PM**	**NISP**	**N with CM**	**Total N of CM**	**N With PM**	**Total N of PM**
Cranial bones	21	7	18	0	0	15	3	8	0	0
Maxillary teeth	18	–	–	–	–	30	–	–	–	–
Mandible	41	15	40	4	5	19	4	7	3	4
Mandibular teeth	39	–	–	–	–	34	–	–	–	–
Humerus	66	10	148	19	23	24	11	38	5	5
Radioulna	86	45	119	16	21	24	10	21	6	6
Metacarpal	46	29	93	5	10	45	21	63	6	6
Femur	65	46	161	22	32	31	14	66	4	4
Tibia	98	54	213	29	37	51	27	70	10	14
Metatarsal	118	60	178	20	28	60	16	32	8	12
Metapodial	62	28	75	14	19	39	10	23	1	1
Prox Phalanges	3	2	3	1	1	7	0	0	0	0
Middle Phalanges	2	0	0	0	0	2	0	0	0	0
Distal Phalanges	4	0	0	0	0	1	0	0	0	0
Atlas	1	0	0	0	0	0	1	1	0	0
Axis	0	0	0	0	0	1	0	0	0	0
Cervical	0	0	0	0	0	0	1	1	0	0
Thoracic	8	6	19	0	0	1	0	0	0	0
Lumbar	10	0	0	0	0	1	1	3	0	0
Sacrum	5	0	0	0	0	2	1	1	0	0
Rib	2	37	156	2	2	1	2	5	0	0
Scapula	53	7	39	2	3	4	0	0	0	0
Sternabre	8	0	0	0	0	2	0	0	0	0
Carpals	4	0	0	0	0	1	0	0	0	0
Tarsals	4	5	18	1	2	0	0	0	0	0
Pelvis	13	1	1	1	1	1	1	1	0	0
Patella	6	1	1	0	0	2	0	0	0	0
Long Bones	534	260	671	105	143	172	59	162	15	19

*Note this table does not include fragments that could not be identified to a specific element.

*TABLE 3.9b. Raw data from Pech IV on the number of size 2/3 bovid/cervid specimens with a minimum of one cut mark (CM) and percussion mark (PM), and the cut mark and percussion mark count per bone.**

	Pech IV I2					**Pech IV YZ**				
Skeletal Element	**NISP**	**N with CM**	**Total N of CM**	**With PM**	**Total PM**	**NISP**	**N with CM**	**Total N of CM**	**With PM**	**Total PM**
Cranial bones	8	1	2	0	0	6	1	1	0	0
Maxillary teeth	18	0	0	0	0	20	0	0	0	0
Mandible	31	6	25	10	19	16	8	23	3	10
Mandibular teeth	43	0	0	0	0	50	0	0	0	0
Humerus	34	19	54	18	42	29	19	47	9	12
Radioulna	35	15	52	12	25	24	17	76	6	11
Metacarpal	24	15	58	11	26	30	7	19	7	10
Femur	31	15	70	11	27	18	13	53	7	11
Tibia	74	41	144	40	84	37	20	78	13	21
Metatarsal	104	46	162	44	78	69	33	89	22	29
Metapodial	22	6	16	7	7	30	3	12	2	3
Prox Phalanges	8	1	0	1	3	5	2	5	1	2
Middle Phalanges	3	1	1	0	0	5	2	3	0	0
Distal Phalanges	2	0	0	0	0	1	0	0	0	0
Atlas	0	0	0	0	0	0	0	0	0	0
Axis	0	0	0	0	0	0	0	0	0	0
Cervical	0	0	0	0	0	0	0	0	0	0
Thoracic	0	0	0	0	0	0	0	0	0	0
Lumbar	1	0	0	0	0	1	1	7	0	0
Sacrum	2	0	0	0	0	1	0	0	0	0
Rib	0	6	37	0	0	0	1	9	0	0
Scapula	15	4	12	0	0	3	3	8	1	1
Sternabre	9	0	0	0	0	3	0	0	0	0
Carpals	0	0	0	0	0	0	1	1	1	2
Tarsals	9	1	2	0	0	8	1	2	0	0
Pelvis	5	3	13	1	1	4	2	8	1	2
Patella	5	0	0	0	0	1	0	0	0	0
Long Bones	29	15	56	12	21	37	26	88	23	32

* Note this table does not include fragments that could not be identified to a specific element.

In order 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, the generalized linear model was applied to the high survival marrow-yielding long bone fragments from each site, including the metapodials and proximal and middle phalanges. A full description of this statistical model and reasons for why it was used can be found in the methods section. Results from this analysis show that for both cut mark (Fig. 3.12) and percussion mark (Fig. 3.13) 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 glacial climates (Level 4 at RDM and I2 at Pech IV) had more cut marks (Wald χ^2= 78.44, p= <0.001) and percussion marks (Wald χ^2= 67.88, $p < 0.001$) than bones excavated from levels deposited during interglacials. For cut marks, the significant effect of climate appears to be driven by the frequency of cut marks found on long bones from RDM, as the 95% confidence intervals (CI) of the least square means overlap at Pech IV. Indeed, site was also a significant effect on the number of cut marks (Wald χ^2= 34.40, p < 0j.001), with bones from RDM showing a heavier frequency (Fig. 3.12). However, percussion marks showed an opposite and significant effect of site (Wald χ^2= 337.25, $p < 0.001$), with Pech IV showing the overall greater frequency of marks per size-controlled bone (Fig. 3.13). As such, for the cut marks, the interaction effect of climate by site was significant (Wald χ^2= 51.33, p= <0.001) with the effect of climate being greater at RDM (Fig. 3.12), while the opposite held for percussion marks (Wald χ^2= 4.92, p= 0.02) for which the effect of climate on the number of marks per size-controlled fragment was greater at Pech IV (Fig. 3.13).

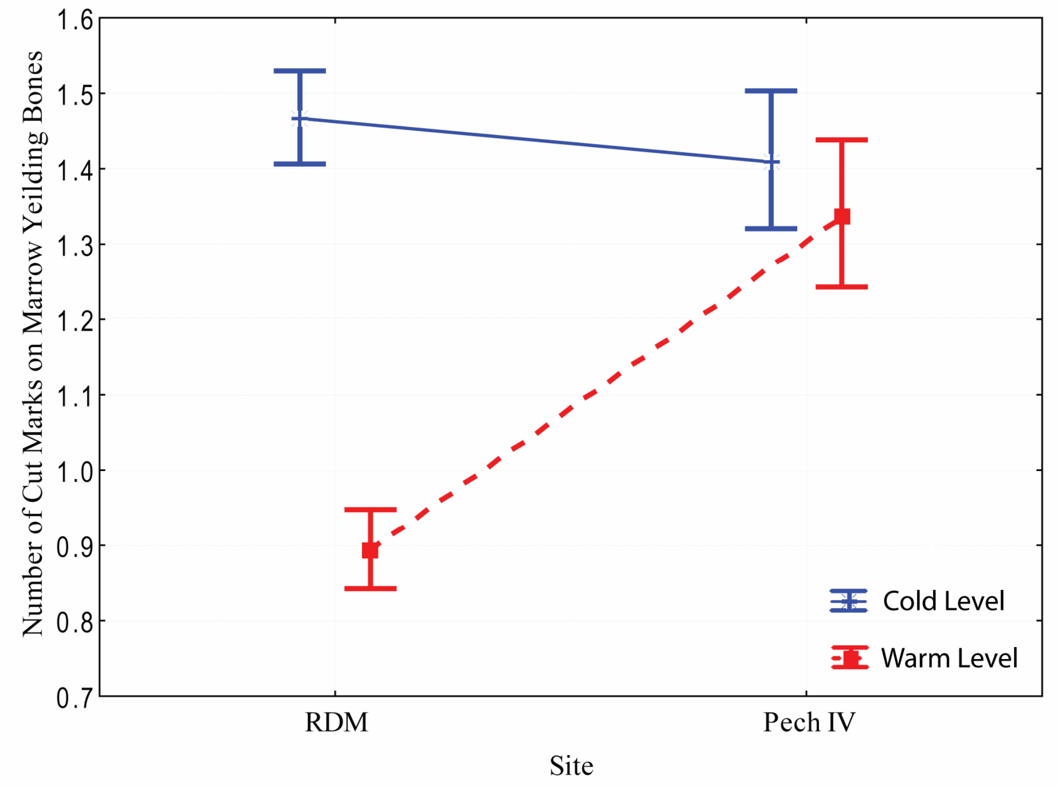

Fig. 3.12. The least-squares means of cut marks on marrow-yielding long bone fragments from Roc de Marsal (RDM) and Pech IV (Bordes' excavations) derived from an analysis of covariance. The geometric mean of fragment length and width was included as a covariate to control for fragment size. To analyze the count data, a generalized linear model was applied assuming a Poisson error distribution.

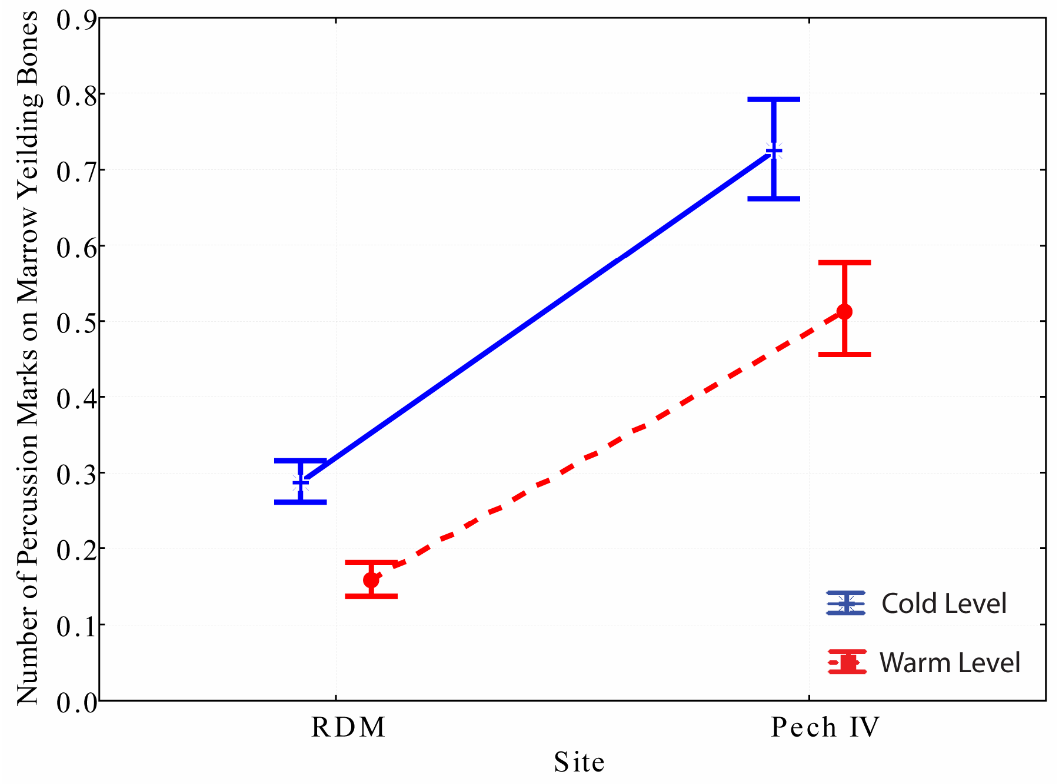

Fig. 3.13. The least-squares means of percussion marks on marrow-yielding long bone fragments from Roc de Marsal (RDM) and Pech IV (Bordes' excavations) derived from an analysis of covariance. The geometric mean of fragment length and width was included as a covariate to control for fragment size. To analyze the count data, a generalized linear model was applied assuming a Poisson error distribution.

While the analyses above demonstrate that percussion marks are more common in levels deposited during glacial cycles, the frequencies of percussion marked long bones in all levels (RDM 4 = 21% 9=12%; Pech I2=43%, YZ = 31%) closely match 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 warm and cold climate oscillations, Neandertals were processing within bone nutrients, but they were doing so more intensively during cold climates. Adding to this pattern of intensive nutrient extraction is the finding that while epiphyseal ends are rare in all levels (Table 3.2), a portion of the epiphyseal ends that are present do have percussion marks (Table 3.10). Interestingly, Table 3.10 shows that the frequency of percussion marked epiphyseal ends is greater in the cold levels than in the warm levels. Another intriguing, although not entirely consistent pattern is that pieces of spongy bone appear in the small-finds bags (Table 3.11). This is important because it has been suggested that if Neandertals were processing epiphyseal ends for bone grease, that activity should have created a lot of small fragments of spongy bone, unless Neandertals were consuming epiphyseal ends directly (Marean, 2005). Findings from this analysis show that at RDM, small pieces of spongy bone are found in a higher abundance in Level 4 (cold level) than in Level 9. However, the reverse pattern is seen at Pech IV, where Level YZ (warm level) has a higher frequency of spongy bone (Fig. 3.14).

*TABLE 3.10. Raw data of the number of marrow-yielding long bone epiphyseal ends recovered from each level along with the number of epiphyseal ends with at least one percussion mark (PM). The frequency of epiphyseal ends with percussion marks from each level is shown.**

Level	Total Long Bone Epiphyseal Ends	Number with PM	Percentage of PM on Epiphyseal Ends
RDM L4	24	6	25%
RDM L9	13	2	15%
Pech IV I2	30	6	20%
Pech IV YZ	24	2	8%

*Note only bones with surfaces that were greater than 25% visible were included.

TABLE 3.11. Number of cortical and spongy bone fragments found in small- finds bags from Roc de Marsal and Pech IV.

Level	Cortical Bone	Spongy Bone	Total N Fragments
RDM L4	5754	457	6211
RDM L9	7132	251	7383
Pech IV I2	1112	24	1136
Pech IV YZ	3172	188	3360

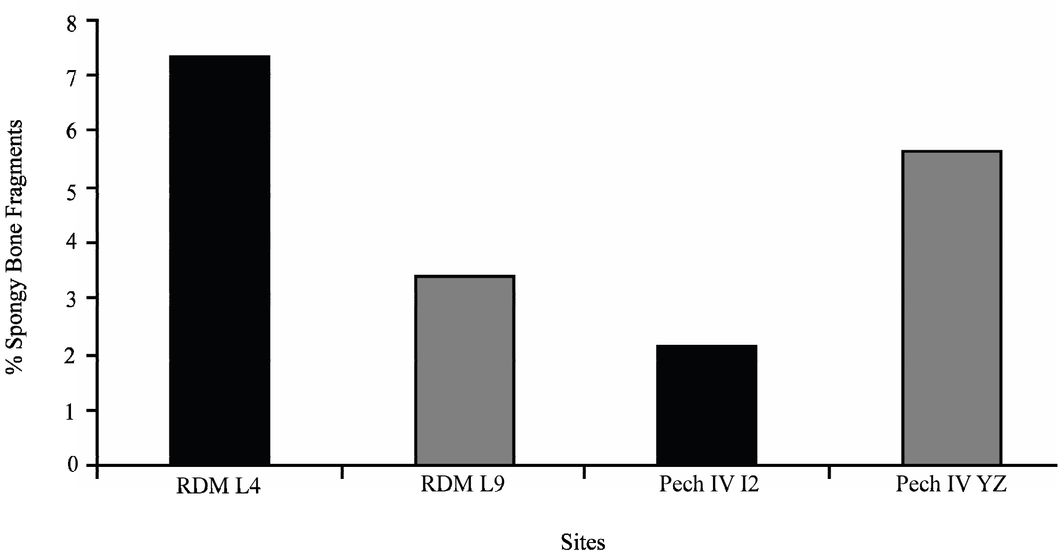

Fig. 3.14. The frequency of spongy bone fragments found in small finds bags from Roc de Marsal (RDM) and Pech IV.

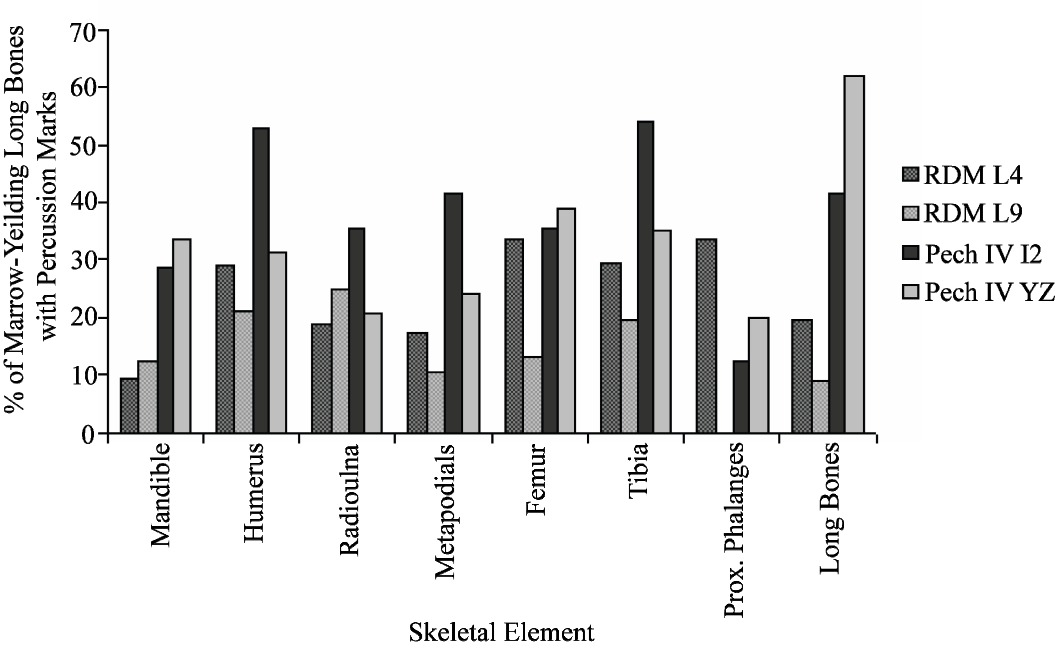

Fig. 3.15. The frequency of percussion marks found on marrow-yielding long bone fragments from archaeological levels at Pech IV and RDM.

Finally, a basic analysis of the frequency of percussion marks on all marrow-yielding long bones from all levels shows that low marrow-yield bones (e.g., proximal phalanges, mandible) have frequencies of percussion marks that matched bones with higher marrow-yields (e.g., tibiae) (Fig. 3.15). Referring back to Tables 3.9a and 3.9b, it can be seen that while a small number of proximal phalanges are found at each site, a portion of those phalanges do contain percussion marks and cut marks. Specifically, in Level 4 at RDM 66% of the proximal phalanges have cut marks and 33% have percussion marks. At Pech IV, 12.5% of proximal phalanges have cut marks, and the same percentage have percussion marks. Finally, in Level YZ 40% of proximal phalanges have cut marks and 20% have percussion marks. Unfortunately, the number of proximal phalanges sampled is quite small, such that the frequencies of modification marks found on them may not be indicative of behavior in response to climate change—as sample size affected the results. However, the fact that a portion of the phalanges found were modified along with all other long bones in the body demonstrates that Neandertals were thoroughly processing skeletal elements through time.

In an attempt to better identify the butchering behaviors utilized by Neandertals, the placement of cut and percussion marks on all high survival skeletal elements was examined. For this analysis, ArcView GIS was employed, as this program made it possible to map all surface modification marks on identifiable skeletal elements (Fig. 3.16, see additional templates in Appendix B).

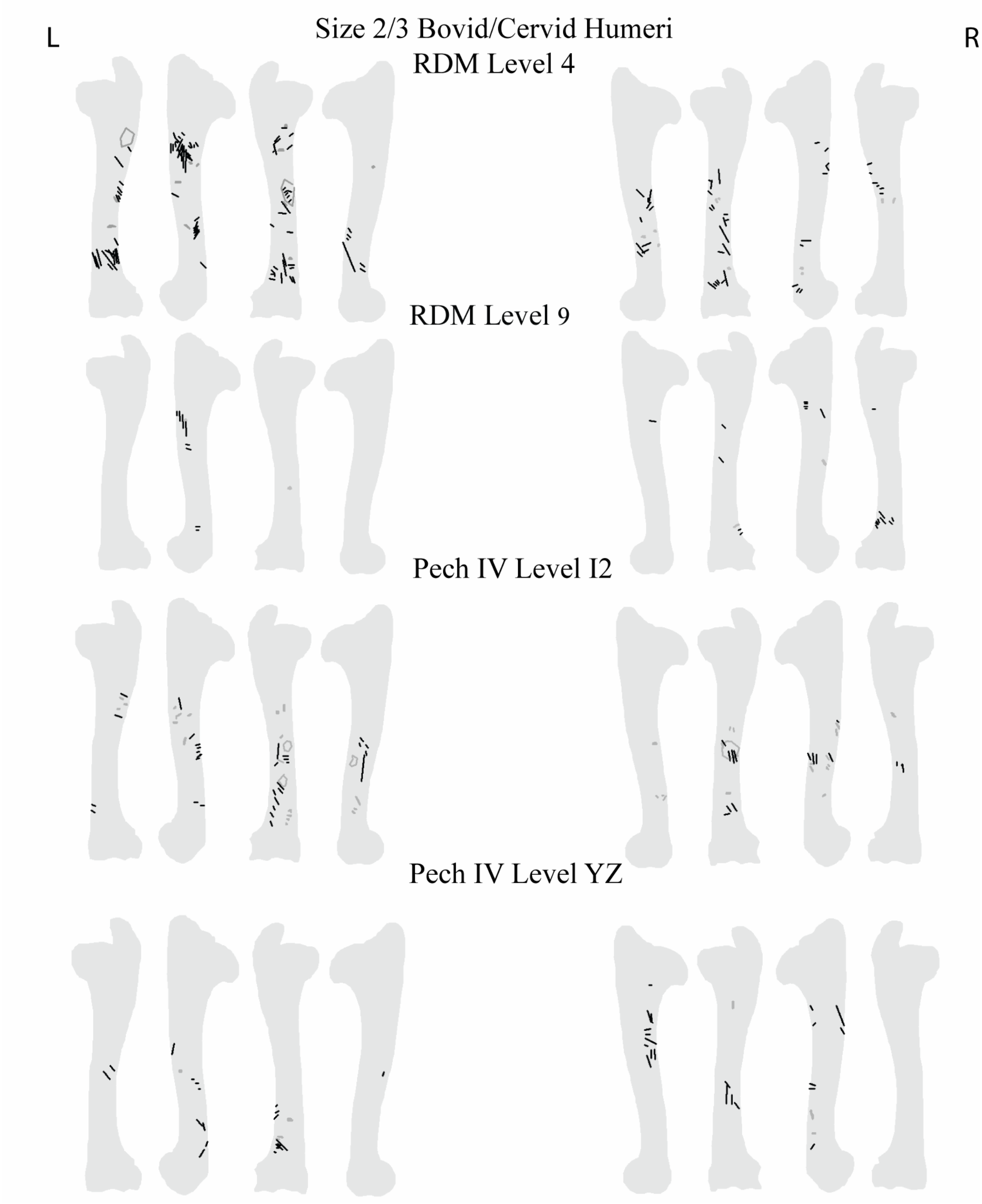

Fig. 3.16. Templates of the medial, lateral, anterior and posterior views of a cervid humerus. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

Once all surface modification marks were drawn on bone templates, the placement of cut marks and the frequency with which they occur in different portions of high survival skeletal elements was calculated (Table 3.12). Then the percentage of bone surface area recorded per anatomical region (e.g. proximal epiphysis, proximal shaft, etc.) was determined (Table 3.13). The purpose of this analysis was to compile data on cut mark frequencies that could be compared to experimental data gathered by Nilssen (2000) regarding the expected frequency of cut marks produced by filleting, or filleting plus disarticulating meat and bones. Here, visual (Figs. 3.17a–d) and statistical (Table 3.14) analyses are provided, comparing the butchering patterns on long bones from RDM and Pech IV to expected butchering patterns reported by Nilssen (2000). The statistical analysis used was a randomized chi-square goodness of fit test, designed to test the null hypothesis that the frequencies of cut marks at RDM and Pech IV were not significantly different from patterns produced by the two butchering practices listed above.

*TABLE 3.12. Number of cut marks recorded per anatomical region on identifiable bovid/cervid Long bone fragments mapped into ArcView GIS at both sites. **

		RDM Level 4						**RDM Level 9**					
		PE	**PS**	**MS**	**DS**	**DE**	**Total Cuts**	**PE**	**PS**	**MS**	**DS**	**DE**	**Total Cuts**
Humerus	Left	0	20	17	28	1	66	0	4	2	2	0	8
	Right	0	7	19	12	7	45	0	8	1	10	0	19
	Total	0	27	36	40	8	111	0	12	3	12	0	27
Radioulna	Left	0	13	40	10	0	63	0	0	0	2	0	2
	Right	0	8	21	6	0	35	0	0	0	0	0	0
	Total	0	21	61	16	0	98	0	0	0	2	0	2
Femur	Left	0	10	10	16	1	37	3	4	5	11	0	23
	Right	0	0	13	42	0	55	0	0	7	3	0	10
	Total	0	10	23	58	1	92	3	4	12	14	0	33
Tibia	Left	0	15	31	56	14	116	0	22	12	11	0	45
	Right	1	19	24	5	0	49	0	6	4	0	0	10
	Total	1	34	55	61	14	165	0	28	16	11	0	55

		Pech IV Level I2						**Pech IV Level YZ**					
		PE	**PS**	**MS**	**DS**	**DE**	**Total Cuts**	**PE**	**PS**	**MS**	**DS**	**DE**	**Total Cuts**
Humerus	Left	0	4	23	22	5	54	0	1	7	10	4	22
	Right	0	0	13	3	0	16	1	9	10	3	0	23
	Total	0	4	36	25	5	70	1	10	17	13	4	45
Radioulna	Left	4	4	4	16	0	28	5	12	6	0	0	23
	Right	1	0	4	7	0	12	13	2	15	0	0	30
	Total	5	4	8	23	0	40	18	14	21	0	0	53
Femur	Left	0	1	12	7	0	20	0	10	4	6	0	20
	Right	6	3	13	23	2	47	0	0	8	4	0	12
	Total	6	4	25	30	2	67	0	10	12	10	0	32
Tibia	Left	0	22	31	27	4	84	0	0	6	2	0	8
	Right	6	6	13	6	0	31	0	19	25	9	0	53
	Total	6	28	44	33	4	115	0	19	31	11	0	61

* Note that only bones that could be sided and placed on a bone template are included.

PE= proximal epiphysis, PS=proximal shaft, MS=midshaft, DS=distal shaft, DE=distal shaft

*TABLE 3.13. The percentage of bone surface area recorded per anatomical region on identifiable bovid/cervid long bone fragments mapped into ArcView GIS at both sites.**

		RDM Level 4					**RDM Level 9**				
		PE	**PS**	**MS**	**DS**	**DE**	**PE**	**PS**	**MS**	**DS**	**DE**
Humerus	Left	0.2	104.9	187.1	159.2	41.3	0.0	19.4	21.0	40.8	5.9
	Right	0.9	66.1	166.0	164.1	15.9	0.0	63.6	22.2	26.6	10.0
	Total	1.1	170.9	353.1	323.3	57.2	0.0	83.0	43.2	67.3	16.0
Radioulna	Left	10.8	163.1	337.5	114.2	0.0	0.0	10.5	43.1	14.4	2.0
	Right	0.0	25.4	120.1	87.1	6.0	0.0	6.4	32.2	29.0	0.0
	Total	10.8	188.5	457.6	201.3	6.0	0.0	16.9	75.2	43.4	2.0
Femur	Left	0.0	45.5	47.9	50.9	5.2	4.7	54.3	16.9	44.6	0.7
	Right	0.0	20.9	112.2	119.5	19.1	0.0	28.7	29.1	57.3	0.0
	Total	0.0	66.3	160.1	170.3	24.4	4.7	83.0	45.9	101.9	0.7
Tibia	Left	24.0	170.5	338.1	227.4	147.2	0.0	81.3	70.6	53.3	0.3
	Right	7.4	72.8	283.2	140.4	85.3	0.0	48.1	80.7	6.5	5.2
	Total	31.4	243.3	621.4	367.7	232.5	0.0	129.4	151.3	59.8	5.5
		Pech IV Level I2					**Pech IV Level YZ**				
		PE	**PS**	**MS**	**DS**	**DE**	**PE**	**PS**	**MS**	**DS**	**DE**
Humerus	Left	0.0	52.6	157.1	140.8	24.8	0.0	2.4	71.8	105.3	15.9
	Right	0.0	7.6	117.2	181.1	6.0	3.3	76.7	104.0	70.7	5.8
	Total	0.0	60.2	274.3	321.9	30.7	3.3	79.1	175.8	175.9	21.7
Radioulna	Left	68.1	78.1	171.4	63.8	0.8	30.6	53.3	35.1	0.0	0.0
	Right	31.2	27.3	39.0	0.0	0.0	31.2	27.3	39.0	0.0	0.0
	Total	99.3	105.4	210.4	63.8	0.8	61.8	80.5	74.1	0.0	0.0
Femur	Left	3.9	23.5	145.7	130.2	25.3	0.0	33.0	37.1	24.2	0.2
	Right	6.9	49.6	99.6	50.8	1.5	0.0	13.3	11.9	25.3	0.4
	Total	10.7	73.0	245.3	181.0	26.8	0.0	46.3	49.1	49.5	0.7
Tibia	Left	25.0	216.8	273.3	132.4	20.5	0.0	33.2	60.0	33.2	8.6
	Right	28.4	182.2	270.9	93.7	74.0	0.0	68.1	43.0	48.6	11.6
	Total	53.4	399.0	544.2	226.2	94.5	0.0	101.2	102.9	81.7	20.2

* Note that only bones that could be sided and placed on a bone template are included. Abbreviations as in Table 3.12.

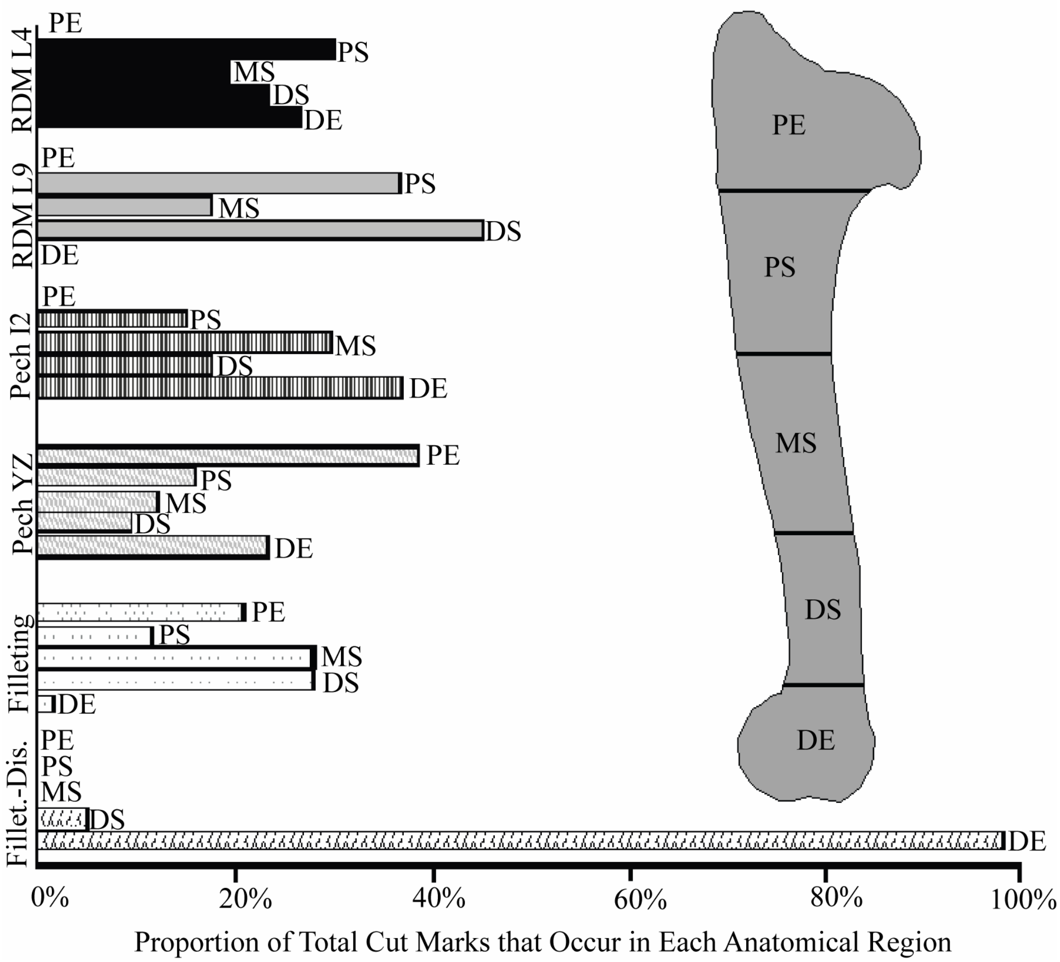

Fig. 3.17a. The proportion of total corrected number of cut marks on the humerus that occur in each anatomical region of bone. Note the bone diagram on the right is for illustrative purposes to show the location of each anatomical region. RDM and Pech IV data are compared to expected proportions based on actualistic experiments of filleting-only and filleting-and-disarticulating butchery strategies (Nilssen, 2000).

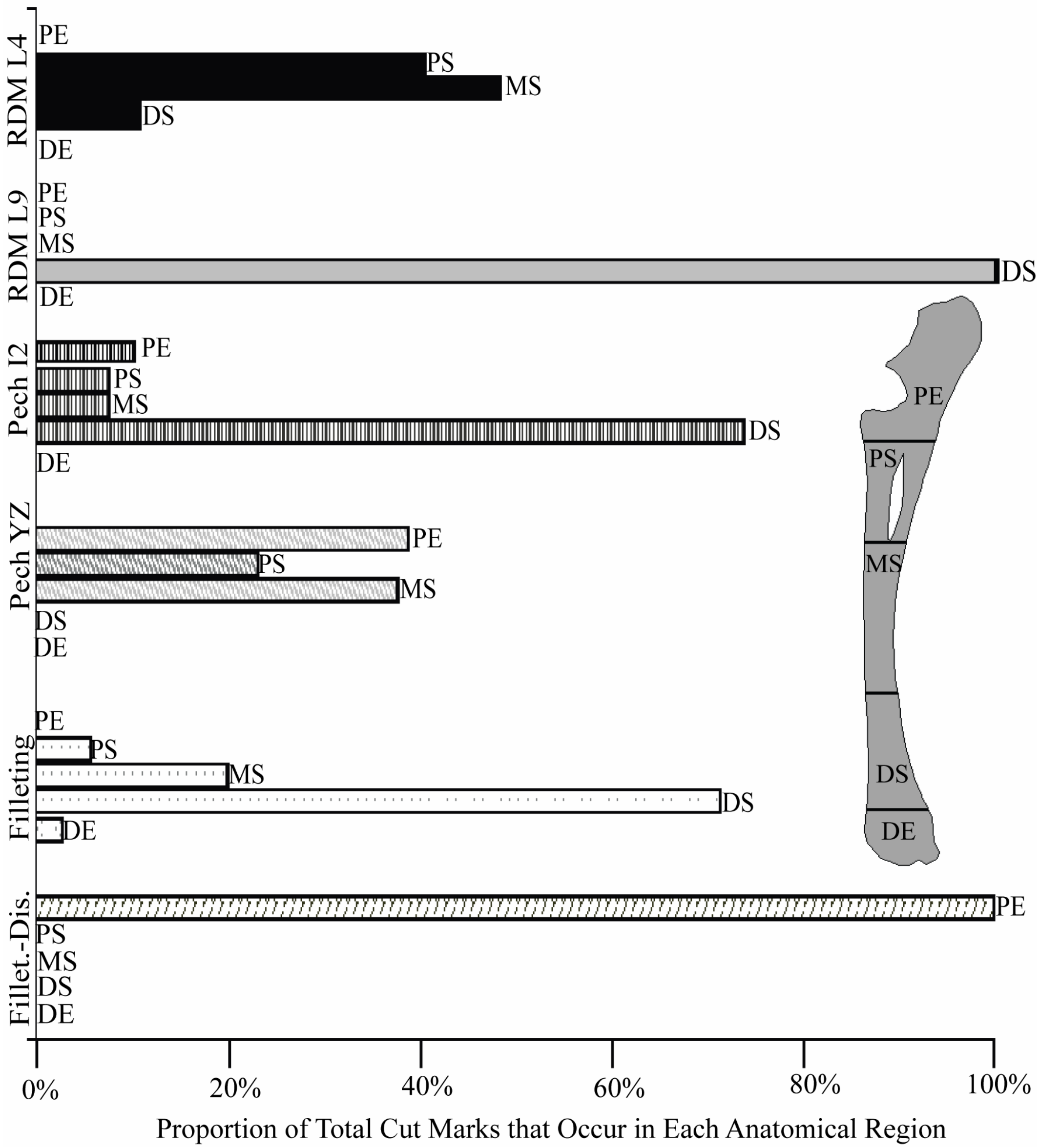

Fig. 3.17b. The proportion of total corrected number of cut marks on the radioulna that occur in each anatomical region of bone. Note the bone diagram on the right is for illustrative purposes to show the location of each anatomical region. RDM and Pech IV data are compared to expected proportions based on actualistic experiments of filleting-only and filleting-and-disarticulating butchery strategies (Nilssen, 2000). For comparison the numbers of cut marks recorded by Nilssen on the radius and ulna individually were combined.

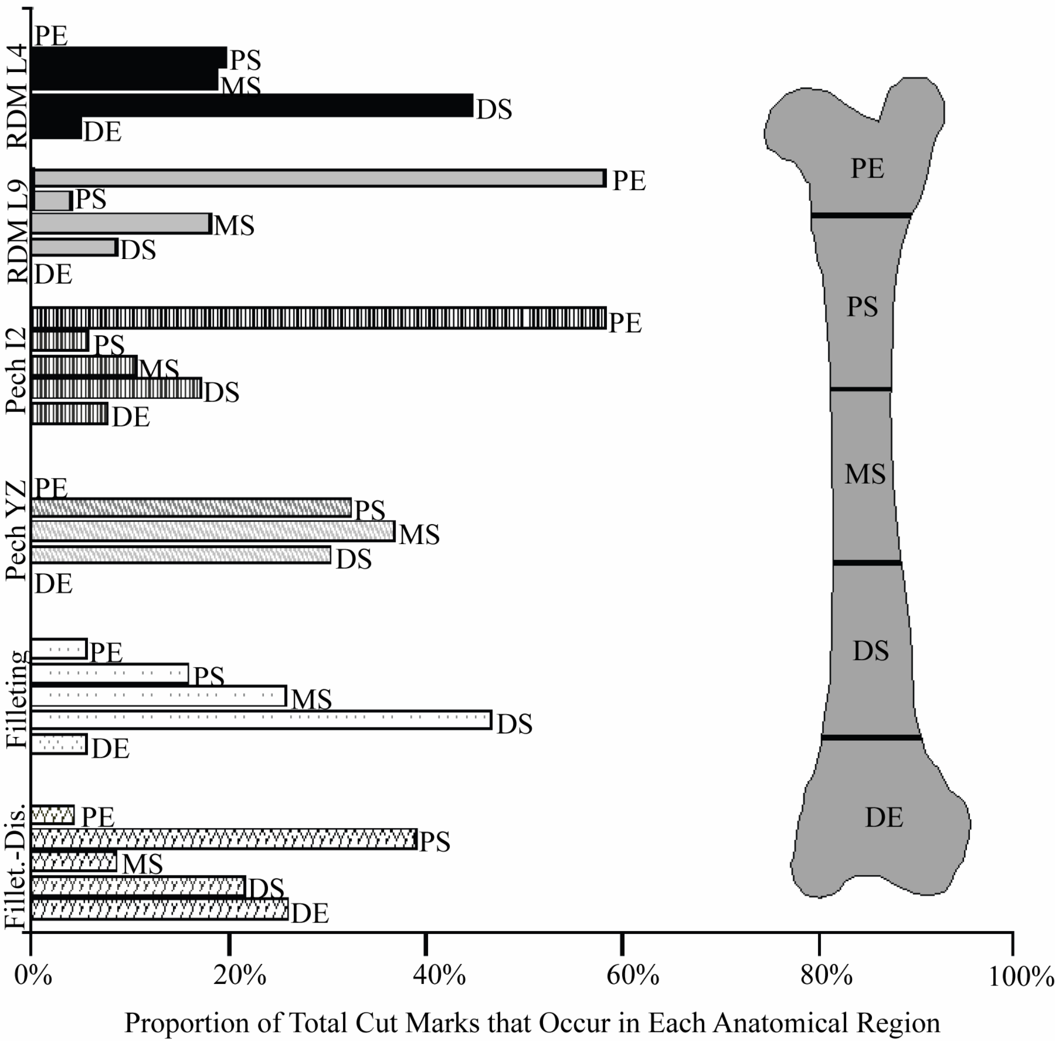

Fig. 3.17c. The proportion of total corrected number of cut marks on the femur that occur in each anatomical region of bone. Note the bone diagram on the right is for illustrative purposes to show the location of each anatomical region. The Roc de Marsal (RDM) and Pech IV data are compared to expected proportions based on actualistic experiments of filleting-only and filleting-and-disarticulating butchery strategies (Nilssen, 2000).

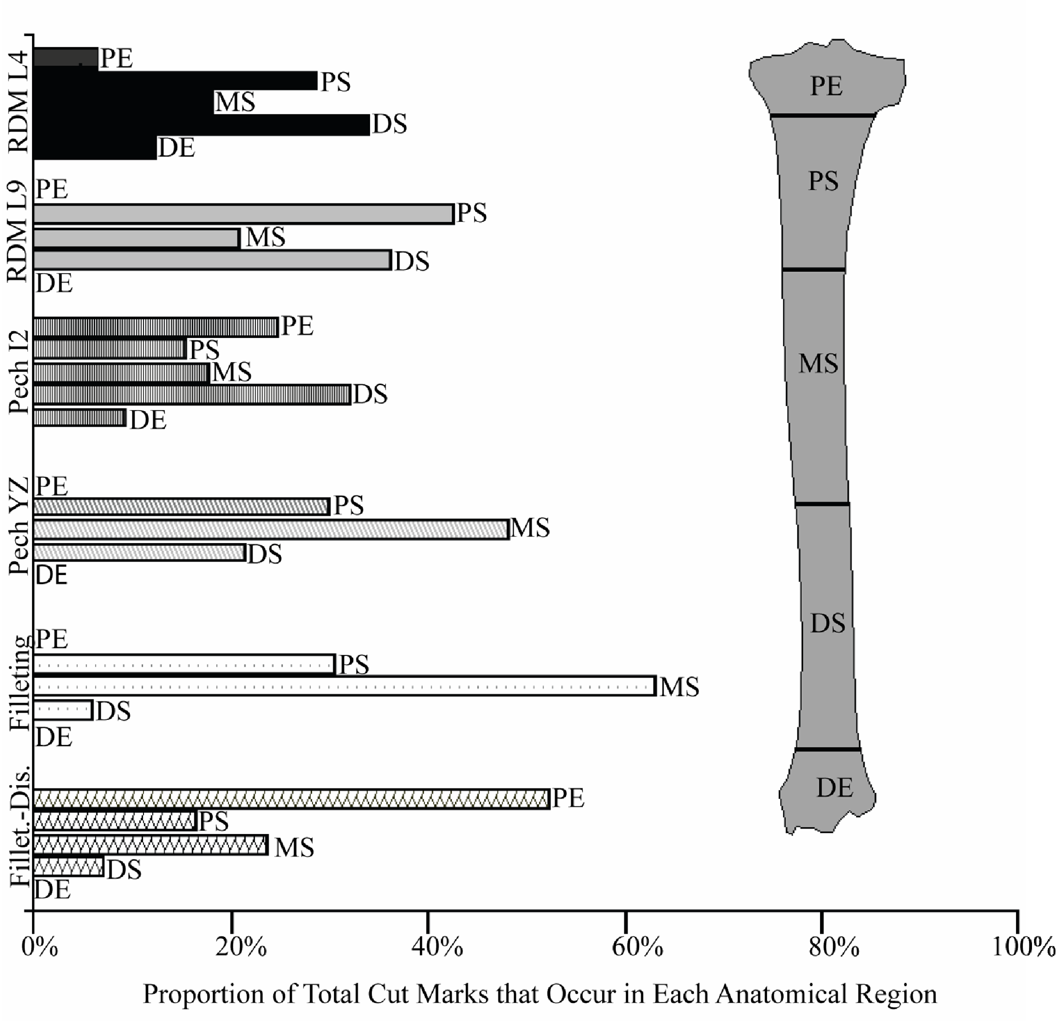

Fig. 3.17d. The proportion of total corrected number of cut marks on the tibia that occur in each anatomical region of bone. Note the bone diagram on the right is for illustrative purposes to show the location of each anatomical region. Roc de Marsal (RDM) and Pech IV data are compared to expected proportions based on actualistic experiments of filleting-only and filleting-and-disarticulating butchery strategies (Nilssen, 2000).

*TABLE 3.14. Randomized Chi-square goodness of fit to test how closely the frequency cut marks recorded on skeletal elements from Roc de Marsal (RDM) and Pech IV matched actualistic data from Nilssen (2000).**

Level	**Skeletal Element**	**Filleting**		**Filleting plus Dissarticulating**	
		$\chi2$	**p-value**	**$\chi2$**	**p-value**
RDM L4	Humerus	24.67	0	64.03	0
	Radioulna	18.67	0.005	231.82	0
	Femur	**24.84**	**0.47**	135.31	0
	Tibia	**21.84**	**0.65**	56.41	0
RDM L9	Humerus	26.59	0	100.13	0
	Radioulna	18.83	0.028	112.7	0
	Femur	285.5	0	85.92	0
	Tibia	**28.27**	**0.52**	100.23	0
Pech IV I2	**Humerus**	35.95	0	**13.11**	**0.24**
	Radioulna	99.57	0.009	638.73	0
	Femur	264.4	0	125.33	0
	Tibia	**53.34**	**0.1**	26.24	0.002
Pech IV YZ	**Humerus**	29.42	0	**35.26**	**0.51**
	Radioulna	197.7	0	40.08	0.007
	Femur	**22.49**	**0.53**	125.34	0
	Tibia	**5.66**	**0.99**	63.73	0
	With epiphyseal ends removed				
RDM L4	**Humerus**	**2.6**	**0.25**	12.99	0.002
	Radioulna	15.48	0	171.6	0
	Femur	15.88	0.007	38.86	0
	Tibia	24.25	0	19.78	0
RDM L9	**Humerus**	**4.1**	**0.12**	6.5	0.037
	Radioulna	17.53	0	86.63	0
	Femur	27.06	0	59.35	0
	Tibia	23.97	0	27.62	0
Pech IV I2	**Humerus**	**2.78**	**0.27**	7.96	0.01
	Radioulna	101.3	0	550.58	0
	Femur	8.41	0.025	24.84	0
	Tibia	26.12	0	15.36	0
Pech IV YZ	**Humerus**	**3.05**	**0.213**	13.32	0
	Radioulna	18.65	0	35.66	0
	Femur	**4.69**	**0.44**	19.776	0
	Tibia	**1.96**	**0.91**	**3.039**	**0.73**

*Exact p-values were determined based on 1000 bootstrap replications of the data. Bolded numbers are not statistically significantly different then Nilssen's data

Results from the randomized chi-square goodness of fit test show that when corrected number of cut marks (CNC) data from Pech IV and RDM are compared to Nilssen's (2000) data (with cut marks recorded on epiphyseal ends included), butchering patterns on many long bones, at RDM and Pech IV are significantly different from cut mark patterns left on long bones from filleting meat or filleting and disarticulating meat and bones (Table 3.14 top). When data recorded by Nilssen (2000) for the number of cut marks found on epiphyseal ends of long bones are removed from the analysis (Table 3.14 bottom), more of the skeletal elements cut mark patterns match Nilssen's data. Clearly, the fact that epiphyseal ends are largely missing at both archaeological sites affected the comparability of the two data sets. Nevertheless, the overall results from both chi-square analyses suggest that the cut mark patterns recorded on most long bones from Pech IV and RDM match butchering patterns produced by filleting meat as there were the fewest significant differences between the observed and expected patterns under this strategy. However, by having missing epiphyses or excluding them in the analysis, it is unlikely that patterns produced by disarticulation can be detected, because the joints are not represented. Some cut mark patterns at Pech IV match patterns produced by both filleting meat and disarticulating skeletal elements. Some long bones from the archaeological sites (the radioulnae in particular) do not match any of the butchering patterns observed by Nilssen. However, in addition to the missing epiphyseal ends in the archaeological sample, the radioulnae are also somewhat problematic to compare between datasets, because Nilssen recorded the number of cut marks on large bovid radii and ulna separately (although he did draw cut marks onto a combined radioulna template). In contrast, in the ArcView GIS program, the radius and ulna templates for caribou are combined into one bone (because these bones are fused in adult bovids and cervids). Thus, for the current comparison, the number of cut marks recorded per butchered bone from Nilssen was combined (summed) for each anatomical portion of the radius and ulna to create the number of cut marks recorded for the radioulna per butchered element. These slight differences in tabulation might have affected the proportions to some degree if the anatomical regions were not defined the same way in the radius versus the ulna under the two methods, which could account for some of the incongruence. Nevertheless, the numbers as they stand suggest that it is at least possible that Neandertals were butchering meat on these skeletal elements somewhat differently than the strategy employed in Nilssen's (2000) analysis.

Bone burning

During the data collection phase of this project, all specimens sampled from archaeological levels at Pech IV and RDM were examined for evidence of bone burning. The results show that fragments sampled from levels deposited during glacial cycles (RDM L4, Pech IV I2) exhibit very little evidence of burning (Table 3.15). In other words, very few specimens from these levels display signs of discoloration caused by smoke or fire. However, a higher proportion of fragments sampled from levels deposited during interglacial cycles were discolored, carbonized or fully calcined (Table 3.16). In fact, 12.3% of the specimens from Level 9 at RDM were grayish in color, while 4.8% were heavily burned: fully carbonized-fully calcined. The number of burned specimens was even greater in Level YZ at Pech IV, with 22% of the fragments showing grayish discoloration and 12.5% heavily burned. Table 3.17 displays the number of burned bone fragments broken down by skeletal element and bone type (cortical versus spongy).

TABLE 3.15. The absolute number and frequency of burned bones (relative to the total number) from Roc de Marsal (RDM) and Pech IV.

Level	**N with evidence of burning**	**Total bones from sites**	**Frequency of Burned Bones**
RDM L4	1	2068	0.05%
RDM L9	330	1922	17.17%
Pech IV I2	20	910	2.20%
Pech IV YZ	252	727	34.66%

TABLE 3.16. The number of specimens found per level that matched descriptions of burning stages outlined by Stiner et al. (1995).

Level	**N <0.5 Carbonized**	**>0.5 Carbonized**	**N Fully Carbonized (black)**	**N <.5 Calcined**	**N >.5 Calcined**	**N Fully Calcined (White)**	**N Carbonized Bone (stages 2-6)**	**N Carbonized Spongy Bone (stages 2-6)**
RDM L4	1	0	0	0	0	0	0	0
RDM L9	184	53	51	22	3	17	129	7
Pech IV I2	5	1	8	4	0	2	13	0
Pech IV YZ	109	52	64	12	1	14	129	13

TABLE 3.17. Number of identifiable specimens (NISP) and frequency of high survival skeletal elements that show signs of alteration caused by fire along with the total number and frequency of spongy bone and cortical bone fragments that show signs of alteration caused by fire.

RDM Level 9

Skeletal Element	**Total Number of Identifiable Specimens**	**N Burned (stages 1-6)**	**% Burned**
Mandible	19	2	10.53%
Humerus	24	3	12.50%
Radioulna	24	16	66.67%
Metacarpal	45	9	20.00%
Femur	31	1	3.23%
Tibia	51	3	5.88%
Metatarsal	60	4	6.67%
Metapodial	39	4	10.26%

Fragment Type	**Total Number of Identifiable Specimens**	**N Burned (stages 1-6)**	**% Burned**
Spongy Bone	89	4	4.49%
Cortical bone	1364	326	23.90%

Pech IV YZ

Skeletal Element	**Total Number of Identifiable Specimens**	**N Burned (stages 1-6)**	**% Burned**
Mandible	16	6	37.50%
Humerus	29	3	10.34%
Radioulna	24	18	75.00%
Metacarpal	30	6	20.00%
Femur	18	6	33.33%
Tibia	37	8	21.62%
Metatarsal	69	13	18.84%
Metapodial	30	13	43.33%

Fragment Type	**Total Number of Identifiable Specimens**	**N Burned (stages 1-6)**	**% Burned**
Spongy Bone	50	29	58.00%
Cortical bone	482	252	52.28%

CHAPTER 4: ZOOARCHAEOLOGY DISCUSSION

Discussion of taphonomic results

The results presented above show interesting patterns in terms of the taxa that were present in each archaeological layer, the transport patterns used by Neandertals, and the butchering strategies carried out through time at Pech IV and RDM. Before discussing the implications of these results, it is important to emphasize that while most of the analyses were focused on capturing information about the behaviors of Neandertals, many of the analyses also support previous findings (Dibble et al., 2005; McPherron, 2005; Dibble et al., 2009; Turq et al., 2009; Aldeias et al., 2012) that the faunal remains at Pech IV and RDM are very well preserved and that the accumulation and modification of bones at each site are the result of anthropogenic activities. For example, very few bones have non-nutritive bone breaks (Fig.3.1), indicating that bones were not extensively broken after they were deposited. Recently, an analysis of combustion features from Levels 7 and 9 at RDM found that a majority of these features are intact and in-place providing strong evidence for the amazing preservation conditions within this site through time. In addition, distinctive charcoal and ash lenses occur at Pech IV (Level YZ) with very little evidence of post depositional disturbance, although evidence exists that hominids actively modified some of the hearths by raking or spreading the charcoal and ash (Sandgathe et al., 2011). Furthermore, epiphyseal ends, which typically do not preserve as well as cortical bone (see Lam et al., 1998, 2003), were found in low frequencies at each site, along with small pieces of spongy bone (Tables 3.2 and 3.11). If these sites had been exposed to heavy sediment compaction, substantial chemical weathering, or heavy water flow these fragments would not be present.

The presence of small fragments of spongy bone (Table 3.11 and Fig. 3.4) and the nearly complete lack of tooth marks on bone fragments (Table 3.3 and Fig. 3.3) demonstrate that carnivores rarely consumed bones at Pech IV and RDM. It should be noted that hyena coprolites have been found in layers at RDM, and carnivore teeth (especially wolf teeth) have been found at both RDM and Pech IV. However, all faunal analyses conducted at these sites are in agreement with the analysis presented here in 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). In addition to faunal analyses at Pech IV and RDM, low levels of carnivore modification have been reported at other Neandertal sites in southern France: Grotte XVI (see Grayson and Delpech, 2003), Jonzac (see Jaubert et al., 2008; Niven, 2012) and Pech de l'Azé I (see Rendu, 2010). It is possible that this lack of carnivore modification may be due to the fact that Neandertals appear to have thoroughly processed skeletal elements (removing meat, marrow, and processing epiphyseal ends). If Neandertals removed most nutrients from skeletal elements, the resulting processed fragments may not have been attractive to carnivores. This idea is consistent with experiments of carnivore consumption, which have shown that carnivores tend to ignore bone fragments that are stripped of meat and bone marrow (Blumenschine, 1988; Marean and Spencer, 1991).

Overall, the taphonomic analysis demonstrates that conditions of preservation were excellent at Pech IV and RDM. All evidence indicates the Neandertals were responsible for accumulating and extracting nutrients from skeletal elements at both archaeological sites. Thus, corrections for post-depositional damage or the effects of carnivore modification are unnecessary in these assemblages, and these taxonomic factors do not need to be considered further in this discussion.

Discussion of taxonomic representation

The patterns of taxonomic representation of cervids from each site add to a large body of literature which shows that the abundance of each species of deer changes in differing climates: within a site *Cervus* and *Capreolus* are more abundant in layers deposited during interglacial cycles, while *Rangifer* are more abundant in colder climates (e.g., Laquay, 1981; Delpech, 1983; Grayson and Delpech, 1998; Grayson et al., 2001; Costamagno et al., 2006; Morin, 2008; Discamps et al., 2011; Guérin et al., 2012). While the abundance of species does change in relation to climatic shifts, it is import to highlight that all species in this study are present in every level analyzed, and *Cervus* exhibit a strong representation in all levels. This result is not unusual for archaeological sites throughout southwestern France (see Grayson and Delpech, 2006). Recently, Discamps et al., (2011) undertook a large, comprehensive study that included an analysis of species representation from archaeological sites dated between MIS 5-3, located in southern France. They concluded that species representation does largely correlate with climatic shifts, and an attempt was made to specifically correlate climate and biozones to species abundance. However, when focusing on smaller time scales, they often found that species representation varied. For example, they state:

> "AnteQuina" [technocomplex dating to approximately 115-73 ka] assemblages are dominated by red deer, but it seems possible to isolate two episodes of dominance by Horse or *Bovinae*. Moreover, at the end of the "AnteQuina", the tops of six sequences show the same pattern. During the transition from the "AnteQuina" to the Quina, the percentage of reindeer increases progressively before reaching its maximum at the Quina (Discamps et al., 2011:2769).

Thus, although climatic factors might have affected individual species abundances to some degree, all species recovered at RDM and Pech IV appear to have existed throughout southwestern France for the entire time period sampled for this dissertation and into the late Pleistocene.

It can be argued that there are two main reasons why most species were able to continue to exist in southwestern France into the late Pleistocene. First, as demonstrated extensively in the background section of this paper, species have remarkable ecological plasticity, and second, environments within southern France may have remained high in productivity. In reference to the latter, it has been reported that pollens typical of boreal forests and Atlantic forests composed greater than 50% of pollen types recovered from sediments within this region during the last interglacial (MIS 5) dating between 133–74 ka, and pollens typically found in boreal forests composed 48% of all identified pollen types between 70–65 ka, which corresponds to dates for the warm and cold phases of Dansgaard-Oeschger 18 (Fig. 4.1, Gentry et al., 2003; Sànchez-Goñi et al., 2008, Discamps et al., 2011; Boch et al., 2011). This suggests that plant productivity was probably maintained at a reasonably high level in southwestern France through time.

While the Discamps et al., (2011) analysis is lacking in its consideration of how transport bias, site type (cave vs. open air), and topography can bias species abundances at archaeological sites, their conclusion that species abundance is tied to climatic shifts is probably sound, as it is consistent with studies that track how species are responding to modern climate change (Parmesan et al., 2000; Parmesan and Yohe, 2003).

In my analysis, species abundance data are especially relevant, because transport bias (only size 2/3 bovid/cervids analyzed), site type (RDM and Pech IV are cave sites) and topography (both are cave sites elevated above a valley floor) were controlled. In addition, the relative abundance of each species (e.g., more *Rangifer* are present in Levels 4 and I2) remained the same after skeletal elements were entered into ArcView GIS and the MNI for each species was calculated (Table 3.1). This step removed the possibility that bones from some species were more fragmented, which might have affected abundance calculations derived from NISP. Therefore, the fact that *Cervus* and *Capreolus* are more abundant than *Rangifer* in Levels 9 and YZ, and *Rangifer* are more abundant in Levels 4 and I2, is consistent with the notion that Levels YZ and L9 were deposited during interglacials, while Levels I2 and L4 were deposited during glacials (Tables 3.4 and 3.5).

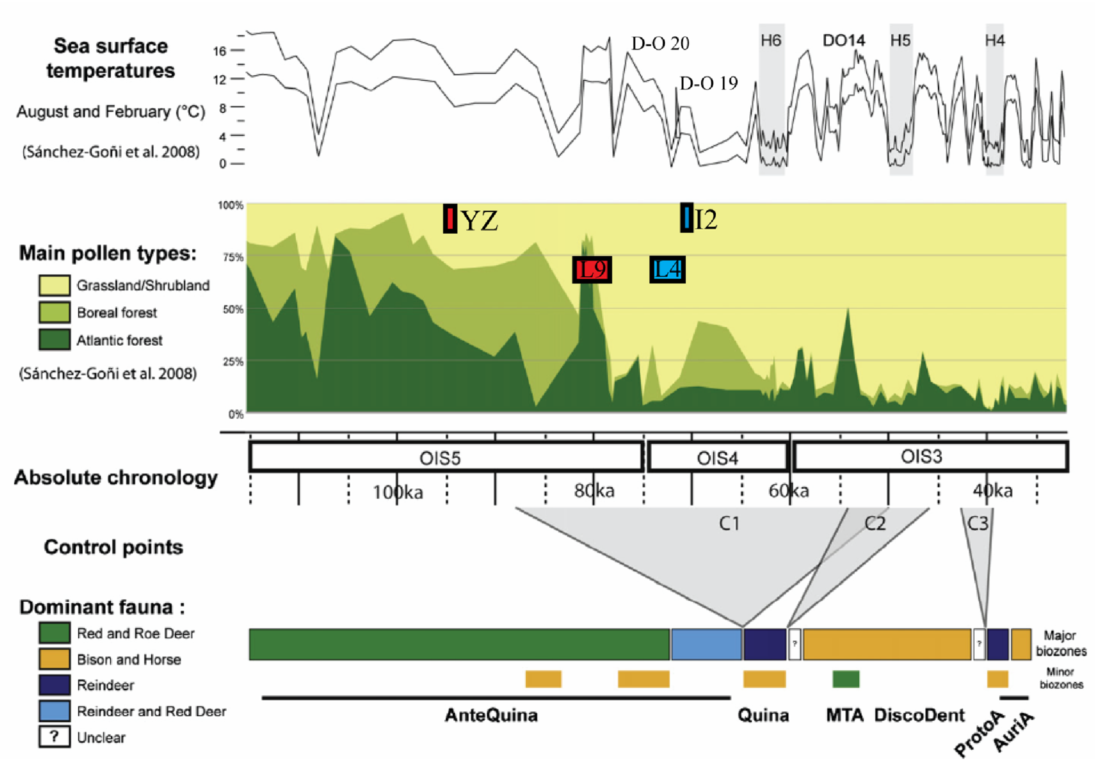

Fig. 4.1. Figure modified from Discamps et al. (2011) showing sea surface temperatures, pollen records, and a summary of species abundance data found at archaeological sites in southern France. The sites of Pech IV and Roc de Marsal (RDM) have been added here.

Discussion of skeletal element abundance

As mentioned in the results section, the abundance of most high survival skeletal elements is fairly similar at each site (Fig. 3.7). In fact, the evenness with which skeletal elements were transported is similar across levels (Tables 3.6a-d). It is interesting that despite the fact that only size 2/3 bovid/cervids were analyzed, full skeletons of these animals were not transported in any of the levels analyzed (Fig. 3.8). Thus, high survival skeletal elements were differentially transported at similar frequencies in all levels, except that mandibles are more abundant at Pech IV than they were at RDM. In addition, tibial fragments are the most abundantly represented skeletal element in all samples except Level YZ at Pech IV. After body size is controlled for, the most frequently invoked explanations for differential transport of skeletal elements are 1) the distance required to move a carcass from a kill site to a butchering site or central place; 2) the number of people available to carry parts of the carcass; and 3) utility of skeletal elements (Binford, 1978; Bunn, 1988; O’Connell et al., 1988, 1990; Marean, 2007; Schoville and Otárola-Castillo, 2009; Schoville and Otárola-Castillo, in prep).

If distance was indeed a constraint on the transport of animal remains to the sampled caves, one explanation for the increased frequency of mandibles at Pech IV, might be that this cave is somewhat closer to the valley floor than RDM. Pech IV is 50 meters above a valley floor while RDM is 80 meters. Studies of transport patterns among the Hadza have shown that the distance traveled does affect transport patterns (Bunn, 1988; O’Connell et al., 1988, 1990). Specifically, it has been found that for larger animals (size 4/5), transport distance has a significant effect on the transport of skulls (crania and mandibles), as heads are not transported when hunter-gatherers are more than fifty minutes away from a kill site (Bunn, 1988; O'Connell et al., 1988, 1990; Schoville and Otárola-Castillo, in prep). However, transport distance does not have a significant effect on the transport of skulls for size 2/3 animals (Bunn, 1988; O'Connell et al., 1988, 1990; Schoville and Otárola-Castillo, in prep). It is also interesting that while the frequency of mandibles is different in all levels at Pech IV and RDM, the frequency of crania are fairly consistent in that cranial remains are rare (Fig. 3.7). In nearly every observation reported by Binford of Nunamiut butchering behaviors, the head is the first body part removed, and this part is often not transported. In fact the head with antlers sticking up is usually used to mark areas where meat is cached (Binford, 1978: 47–91). The usage of heads in this way is not just reported for *Rangifer*, but also for *Alces* (Binford, 1978:55). A similar behavior among Neandertals may account for the low abundance of cranial remains recovered from each level at Pech IV and RDM, although the use of a caching site is hard to prove. The behavior also does not explain the high abundance of mandibles at Pech IV. Overall, when the full range of skeletal element abundance is considered at Pech IV and RDM, the cost associated with transport distance does not appear to explain the observed pattern.

The number of people present to transport carcasses has also been shown to have a significant effect on transport behaviors (Bunn, 1988; O'Connell et al., 1988, 1990; Schoville and Otárola-Castillo, 2009; Schoville and Otárola-Castillo, in prep). Specifically, among size 3 bovids the number of carriers significantly increases the likelihood that the skull, mandible, humerus, femur, tibia and metatarsals will be taken back to a central place (Bunn, 1988; O'Connell et al., 1988, 1990; Schoville and Otárola-Castillo, 2009; Schoville and Otárola-Castillo, in prep). It has been found that above six carriers, the probability of transporting the skull is 100% (Schoville and Otárola-Castillo, 2009; Schoville and Otárola-Castillo, in prep). In a study of the Evenki, Abe (2005:125) found that *Rangifer* were transported completely (although sleds and domesticated *Rangifer* were used to transport carcasses), but she stated that field butchering required more than one person. Thus, it seems likely that the number of carriers present at any given hunting event would have influenced the transport behaviors of Neandertal for size 2/3 bovid/cervids. It is possible that more carriers were able to transport skeletal elements at Pech IV than at RDM. This could have implications for Neandertal demography; however, a true analysis of this would have to include some control for time averaging within stratigraphic levels. It is also important to note that if more carriers were transporting animals at Pech IV, then the number of carriers was still not enough to transport a complete skeleton.

The most common approach to inferring transport patterns is to see if the abundance of bones found at a site is related to the utility, in terms of nutrient availability, calculated for each skeletal element (Binford, 1978; Metcalfe and Jones, 1988). Results from the current study have shown that the abundance of skeletal elements from each site fit most closely to Binford's bulk transport strategy (Fig. 3.8 and Fig. 3.11). Although skeletal elements from all levels deviated from the bulk strategy in the lack femoral fragments (Fig. 3.8, far right portion of the graph). In addition, mandibles (Fig. 3.8, far left portion) were more abundant in both Levels at Pech IV than would be predicted based on their calculated utility. Level YZ also stood out as having a lower than expected abundance of tibia. The lack of femora and abundance of mandibles has also been reported from the Middle Paleolithic site of Les Pradelles (Costamagno et al., 2006). Costamagno and colleagues suggested that the deficit of femora was cause by the transport of these elements to another site. This interpretation is possible, however it seems likely that femora were never transported to the site to begin with. Binford (1978:54) observed femora being processed at a kill site for the purposes of snacking, which were then left behind:

> While the hunter was butchering the animal, she (a woman accompanying the hunter) stripped all the meat from the left rear quarter with an *ulu* (an Eskimo woman's knife) and cracked the femur, tibia, and metatarsal for marrow. She did this by holding the bones in her left hand and striking the bone with a sharp blow just below the articular end with the handle of a knife. She then grabbed the articular end and twisted, and it came free with a typical spiral fracture…In this case the woman used the knife blade and a sharpened willow stick to dig the marrow from the cavity in the articular end. Only the stick was used for pushing the marrow from the sections of the bone shaft.
>
> All the dismembered parts and the skin were transported back to the village by sled. Remaining at the site were the broken bones of the left rear quarter and the articulated left rear foot.

The abundance of skeletal elements at Pech IV and RDM do not perfectly fit Binford's bulk strategy; therefore, it is possible that rather than focusing on the utility of meat marrow and bone grease, Neandertals were prioritizing bones with high marrow content. To test this, skeletal element abundance data were compared to two indices that quantify the quantity and quality of bone marrow and grease in long bones (see Fig. 3.9 and Fig. 3.10). However, results from these analyses do not suggest that Neandertals were focusing on marrow utility, as no positive significant correlations were found between measures of marrow utility and skeletal element abundance. However a significant negative correlation between skeletal element abundance and quantity of unsaturated fat is exhibited for Level YZ, suggesting that bones high in unsaturated fat were actively excluded from the assemblage. Figure 3.10 shows that in a comparison of %MAU and standardized UMI, Level YZ was unique from other levels analyzed in the low abundance of tibiae, femora, and radioulnae. It should be reiterated here that taphonomic data from this study demonstrate that carnivores played a very minor to non-existent role in consuming bones at Pech IV. In addition, high survival shaft fragments were analyzed throughout this analysis; thus, the taphonomic factors of carnivore bone consumption and the natural degradation of low density bones do not explain the under representation of “fatty” bones in Level YZ. Therefore, either these bones were not transported to Level YZ by Neandertals, or they were transported, but they were then removed from the archaeological record. One way this could happen is if tibiae, femora and radioulnae, which have the highest, third highest and fourth highest quantity of natural fuel in the form of unsaturated fat (Table 3.9), were used for fires. Morin (2007) points out that unsaturated fat (oleic acid) has a low melting point and is liquid at room temperature. Experiments in which bones were used as the primary source of fuel found that in order to get a fire started, it was necessary to use either grass (Glazewaki, 2006) or wood (Théry-Parisot, 2002), because heat was needed to melt grease within the bones before they would ignite. Thus, bones with a high content of grease with a low melting point may be beneficial for fires. Importantly, the highest frequency of burned bones were found in Level YZ, it therefore seems likely that tibiae, femora and radioulnae were used to fuel fires in this level, thus removing them from the archaeological record (Table 3.16).

Based on the discussion above, it appears that Neandertals were generally following a bulk transport strategy at both Pech IV and Roc de Marsal in which they maximized the quantity of all but the lowest utility parts, although mandibles were being transported at higher frequency and femora at a lower frequency than expected by the bulk strategy. In Level YZ, it appears likely that once bones were transported those bones with the highest unsaturated fat content were then used to fuel fires. Femora are included in the bones that may have been used to fuel fires in Level YZ; however, I am not suggesting that an under representation of femora in all levels was caused by their use as fuel. Femora in Level YZ have a lower %MAU (YZ=36%) than in other levels (L4=48%, L9=54%, LI2=36%). In addition, Figure 3.10 shows that in level YZ, other bones with high quantities of unsaturated fat (e.g., tibiae, and radioulna) are all under represented. Finally, evidence for hearth lens and burned bones exist in Level YZ, but not in Level 4 and I2. Thus, the under representation of femora in Levels 4, 9 and I2 indicates that they were either not always transported (possibly because they were used as snacks) or they were removed from the archaeological record (possibly by being transported to another site).

Discussion of surface modification

Overall results from this dissertation show that Neandertals extensively extracted nutrients from bones across time as demonstrated by an abundance of nutritive bone breaks on long bone fragments in all levels analyzed. However, Neandertals do appear to have increased their processing efforts during cold climates. The strongest evidence for this comes from the statistical analysis of the number of cut marks (Fig. 3.12) and percussion marks (Fig. 3.13) found on all marrow-yielding long bone fragments. The statistical analysis of the number of cut marks shows that levels deposited during cold climates have 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) has significantly more cut marks than Level 9 (warm level). At Pech IV, bones deposited in Level I2 (cold level) also contain more cut marks than Level YZ (the warm level), but the 95% confidence intervals overlap, so the difference is not as pronounced as at RDM. Statistical analysis of the frequency of percussion marks at both sites also shows that levels deposited during cold climates have more percussion marks than levels deposited during warm climates. In this analysis the magnitude of the difference was again affected by the site being analyzed. While the relative difference is greater between the number of cut marks in warm and cold layers at RDM, for percussion marks the relative difference in the number of percussion marks between warm and cold layers is greater at Pech IV. However, the pattern that frequency of percussion marks is statistically significantly greater in levels deposited during cold climates than in warm climates is clear for both sites.

Additional evidence that Neandertals were processing bones more intensively in cold climates than they were in warm climates is that while epiphyseal ends are rare in all levels (Table 3.2), of the ones that remain, more percussion marks are found on the epiphyseal ends deposited during glacials than those deposited during interglacials (Table 3.10). This last finding matches expectations published by Marean (2005: 21) of what an archaeological assemblage would be like if Neandertals were processing epiphyseal ends for consumption. It is also interesting that in the small finds bags from each site, small fragments of spongy bone are found in higher abundance in Level 4 (the cold level) from RDM than in 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 YZ from this site (Fig. 3.14). It is possible that a lower frequency of spongy bone fragments in Level I2 at Pech IV is simply due to sampling error. Fewer small finds were analyzed from this level than all other levels (Table 3.11). It is also possible the extensive amount of bone burning in Level YZ created an abundance of small fragments of spongy bone. This might be the case if greasy epiphyseal ends were used to fuel fires and the fires caused the bones to crack into small pieces while being burned.

As mentioned in the methods section, experimental butchering studies have found that there is not a one to one correlation with the number of cutting strokes or the number of percussion hits taken and marks left on the bone (Egeland, 2003; Lyman, 2005; Pickering and Egeland, 2006). In fact, a negative correlation has been reported between these variables (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 that protect the bone from the tool being used. With this in mind, it is safe to say that the number of modification marks found at Pech IV and RDM does not reflect the full amount of effort that Neandertals put into extracting nutrients from the bones. Neandertals would have made many more cutting strokes and percussion hits than were recorded. This realization makes the results from this analysis that significantly more surface modification marks were found in layers deposited during cold climates than warm climates at two different sites all the more interesting.

One other criterion that needs to be met in order to make a strong case that Neandertals were intensively processing skeletal elements at Pech IV and RDM is that bones with low marrow yields should show evidence of processing (Bar-Oz and Munro, 2007). Bar-Oz and Munro (2007) specifically single out phalanges for this type of analysis; however, Binford's marrow index also shows that mandibles have fairly low marrow yields (Binford, 1978). Tables 3.9a and 3.9b show that while very few phalanges have been analyzed high frequencies of those phalanges have surface modification marks. Interestingly, mandibles were well represented at Pech IV and RDM and frequencies of percussion marks on mandibles match those for other high marrow-yield long bones (Fig. 3.15). In a study of the Evenki, Abe (2005: 185) observed that *Rangifer* mandibles were separated from the rest of the skull. The right and left halves of the mandibles were disarticulated and the mandibles were broken open using a knife as a hammer for the consumption of marrow. On page 185, Abe writes, “The marrow was not thoroughly eaten, unlike the case with other marrow bones. Usually the person ate what s/he could extract from whatever size hole [was] made on the first attempt.” At RDM, and especially at Pech IV, it appears that often more than one attempt was made to expose the marrow inside of mandibles. In RDM’s Level 4, out of four mandibles with percussion marks five total marks were recorded, while in Level 9 out of three mandibles with percussion marks four total marks were recorded. In Pech IV’s Level I2, out of 10 mandibles with percussion marks a total of 19 percussion marks were found, and in Level YZ out of three mandibles with percussion marks 10 percussion marks were recorded (Table 3.9b). These results may indicate that effort was put into extracting all of the marrow stored in mandibles at these sites. The fact that mandibles at Pech IV contain more percussion marks than those at RDM suggests that Neandertals at this site really utilized this resource through time, and this may explain why mandibles were transported to this site in higher abundances.

Finally, in order to understand how Neandertals were butchering the meat from particular skeletal elements, a comparison of the frequency of cut marks recorded in all anatomical regions of long bones was undertaken and compared to patterns reported by Nilssen (2000) for cut marks produced by filleting, and filleting and disarticulating. While the cut mark patterns on some long bones did match Nilssen’s data for patterns produced by filleting and filleting and disarticulating meat and skeletal elements, cut mark patterns on many skeletal elements did not match Nilssen’s data (Table 3.14). One of the reasons that most patterns of cut marks at RDM and Pech IV do not match patterns observed by Nilssen is that epiphyseal ends are so poorly represented at this site. Another reason is that of the epiphyseal ends that are present some of them have higher frequencies of cut marks than predicted by filleting meat, and less than predicted for filleting and disarticulating. This discrepancy can be seen in Figures 3.17a-d. While the corrected number of cut mark (CNC) method is a good tool, which analyzes the frequency of cut marks recorded on fragmentary pieces of long bone shafts, and then estimates the number of cut marks that would be recorded if a whole bone had been analyzed, this method cannot correct for a zero occurrence of certain portions of bones. With this problem in mind additional randomized chi-square analyses were run in which cut marks reported on epiphyseal ends by Nilssen were removed. These analyses did increase the correspondence of data from Pech IV, RDM and Nilssen's expected patterns somewhat (Table 3.14). Overall, analyses of cut mark frequencies on long bones visually demonstrate that cut marks are found in high abundance on long bone shaft fragments from Pech IV and RDM (Fig. 3.17a-d). They also show that of the epiphyseal ends that are present many of them contained cut marks.

Discussion of the results of bone burning

Pech IV and RDM are interesting assemblages in terms of evidence for bone burning behaviors among Neandertals. In a recent publication, Sandgathe et al. (2011) point out that at both Pech IV and RDM evidence for burning and use of hearths only exist in layers deposited during warm climates. Evidence for bone burning becomes much less frequent in layers deposited during glacial cycles.

This pattern is the opposite of what would be expected (based on “common sense”) as it seems more logical that Neandertals would want to warm themselves when it was cold. However, Sandgathe and colleagues propose that one possible reason for a lack of fire during cold climatic cycles is that while Neandertals could maintain fires they could not produce them. Natural fires occur more frequently on the landscape during warm time periods; thus, Neandertals had the opportunity to find fire on landscape, collect it, and maintained it during interglacial cycles.

The conclusion reached by Sandgathe and colleagues is compelling. The lack of fire during cold time periods, as well as the general intermittence of fire use over time is a strange phenomenon. Results from this dissertation uphold the observation that evidence for fire is much more common during interglacial cycles than in glacials (Table 3.15). Levels 4 and I2, both deposited during glacial cycles, have very few burned bones. Therefore the rest of this discussion will focus on Levels 9 and YZ. For these levels, the extent of bone burning and the proposed use of fire in each level will be discussed.

In an effort to reconstruct the bone burning behaviors of Neandertals Costamagno et al. (2009) ran a series of 30 experiments. The humeri of ox (*Bos taurus*) were employed in these experiments and portions of these bones were placed in different categories including: fresh whole unbroken humeri, dry whole unbroken humeri, fresh humeral epiphyses only, dry humeral epiphyses, fresh fragmented humeri, dry fragmented humeri, humeral diaphyses with marrow, and humeral diaphyses without marrow. Specimens in each category were then subjected to a range of different burning experiments in which attempts were made to use each category of specimens as fuel, where meat was cooked from specimens in all categories, and where specimens in different categories were thrown on a fire at random to simulate cleaning. From these experiments, Costamagno et al. (2009) calculated the expected frequencies of burned specimens in assemblages where specimens were burned as fuel, where specimens were burned unintentionally (through cooking), and where specimens were burned both for the purpose of cleaning camp and also for use as a fuel source. In establishing criteria for classifying bone burning behaviors into each of these categories, Costamagno et al. (2009) focused on specimens from their experiments that were mostly carbonized (> 50% black, burning stages 2–6, Stiner et al., 1995).

Using the range of values reported by Costamagno et al., (2009) as a reference for interpreting burning patterns at archaeological sites, previously published reports found that Level 9 at RDM matched assemblages where bones were burned unintentionally and also where bones were burned for site cleaning and as fuel (Costamagno et al., 2009, study conducted by Castel in Sandgathe, 2005). Level YZ matched sites where bones were burned for the purposes of cleaning camp and also as fuel (Dibble et al., 2009; study by L. Niven). Results from the current dissertation show that bones from RDM and Pech IV match assemblages where bones were unintentionally burned (Table 4.1). However, the sample size of burned bones from Niven’s analysis of Level YZ (level 8, Dibble et al. excavation) was larger than the sample analyzed in this study, and therefore her results are likely more reflective of burning behaviors at the site. Thus, it appears that bones in Pech IV's Level YZ were burned for both site maintenance and to fuel fires, whereas in RDM's Level 9 bones may have been unintentionally burned.

Unintentional burning may result from such activities as cooking meat, or from bones being placed close to a hearth. It is worth mentioning that when all stages (1–6) of burned bones are considered, a higher frequency of spongy bone fragments (58%) show signs of burning in Level YZ, compared to cortical bone fragments (52%). This is in contrast to the situation in Level 9 for which 4.49% of spongy bones fragments were burned compared to 23.9% of cortical bone. This analysis demonstrates clearly that bones were burned more intensively in level YZ at Pech IV than they were in Level 9 at RDM.

TABLE 4.1. The frequency of burned bones found at sites where bones were burned for fuel, bones were burned accidentally, and bones were burned for cleaning and combustion compared to frequencies from RDM and Pech IV.

Site Types from Costamagno et al. (2009)	% spongy bone burned	% carbonized	% burned bones
Range of Frequencies From Bones Used As Fuel	34.9%-77%	77%-100%	32.2%-78.5%
Range of Frequencies From Bones Accidentally Burned	0.65%-30.4%	33.5-63.7	3.4-61
Range of Frequencies From Bones Burned for Cleaning and Combustian	5.49%-23%	77.9%-100	14.8%-98.7
RDM L9 (Hodgkins study)	5.30%	39.00%	34%
RDM L9 (Castel study)	4.49%	76%	17.17%
Pech IV L YZ (Hodgkins study)	10.08%	51.00%	17.17%
Pech IV L YZ (Niven study)	19.10%	99.10%	54.00%

The use of fire in Level YZ has been referenced previously in this discussion, because it was proposed that the uniquely low representation of skeletal elements with high quantities of unsaturated fat (tibiae, femora, radioulna) may be the results of these specimens being used to fuel fires. Experiments in bone burning have shown that only spongy bone can be considered a good fuel source (Théry-Parisot, 2002; Glazeski, 2006; Costamagno et al., 2009). At equivalent weights, spongy bone will remain burning twice as long as compact bone (Costamagno et al., 2009). It is also interesting that in a bone burning experiment conducted by Glazeski (2006: 21), whole deer legs were placed on top of the fire so that grease from the legs would drain into the fire helping to keep the fire going. This experiment resulted in a fire that reached 540°C. While the results from the frequencies of burned bone suggest that Neandertals at Level YZ were burning bones in order to clean out the site and also to help fuel their fires, the fact that a high frequency of spongy bone was burned may suggest that the bones preferentially chosen to help fuel fires were bones with high quantities of unsaturated fat. The burning of these bones would effectively delete them from the archaeological record. This behavior would explain why tibiae and radioulnae are represented at higher frequencies in Level 9 where bone burning behaviors appear to have been unintentional.

It is hard to comment on why Neandertals were primarily burning bones during warm interglacial cycles. The hypothesis that Neandertals lacked the knowledge of how to build a fire is not farfetched given that some modern hunter-gatherers have been found to lack fire making knowledge, although these hunter-gatherers do have constant access to fire (Hill et al., 2011; Stearman, 1991). However, since a number of bone burning experiments have shown that only the grease rich portion of bones can be used as a fire source, an alternative explanation is that during times when Neandertals were nutritionally stressed (e.g., during glacial cycles) they may not have been able to waste high caloric and nutrient rich spongy bone for the use of fires (see Marean, 2005). Instead as shown in this study, Neandertals may have been percussing long bone ends and processing the grease for consumption.

CHAPTER 5: RESULTS OF THE RADIOGENIC STRONTIUM ISOTOPE ANALYSIS

Major, minor, and trace elemental concentrations

When analyzing isotopic values from archaeological remains it is important to demonstrate that the values have not been altered by diagenetic processes. Therefore, as mentioned in the methods section, a number of teeth from multiple levels in each cave were selected for major, minor, and trace element analysis. Examinations of calcium/phosphate (Ca/P) ratios have been used to indicate whether archaeological material has undergone diagenesis (Price et al., 1992). It is known that modern hydroxyapatite contains by weight approximately 37% Ca and 17% P, giving modern teeth Ca/P values of approximately 2.14 (Sillen, 1989; Price, 1992; Balasse, 2002; Burton, 2008; Papageorgopoulou and Xirotiris, 2009). Results from this analysis demonstrate that most enamel samples from Pech IV and RDM have been robust to diagenetic contamination. The Ca/P values from these enamel samples (mean Ca/P = 2.14±0.08, 2σ, n=12) closely match the value found in modern teeth, as well as values obtained from samples of the international standard NIST-1400 of ashed bone that is certified by the National Institute of Standards and technology (Ca/P=2.10±0.03, 2σ), and values obtained from samples of the internal standard CUE-0001 of ashed llama bone used in the ACL lab at ASU (Ca/P=2.13±0.06, 2σ) (Table 5.1). Samples of the NIST-1400 (n=9) and the CUE-0001 (n=5) were measured repeatedly to ensure accuracy and precision. The one exception is specimen F16-3786 (a horse tooth) from Pech IV, layer YZ, which has an elevated Ca/P ratio (Ca/P =2.24), suggesting some contamination has occurred in this specimen. It is also interesting that Ca/P values were elevated in the dentin samples. Like bone, dentin has a more porous structure than enamel resulting in greater susceptibility to diagenesis (Lee-Thorp et al., 1989; Lee-Thorp and van der Merwe, 1991, Budd et al., 2000; Balasse, 2002). The fact that dentin samples from RDM appear to have undergone some chemical alteration, suggests that bones from these levels may be altered as well. Fortunately, results from this analysis show that nearly all enamel samples have been robust to contamination.

Other tests for diagenetic contamination included analyzing levels of neodymium (Nd) and uranium (U). These rare earth elements (REEs) are key tools for identifying whether or not a bone has undergone chemical alteration. REEs should only be present in very low concentrations (sub-ppm, 1×10^{-5}) within living animals (Kohn et al., 1999). Thus, if a higher concentrations of U and Nd are found in fossilized bone, this provides evidence that diagenetic activity has occurred (Millard and Hedges, 1995). Analysis reveals that none of the enamel samples have undergone contamination as the U/Ca and the Nd/Ca values are within one standard deviation of values obtained from samples of the international standard NIST-1400 (n=9) and the internal standard CUE-0001 (n=5) (see Table 1.5). Additionally, U concentrations in all tooth samples were less than 1×10^{-8}, which is within the range that has been reported from modern bones (Williams and Marlow, 1987; Burton, 2008). It has been noted that since U and Nd are universally present in soils, finding low values of these elements in archaeological samples is a good indication that the samples have largely been resistant to chemical alteration (Burton, 2008). Thus, these results suggest that strontium measured in archaeological teeth from RDM and Pech IV (with the possible exception of specimen F16-3786) will likely reflect biogenic and not diagenetic values.

TABLE 5.1. Results from major, minor, and trace element analysis.

Site, Level	**Specimen**	**Sample**	**44Ca/31P**	**238U/44Ca**	**146Nd/44Ca**
RDM, L4	J18-4657 *Equus*	ACL-2328 enamel	2.09	1.73E-07	5.19E-07
	K17-1338 *Cervus*	ACL-2340 dentin	2.79	3.02E-06	3.50E-07
	K17-1338 *Cervus*	ACL-2340 enamel	2.15	2.55E-07	5.12E-07
	J16-1572 *Rangifer*	ACL-2337 enamel	2.10	1.46E-07	1.11E-06
	K16-2238 *Equus*	ACL-2341 enemel	2.15	1.64E-07	1.23E-06
RDM, L8	K17-2382 *Rangifer*	ACL-2330 dentin	2.35	4.18E-06	4.55E-06
	K17-2382 *Rangifer*	ACL-2330 enamel	2.11	6.07E-07	7.02E-07
	G18-1882 *Rangifer*	ACL-2329 enamel	2.17	1.20E-07	3.46E-06
	K17-1418 *Equus*	ACL-2334 enamel	2.10	1.03E-07	3.03E-07
RDM, L9	G18-6729 *Cervus*	ACL-3434 enamel	2.13	3.87E-07	3.63E-07
Pech L I2	E11-3125 *Rangifer*	ACL-2325 enamel	2.14	8.13E-06	2.85E-06
	D11-3951 *Rangifer*	ACL-2338 enamel	2.15	3.05E-07	9.61E-07
Pech, L YZ	F17-2845 *Cervus*	ACL-3435 enamel	2.10	1.90E-07	4.58E-07
	F16-3786 *Equus*	ACL-3436 enamel	2.24	9.60E-07	2.07E-07
CUE-0001 average		n= 5 (2σ)	2.13 ±0.06	2.35E-07± 1.96E-07	2.91E-08± 1.85E-07
NIST 1400 average		n=9 (2σ)	2.10 ±0.06	1.03E-07 ± 1.17E-05	5.09E-07 ± 1.98E-06

Radiogenic strontium isotope analysis

Results from radiogenic strontium isotope analysis of large herbivore teeth from RDM and Pech IV are provided in Table 5.2a-c. These data reveal that all isotope values (herbivore range $^{87}Sr/^{86}Sr= 0.7093-0.7137$) are above local ratios (local range $^{87}Sr/^{86}Sr=0.7087-0.7092$, mean $^{87}Sr/^{86}Sr= 0.70899\pm0.00017$, 1σ, N=7). Here the "local ratios" refer to radiogenic strontium isotope values obtained from archaeological rodent teeth excavated from Levels 7, 8 and 9 at RDM (Table 5.2a-c). Modern water and snail shell samples collected from the town of Les Eyzies, which is located 10 km from RDM and 30 km from Pech IV were also used to establish the range of radiogenic strontium isotope values found in and around the sites of RDM and Pech IV (Table 5.3). A modern snail shell sample from Mansle located 158 km away from the archaeological sites, but still located within the Aquataine Basin was used to help establish a broader local radiogenic strontium isotope signature for the sedimentary Aquatine Basin. The fact that $^{87}Sr/^{86}Sr$ values in herbivore teeth from the sites of Pech IV and RDM are above local values, suggests that they are not the product of diagenetic changes (Williams and Marlow, 1987; Williams and Potts, 1988; Williams, 1988; Price, 1992; Budd et al., 2000). Contaminates in fossils are often introduced through precipitation from ground water or from incorporation of minerals into archaeological specimens from soils surrounding the archaeological remains (Williams and Marlow, 1987; Williams and Potts, 1988; Williams, 1988; Price, 1992; Budd et al., 2000). Contamination by these processes causes values in archaeological specimens to match local water values (Price, 1992; Budd et al., 2000). Thus, the ratios found in herbivore teeth from Pech IV and RDM are more likely reflective of where the animals were eating when their teeth were developing (Fig. 5.1). While the ratios measured from large ungulate teeth are higher than levels found at RDM, Les Eyzies and Mansle, they are within the range of published values from other areas of the Aquitaine and Paris basins (see Fig. 5.2; range $^{87}Sr/^{86}Sr$=0.7086-0.7109; Tricca et al., 1999; Semhi et al. 2000; Barbaste et al. 2002; Kelly et al. 2007; Britton et al., 2011). Additionally, a majority of values found in herbivore teeth are lower than values recorded from clay and most granitoid sediments (range $^{87}Sr/^{86}Sr$= 0.7098-0.7272, mean $^{87}Sr/^{86}Sr$ =0. 7164 ± 0.005, 1σ, n =10, see Kelly et al. 2007) from the nearby mountain range of the Massif Central (see Fig. 5.1 and Figs. 5.3 and 5.4). In addition, ratios found in all *Rangifer* (mean $^{87}Sr/^{86}Sr$=0.7098± 0.00026, 1σ, n=24) and most *Cervus* (mean $^{87}Sr/^{86}Sr$= 0.7108±0.0012, 1σ, n= 15) , *Bison* (mean $^{87}Sr/^{86}Sr$=0.7100±0.00046, 1σ, n=12) and *Equus* (mean $^{87}Sr/^{86}Sr$ 0.7101±0.00085, 1σ, n=12) enamel samples are lower than values reported from archaeological ungulate teeth from the site of Les Pradelles (range $^{87}Sr/^{86}Sr$=0.7105-0.7125, mean $^{87}Sr/^{86}Sr$=0.7113 ±0.0005, 1σ, n= 14, see Kelly, 2007) located on the eastern edge of the Massif Central (see Fig. 5.1, bar B).

TABLE 5.2a. Results from $^{87}Sr/^{86}Sr$ analysis.

Site, Level	**Specimen**	**Sample**[1]	**$^{87}Sr/^{86}Sr$**
RDM, L4	J17-2266 *Bison* (mid wear)	ACL-3424a (m_1)	0.70973
		ACL-3424b (m_1)	0.70966
		ACL-3424c (m_1)	0.70958
		ACL-3424d (m_2)	0.70966
		ACL-3424e (m_2)	0.70969
		ACL-3424f (m_2)	0.70958
	J18-1379 *Rangifer* (early wear)	ACL-3425a (m_1)	0.70992
		ACL-3425b (m_1)	0.71026
		ACL-3425c (m_2)	0.71014
		ACL-3425d (m_2)	0.70973
		ACL-3425e (m_3)	0.70985
		ACL-3425f (m_3)	0.70964
	K16-1865 *Rangifer* (mid wear)	ACL-2336a ($M^{1 or 2}$)	0.70953
		ACL-2336b ($M^{1 or 2}$)	0.70962
		ACL-2336c ($M^{1 or 2}$)	0.70949
	K17-1338 *Cervus* (mid wear)	ACL-2340a (M^1)	0.70989
		ACL-2340b (M^1)	0.70986
		ACL-2340c (M^1)	0.70973
	K16-2238 *Equus* (early wear)	ACL-2341a (M^2)	0.70935
		ACL-2341d (M^2)	0.70951
		ACL-2341g (M^2)	0.70944

TABLE 5.2b. Results from ^{87}Sr/^{86}Sr analysis.

Site, Level	**Specimen**	**Sample^1**	**^{87}Sr/^{86}Sr**
RDM, L7	J17-6775 *Microtus*	ACL-2344	0.70890
RDM, L8	G18-1882 *Rangifer* (unworn)	ACL-2329a (m_3)	0.70971
		ACL-2329b (m_3)	0.70978
		ACL-2329c (m_3)	0.70996
	K17-2382 *Rangifer* (early wear)	ACL-2330a (m_1)	0.71025
		ACL-2330b (m_1)	0.71009
		ACL-2330c (m_1)	0.71008
	K17-1418 *Equus* (mid wear)	ACL-2334a (p_4)	0.71033
		ACL-2334d (p_4)	0.70971
		ACL-2334g (p_4)	0.70993
	K17-1396 *Cervus* (early wear)	ACL-2331a (m_1)	0.71061
		ACL-2331c (m_1)	0.71091
	K18-5419 *Microtus*	ACL-2343	0.70905
RDM, L9	G18-6729 *Cervus* (Very early wear)	ACL-3427a (M^3)	0.71007
		ACL-3427b (M^3)	0.70998
	F18-2860 *Cervus* (mid wear)	ACL-3426 (m_1)	0.71021
		ACL-3426 (m_1)	0.71051
	K17-5969 *Microtus*	ACL-2345	0.70922

TABLE 5.2c. Results from ^{87}Sr/^{86}Sr analysis.

Site, Level	**Specimen**	**Sample[1]**	**^{87}Sr/^{86}Sr**
Pech IV, L I2	D11-3951 *Rangifer* (unworn)	ACL-2338a ($M^{1 \text{ or } 2}$)	0.70977
		ACL-2338b ($M^{1 \text{ or } 2}$)	0.70966
		ACL-2338c ($M^{1 \text{ or } 2}$)	0.70961
	C13-636 *Rangifer* (very early wear)	ACL-2324a ($M^{1 \text{ or } 2}$)	0.70981
		ACL-2324b ($M^{1 \text{ or } 2}$)	0.70944
	E11-3125 *Rangifer* (mid wear)	ACL-2325a (m_1)	0.71011
		ACL-2325b (m_1)	0.71006
	D14-3358 *Bison* (mid wear)	ACL-3429a (M^1)	0.71076
		ACL-3429b (M^1)	0.71068
		ACL-3420c (M^1)	0.71055
	F16-706 *Bison* (mid wear)	ACL-3416a (m_2)	0.71019
		ACL-3416b (m_2)	0.71034
		ACL-3416c (m_2)	0.71041
	D17-1142 *Equus* (early wear)	ACL-3428a (M^1)	0.70963
		ACL-3428b (M^1)	0.70958
		ACL-3428c (M^1)	0.70942
	D11-4434 Rangifer (early wear)	ACL-2327a (m_3)	0.70949
		ACL-2327b (m_3)	0.70949
Pech IV, L YZ	F16-3786 *Equus* (early wear)	ACL-3421 (m_2)	0.71139
		ACL-3418 (m_2)	0.71141
		ACL-3419 (m_2)	0.71155
	M15-640 *Cervus* (early wear)	ACL-3423 (M^1)	0.71378
		ACL-3417 (M^1)	0.71376
	F17-2845 *Cervus* (mid wear)	ACL-3422a (m_2)	0.71115
		ACL-3422b (m_2)	0.71098
		ACL-3422c (m_3)	0.71057
		ACL-3422d (m_3)	0.71106

[1] An upper case M indicates maxillary dentition. Numbers in superscript refer to the specific maxillary tooth analyzed (e.g., M^1 =maxillary first molar). A lower case m indicates a mandibular molar and a lowercase p indicates a mandibular premolar. Numbers in subscript indicate the specific mandibular tooth analyzed (e.g., m_1 = mandibular first molar).

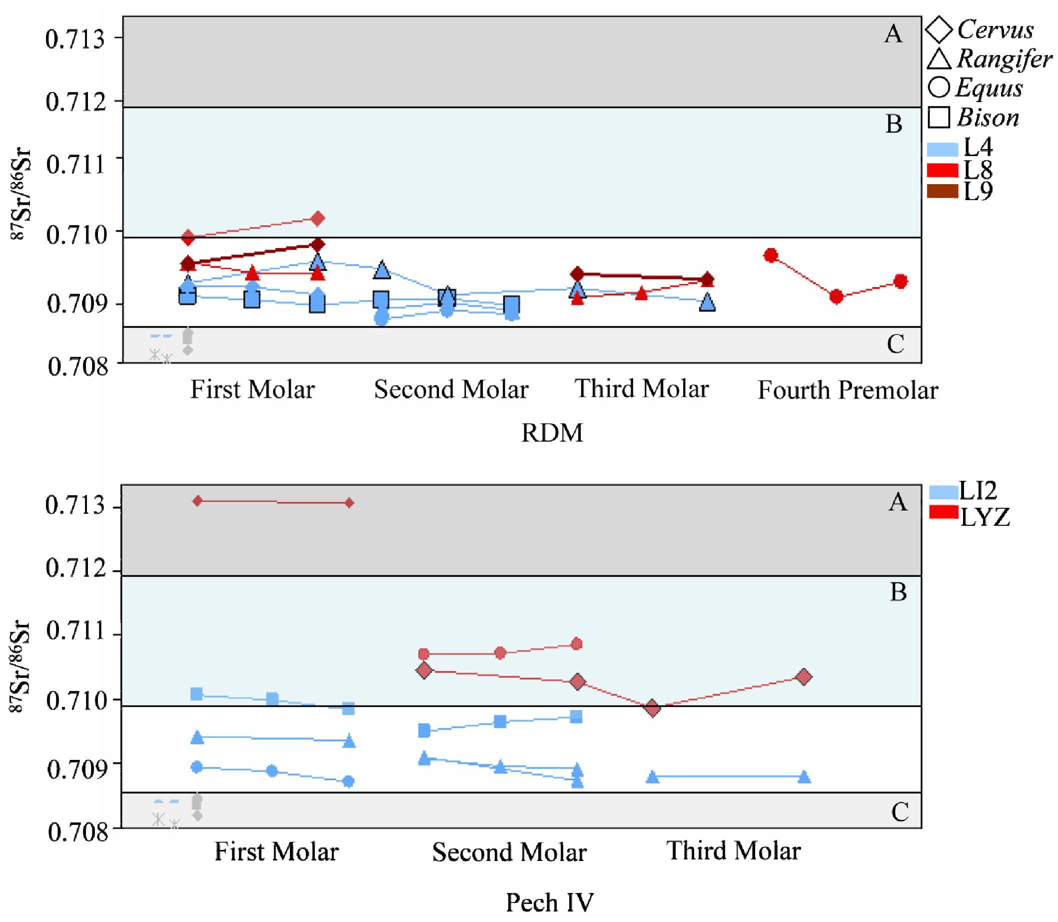

Fig. 5.1. $^{87}Sr/^{86}Sr$ values obtained from the first, second and third molars and the fourth premolar of *Cervus elaphus*, *Rangifer tarandus*, *Equus caballus, and Bison priscus*. A) The $^{87}Sr/^{86}Sr$ values obtained from clay and granites on the eastern edge of the Massif Central (Kelly, 2007). B) The range of $^{87}Sr/^{86}Sr$ values obtained from archaeological herbivore teeth excavated from the site of Les Pradelles, on the eastern edge of the Massif Central (Kelly, 2007). C) The $^{87}Sr/^{86}Sr$ values from the cave site of RDM, Les Eyzies and the town of Mansle in the Aquitaine Basin.

In area C) grey triangle, square and circle= $^{87}Sr/^{86}Sr$ values from archaeological rodent teeth from Roc de Marsal levels 9, 8 and 7. Blue lines = $^{87}Sr/^{86}Sr$ values of water samples from rivers in the towns of Les Eyzies and Mansle. The grey asterisk = $^{87}Sr/^{86}Sr$ values of snail shells from the towns of Les Eyzies and Mansle.

Symbols outlined in black indicate that multiple teeth from the same specimen were sampled.

TABLE 5.3. Results from ^{87}Sr/^{86}Sr analysis from modern samples.

Region	**Location**	**Elevation**	**Sample**	**^{87}Sr/^{86}Sr**
Alps	Foot of the Alps, La Voûte 46°10'4"N 5°43'5"E	588m	Snail Shell	0.70722
			Soil	0.70826
			Water	0.70761
	Chamonix, Lacs des Gaillands 45°54'54"N 6°50'49"E	1017m	Water	0.72280
	La Fontaine 45°54'57"N 6°46'2"E	825m	Soil	0.72502
			Water	0.71537
	Saint-Nicolas-la-Chapelle 45°48'28"N 6°30'15"E	504m	Snail Shell	0.70803
	Saint Amour 46° 26'11" N 5° 20'42"	252m	Wine	0.71129
Pyrénées	Montferrier 42°52'44"N 1°49'10"E	981m	Snail Shell	0.70856
			Snail Shell	0.70858
			Water	0.71501
	Base of Montségur 42°52'09"N 1° 50"05"E	883m	Snail Shell	0.70843
			Wine	0.71112
	Montségur hiking path 42° 52'52"N 1°51'22"E	734m	Soil	0.71038
	Fontaine de Fontestobes 42°53'33"N 1°55'36"E	502m	Soil	0.71554
			Water	0.70875
Aquitaine Basin	Les Eyzies 44°55'50"N 1°00'50"E	144m	Snail Shell	0.70874
			Water	0.70910
			Water	0.70910
	Mansle 45°52'44"N 0°11'04"E	61m	Snail Shell	0.70883
Edge of Massif Armoricain	Chinon 47° 10' 2" N 0° 14' 25" E	60m	Soil	0.71382
			Wine	0.71373

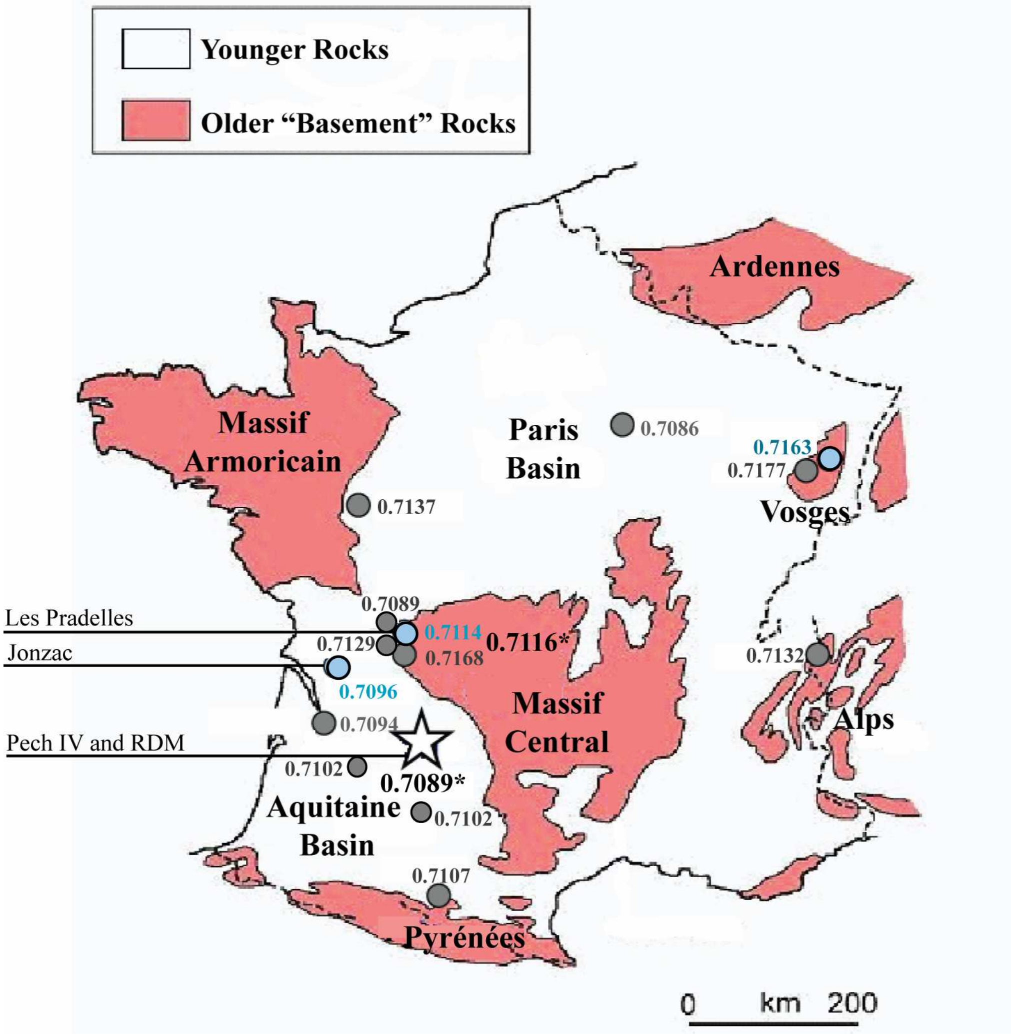

Fig. 5.2. Map of France depicting the areas with younger versus older rocks and the average ^{87}Sr/^{86}Sr values determined from modern and archaeological samples. Map adapted from http://www.virtual-geology.info/lozere/lozere.html

Grey circles = modern samples composed of soil, plants, snail shells, water, and wine (data from Semhi et al. 2000; Tricca et al. 1999; Kelly et al. 2007; Barbaste et al. 2002; and data collected in this study, see Table 5.3)
Large black numbers with a * indicate the site average calculated from modern samples at the sites of Les Pradelles and Pech IV and RDM

Blue circles = values from archaeological tooth samples
(see Bentley and Knipper 2005; Kelly et al. 2007, Britton et al., 2011 and data collected in this study, see Table 5.2).

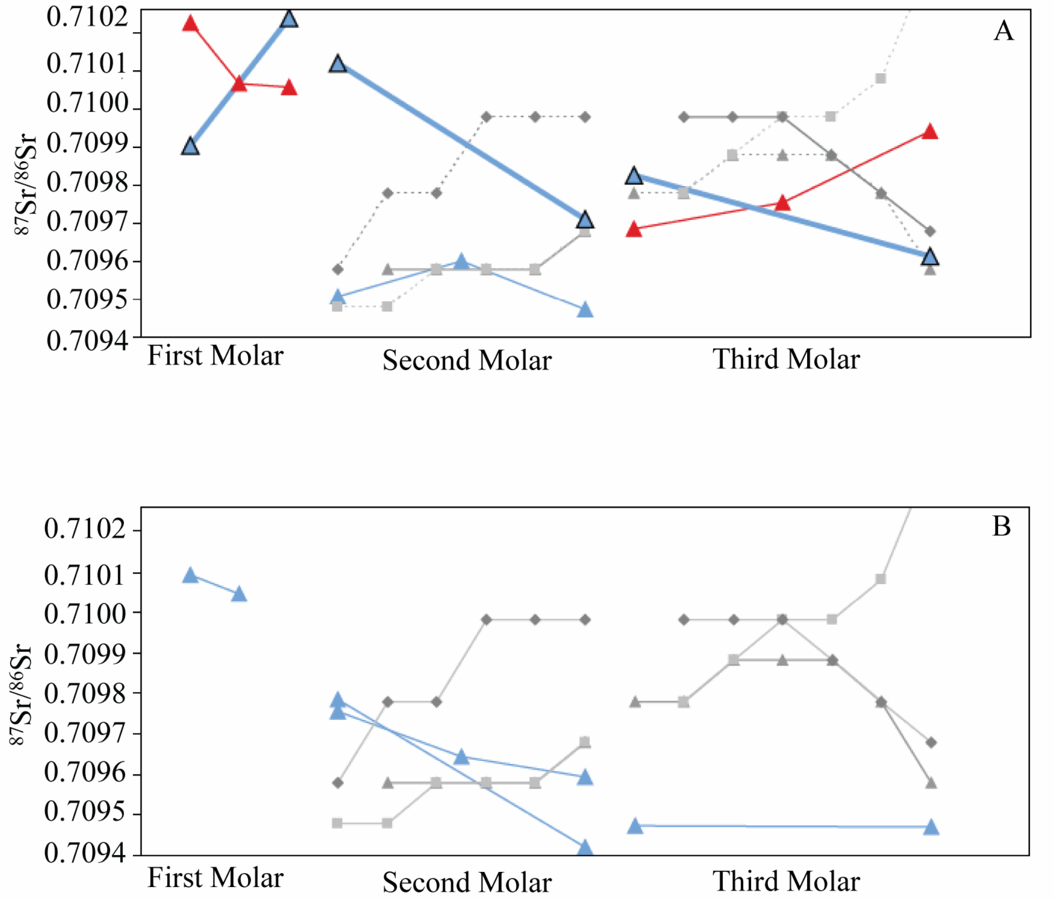

Fig. 5.3. A) $^{87}Sr/^{86}Sr$ values obtained from *Rangifer* teeth in Level 4 (blue) and 8 (red) at Roc de Marsal, compared to values obtained from *Rangifer* teeth at the archaeological site of Jonzac (grey) in the Charente-Maritime region of France (Britton et al., 2011). The blue triangles with the black border indicate that the first, second and third molars came from the same individual.

B) $^{87}Sr/^{86}Sr$ values obtained from *Rangifer* teeth from Level I2 at Pech IV, compared to values obtained from *Rangifer* teeth at the archaeological site of Jonzac (Britton et al., 2011).

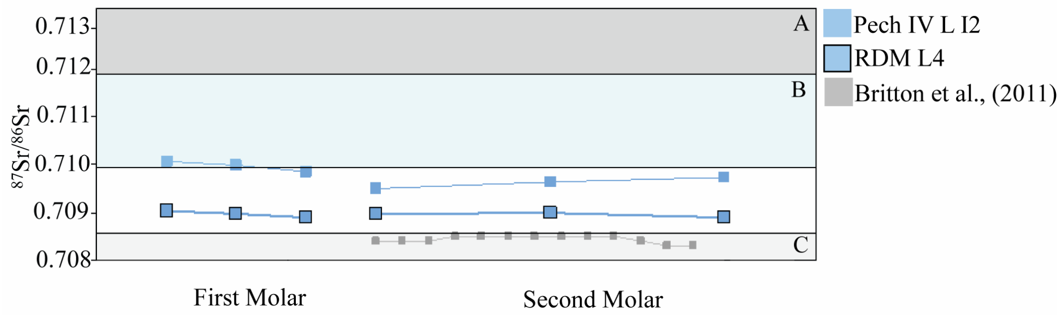

Fig. 5.4. ^{87}Sr/^{86}Sr values obtained from *Bison* teeth from Pech IV and Roc de Marsal (blue) compared to values obtained from *Bison* teeth at the archaeological site of Jonzac (grey) in the Charente-Maritime region of France (Britton et al., 2011). The blue squares with the black border indicate that the first and second molars came from the same individual.

A) ^{87}Sr/^{86}Sr values obtained from clays and granites on the eastern edge of the Massif Central (Kelly, 2007). B) The range of ^{87}Sr/^{86}Sr values Obtained from archaeological herbivore teeth excavated from the site of Les Pradelles, on the eastern edge of the Massif Central (Kelly, 2007). C) The ^{87}Sr/^{86}Sr values from the cave site of Pech IV, Les Eyzies and the town of Mansle in the Aquitaine Basin.

Some individuals of *Cervus*, *Bison* and *Equus* do appear to have been moving between areas with low strontium isotopic values to areas with higher strontium isotopic values. In fact, most radiogenic strontium ratios from herbivores at RDM and Pech IV are lower than average values determined from modern samples collected in the Alps (range $^{87}Sr/^{86}Sr$= 0.7072-0.7250, mean $^{87}Sr/^{86}Sr$= 0.71320±0.00715, 1σ, n=8, Table 5.3) situated 683 km to the west of Pech IV and RDM (Fig. 5.2), particularly from the granitoid regions of the Alps (Chamonix Lacs des Gaillands, La Fontaine, Saint Amour) and from the edge of the Massif Armoricain (range 0.7137-0.7138, mean $^{87}Sr/^{86}Sr$= 0.71378±0.0001, 1σ, n=2, Table 5.3) roughly 341 km to the north of both sites (Fig. 5.2). Finally, radiogenic strontium isotope ratios from most herbivores sampled here are also lower then modern samples collected from the mixed sedimentary and granitoid rocks on the northern edge of the Pyrénées (range $^{87}Sr/^{86}Sr$= 0.7084-0.7155, mean $^{87}Sr/^{86}Sr$= 0.71079±0.00293,1σ, n=8, Table 5.3), located 322km to the south of both sites (Fig. 5.2).

The comparison of ratios from herbivore teeth within the geological context of France enables a more detailed analysis of the movement of animals themselves across the landscape. The major results to come out of this analysis are that large scale climate shifts do not appear to have created discernable patterns of mobility in large herbivores (Fig. 5.1). As mentioned above, *Rangifer* from warm and cold levels at both RDM and Pech IV appear to have been moving within the sedimentary basins of France (range $^{87}Sr/^{86}Sr$ =0.7094-0.7103). A majority of the *Cervus* specimens from RDM (specimens RDM K17-1338, RDM

G18-6729, RDM F18-2860) sampled from layers deposited during both glacial and interglacial cycles (Table 5.2a-c) also appear to have stayed within the sedimentary basins of France (range $^{87}Sr/^{86}Sr$ =0.7097-0.7105). However, a *Cervus* specimen (RDM K17-1396) sampled from a warm level at RDM and two sampled from the warm level at Pech IV (M15-640, F17-2845) have much more elevated ratios (range $^{87}Sr/^{86}Sr$ =0.7105-0.7137) than other herbivores, which suggests they were foraging in areas with higher strontium isotope values, most likely the Massif Central or the Pyrénées, although they could have been moving within the Massif Armoricain or the Alps. Mobility patterns of horses sampled from both sites are also variable.

Most horse specimens sampled from glacial cycles and interglacial cycles at both RDM and Pech IV (RDM K16-2238, RDM K17-1418 Pech D17-1142) appear to have been ranging within the Aquitaine and Paris Basins (range $^{87}Sr/^{86}Sr$ =0.7093-0.7103). However, one horse specimen sampled from the warm level at Pech IV (F16-3786) has elevated values (range $^{87}Sr/^{86}Sr$ =0.7113-0.7115) that match those of herbivores sampled from the Massif Central. Finally, for the most part *Bison* specimens sampled from layers deposited during glacial cycles (RDM J17-2266 and Pech F16-706) exhibit results indicating that these animals mostly remained within the sedimentary basins of France (range $^{87}Sr/^{86}Sr$ =0.7095-0.7104), although one *Bison* from Pech IV Level I2 (D14-3358) appears to have moved from an area with higher strontium isotope values to an area with lower strontium isotope values (range $^{87}Sr/^{86}Sr$ = 0.7107-0.7105). Thus, the results from this analysis suggest that *Rangifer* were consistently ranging within the limestone basins of France. Many of the *Cervus*, *Equus* and *Bison* specimens analyzed in this study were also ranging within French basins with a few individuals of each of these species ranging between the sedimentary basins into areas with higher strontium isotope values—most likely the Massif Central or the Pyrénées.

CHAPTER 6: DISCUSSION OF RADIOGENIC STRONTIUM ISOTOPE ANALYSIS

The results from this analysis do not show clearly defined migratory patterns (as defined as round trip movements from the place of birth) among any of the species analyzed. Instead Pleistocene herbivores in southwestern France appear to have been roaming within sedimentary basins, with some variation observed in the inferred mobility patterns of *Cervus*, *Equus* and *Bison*. The lack of a strong migratory signal is especially interesting in *Rangifer* and *Bison* specimens, as non-migratory movements observed in these species has been tied to mosaic habitats rich in resources such as pine and spruce woodlands and boreal forests. These behaviors may support hypotheses that southwestern France (particularly areas surrounding Pech IV and RDM) was sheltered from some of the major global climatic changes that occurred throughout the Pleistocene (Barron et al. 2003; de Beaulieu and Reille 1992; Huntley and Allen 2003). If wooded environments in the Dordogne Valley had become open grasslands, or tundra ecosystems, *Rangifer* in this region would have become migratory, thus behaving like tundra *Rangifer* today (given what we know of variability in modern *Rangifer* behavior). However, it is also possible that if areas surrounding the Dordogne were uninhabitable, herbivores would have had nowhere to go and their mobility patterns would not have increased, even if the forested environments became more open.

Mobility comparisons among Pleistocene *Rangifer* for southwestern France

In discussing the mobility patterns obtained in this study, especially with regard to reindeer, it is important to reiterate that Britton et al., (2009) demonstrated that radiogenic strontium isotope analysis can successfully track the movement behaviors of *Rangifer* over the extent of their migration. These researchers found that an overall pattern of movement was apparent in most *Rangifer* sampled from the Western Arctic Caribou Herd such that across tooth development, the ratios went from high to low (reflecting movement away from the birthplace) with a final return to higher ratios as the animals moved back into the geological setting from which they had started (Britton et al., 2009). Britton and colleagues (2011) used this method to analyze enamel layers from the second and third molars of three archaeological *Rangifer* specimens from the site of Jonzac in southwestern France (Fig. 5.5). Their results demonstrated that two of the individuals showed very similar trends, changing from lower strontium isotope values to slightly higher values and back to lower values. The third individual did not follow the same trend, with ratios in this *Rangifer* specimen increasing throughout ontogeny, but this variation was not considered to be outside of the range of variation observed in modern migratory herds.

When the radiogenic strontium isotope values measured from *Rangifer* teeth at RDM, Pech IV and Jonzac are compared (Fig. 5.3), the range of values found are nearly identical at all three sites (Jonzac: range $^{87}Sr/^{86}Sr$ =0.7095-0.7104, mean $^{87}Sr/^{86}Sr$ =0.7098 ±0.0002, 1σ, n=36; RDM and Pech IV: range $^{87}Sr/^{86}Sr$ =0.7094-0.7103, mean $^{87}Sr/^{86}Sr$ = 0.7098 ± 0.0008, 1σ, n=24).

However, *Rangifer* from these sites do not display similar trends in values across tooth development. Unlike what is observed in modern migratory herds, there is no indication that *Rangifer* at Pech IV and RDM moved away from their place of birth and returned to it at a later date. This pattern is apparent for specimen J18-1379 at RDM where the first, second and third molar of one individual were sampled. If strontium isotopes from individual molars allow brief glimpses into the mobility patterns of *Rangifer* then, at RDM, the ratios established from different individuals show no apparent patterns at all, while at Pech IV *Rangifer* appear to have been born in areas with higher strontium isotope values and moved into areas with lower strontium isotope values. The pattern at Pech IV is opposite of that seen at Jonzac.

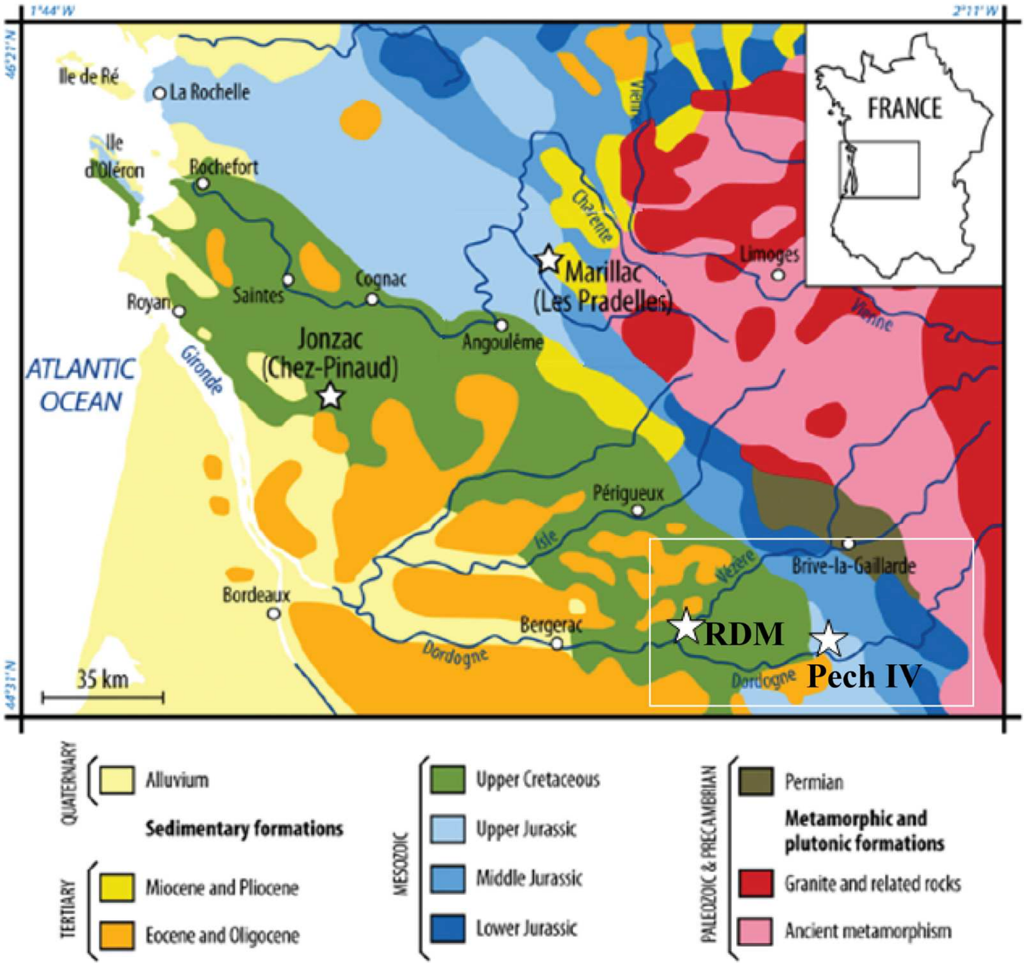

Fig. 5.5. Map of southwestern France showing the location of Roc de Marsal (RDM) and Pech IV in relation to Jonzac and Les Pradelles along with the regional geology. This figure is modified from Britton et al. (2011).

A number of temporal, spatial and dietary factors, along with the possibility of sampling error, could explain why the results of the present study differ from those of Britton and colleagues (2011) regarding Pleistocene *Rangifer* migratory behaviors. One difficulty with comparing studies and attempting to establish the behavioral norm for a species is the imprecision of archaeological dating. The *Rangifer* specimens analyzed from Jonzac come from a level older than 49 ka (Britton et al., 2011), placing it within MIS 3- 4. Dates from RDM and Pech IV suggest that levels at these cave sites maybe older than the level analyzed at Jonzac. Thus, *Rangifer* from these assemblages are likely separated by thousands years. Even when the deer were excavated from the same archaeological level at the same site, the fauna sampled could have been separated by considerable temporal gaps. It is possible that behavioral heterogeneity in *Rangifer* might have occurred across even relatively brief periods of time due to short-term environmental disturbances (e.g., rapid climatic shifts, occasional winters with above average snowfall, etc.), and that the *Rangifer* selected from each site reflect these temporary ecological shifts, causing *Rangifer* from Pech IV and RDM to deviate from their migratory patterns. However, based on the data from the current study, no consistent differences in the mobility patterns undertaken by animals in warm versus cold time periods could be identified. This result is important because at Pech IV and RDM large herbivores from archaeological levels dated to different marine isotope stages and correlated with global glacial and interglacial cycles did not show patterned changes in their mobility behaviors (Fig. 5.1). If climate changes in southwestern France were strong enough to change the behaviors of prey species, the change is much more likely to be captured in the archaeological record by gross comparisons between different marine isotope stages rather than within stages. Therefore, the results from this analysis suggest that local environments within the Aquitaine Basin may not have tracked the drastic changes observed in global climate. Thus, rapid climate-driven temporal variation does not appear sufficient for explaining why Britton et al. (2011) found a different pattern of *Rangifer* movement at Jonzac than what is observed at RDM and Pech IV.

In living *Rangifer* populations, there is also a spatial component to intraspecific variation in movement patterns, which corresponds to the biomes in which the animals are living. As discussed previously, large herbivore populations that live in open tundra environments migrate long distances while those in the boreal forests are non-migratory (Skogland, 1984; Senft et al., 1987; Tyler and Oritsland 1989; Johnson et al. 2001, 2002a, 2002b). Burch (1972:343) points out that, “it would be quite in line with our current understandings of the species [*Rangifer tarandus*] to find evidence of forest forms in the south, and tundra forms in the north, as is the case in both North America and Eurasia today.” Jonzac is located toward the northern extent of the Aquitaine Basin, roughly 200 km to the northwest of RDM and Pech IV.

The site of Jonzac is positioned close to where the Aquitaine and Paris Basins meet (Figs. 5.4 and 5.5). Recently, an analysis of microfauna from Jonzac found that species representation was fairly homogeneous throughout stratigraphic sequences and that the species present within each level indicated harsh and dry climatic conditions, with some wetland areas close by. *Rangifer*, *Equus* and *Bison* were the most abundantly represented herbivores at the site, which led to the conclusion that the site was located in an open environment (Jaubert et al., 2008). The migratory behaviors of *Rangifer* are ecologically driven. Thus, while Jonzac is not far from Pech IV and RDM, it is located to the north of both sites. Based on environmental reconstructions from Jonzac, and the results of Britton et al.'s paleomobility analysis, it is possible that *Rangifer* in this region may have been undertaking seasonal migrations (possibly into the Paris Basin), behaving more like modern *Rangifer* who occupy open tundra biomes, while *Rangifer* from Pech IV and RDM appear to have been non-migratory, behaving like modern species who live in more southern boreal forest biomes today.

Reconstructed distances traveled by *Rangifer* in southwestern France

While the movement behaviors of *Rangifer* from Jonzac, RDM and Pech IV may have been different with regard to migratory or non-migratory movements, the data presented from all three sites are unable to resolve the distance that the *Rangifer* may have moved. Britton and colleagues suggest that because ratios in *Rangifer* teeth do not match values from limestone deposits located directly at Jonzac, *Rangifer* from this site may have spent a considerable portion of their time in non-local sediments. These authors also argue that perhaps the *Rangifer* were moving quickly and undertaking very long distance migrations across different geologic regions such that the ratios found in the teeth are a result of an averaging of values.

As discussed in the methods section, radiogenic strontium isotope values sampled from fast-growing herbivore teeth are likely affected by the time it takes for enamel to fully mineralize and by the amount of time that strontium stays in the body after it has been ingested by an animal. Therefore, it is probable that the ratios measured by both Britton and coworkers (2011) and in this study are averaged numbers that reflect *Rangifer* foraging across the landscape. However, the full range of isotope ratios obtained from *Rangifer* teeth at Pech IV, RDM and Jonzac (Table 5.2 and Fig. 5.2) have been found in river water, soil, plant, snail shell and wine samples collected from the Aquitaine and Paris Basins (Semhi et al., 2000; Barbaste et al., 2002; Kelly et al., 2007). It is therefore reasonable to conclude that *Rangifer* were moving within these regions, but not venturing into areas with granitoid sediments. When the strontium isotope ratios of *Rangifer* are compared to *Cervus*, *Equus* and *Bison* from RDM and Pech IV, it is clear that unlike *Rangifer*, some individuals of other species were moving into regions with higher strontium isotope values (perhaps the Massif Central, or the Pyrénées) and those higher values were picked up in the teeth of these animals (Fig. 5.1).

Given the considerations above, the question therefore becomes, do *Rangifer* move much more quickly across the landscape than other species resulting in averaged radiogenic strontium isotopic values that do not allow movement into granitoid regions to be detected? This seems unlikely for two reasons: 1) Britton et al. (2009) were able to successfully track (through radiogenic strontium isotope analysis) the migratory behavior of *Rangifer* from the Western Arctic Caribou Herd in Alaska; and 2) radiogenic strontium isotope ratios sampled from large herbivores (including *Rangifer*) at the site of Les Pradelles (Kelly, 2007) (on the edge of the Massif Central) had values that were much higher than values found in herbivores from RDM, Pech IV and Jonzac. The most parsimonious explanation for these elevated ratios is that the *Rangifer* excavated from Les Pradelles were foraging close to and in the Massif Central. For these reasons, and because it is well documented that not all extant *Rangifer* undertake long distance round trip migrations, it should not be assumed that Pleistocene *Rangifer* from southwestern France had to migrate long distances. Instead data collected from Pech IV, RDM and Jonzac strongly suggest that *Rangifer* were staying within the sedimentary basins of France, which means they were not crossing the Pyrénées into Spain, they were not moving into the Massif Central, and they were not crossing the Vosges or Alps to venture further east in the European continent. That being said the Aquitaine and Paris Basins are expansive, and it is possible that *Rangifer* living within the basins were moving long distances, but at this point the distance traveled cannot be inferred from radiogenic strontium isotope analyses.

Comparison of diet among *Rangifer*, *Cervus*, *Equus* and *Bison*

If *Rangifer* were not moving too quickly to pick up elevated radiogenic values in their teeth, then one other reason that could explain the constantly lower radiogenic values of their teeth over time compared to other animals is diet. The diet consumed by an animal directly influences the radiogenic strontium isotopes present in dentition. If *Rangifer* diets included an item that had strontium isotope ratios out of line with values found in the geology of southwestern France it would affect values sampled from their teeth (e.g., a less radiogenic item could drive the overall ratio down).

The diet of modern *Rangifer* is made up of horsetails (*Equisetum* sp.) and sedges (i.e. *Carex* sp., *Eriophorum angustifolium*), which serve as a source of protein (Jefferies et al., 1994; Rettie and Messier, 2000). They also consume grasses (i.e. *Alopecurus* sp., *Arctagrostis* sp., D*upontia* sp., *Altai fescue*), buckbean (*Menyanthes* sp.*)* moss (*Drepanocladus* sp.) and lichens (C*ladina* sp., *Cladonia* sp., *Umbilicaria* sp., *Cetraria* sp., *Stereocaulon* sp., *Bryoria* sp.) (Jefferies et al., 1994; Sharnoff and Rosentreter, 1998; Rettie and Messier, 2000; Johnson et al., 2002). Most of the food consumed by caribou is 40-70% digestible, with the exception of mosses which are only 10% digestible (Jefferies et al., 1994). Lichen is high in carbohydrates, which provide caribou with energy, but it is low in other nutrients (Jefferies et al., 1994). While *Rangifer* are unique in their ability to consume and digest large quantities of lichen, there is no reason to believe that the radiogenic strontium isotopes in lichen would not directly reflect the ratios available in the geological setting on which the plant was growing. In fact, lichens are known to contribute to the chemical weathering of rocks and observations have been made of fungus (one component of lichen) extracting (solubilizing) strontium from the rock on which the plant was growing and transferring the strontium across the body of the fungus (Dighton, 2003). Furthermore, other herbivores discussed in this paper would have consumed many of the same plants eaten by *Rangifer*. *Cervus* are intermediate, opportunistic mixed feeders who are able to consume and digest a wide variety of plant types and therefore would have consumed many of the same foods as *Rangifer* (Peek, 2003), while *Bison* and *Equus* would have consumed large quantities of the grasses, sedges and herbs also consumed by *Rangifer* (Speiss, 1975; Moehlman, 2002; Reynolds et al., 2003; Pucek et al., 2004).

In human populations, the inclusion of imported sea salt in the diet has been observed to change the radiogenic strontium isotope ratio of teeth, causing the teeth to stray from the local signal (Wright, 2005). Sodium is an important component in the diet of all mammals, and a lack of sodium can decrease milk production in females, decrease infant growth rate, and contribute to a host of other health issues (Staaland and Hove, 2000). Thus, in areas where sodium is not present in sufficient quantities, mammals will migrate to attain it. However, France is rich in salt deposits, which resulted from the evaporation of sea water over time (Müller and Mueller, 1991; Fontes and Matray,1993; Geslin, 2002). Typically salt deposits evaporated from sea water have radiogenic strontium isotopes ratios that range from 0.70772 to 0.7092 (Palmer and Elderfield, 1985; HongBing et al., 2010); however, salt deposits from the Paris Basin, the Mediterranean Sea and Spain have ratios that are slightly more elevated (range $^{87}Sr/^{86}Sr = 0.7084\text{-}0.7096$) (Müller and Mueller, 1991; Fontes and Matray, 1993; Lu and Meyers, 2003). This range of isotope values from French salt deposits is within the range of geological values found throughout the Paris and Aquitaine Basins and also at the lower end of the range of values found in herbivores from RDM, Pech IV and Jonzac. Since salt values are at the lower end of the ratios observed in herbivore teeth, it is possible that consumption of salt could have lowered the overall values sampled. However, all herbivores sampled would have consumed salt; thus, the inclusion of salt in the diet must not have been sufficient to prevent the elevation of radiogenic strontium isotope ratios in the *Cervus*, *Bison* and *Equus* teeth. Therefore, diet and salt consumption cannot explain why *Rangifer* have constantly lower radiogenic isotope values than other herbivores.

Discussion of sampling error

Finally, sampling error could also explain why the results of the current study are different from those obtained by Britton and colleagues (2011) regarding Pleistocene *Rangifer* migratory behaviors. The studies conducted at RDM, Pech IV, and Jonzac have been conducted on small sample sizes. Data from Jonzac were based on three individual *Rangifer*. The individuals sampled had complete molar rows allowing the second and third molars to be sampled from all specimens. Two of the *Rangifer* specimens analyzed fit expectations for isotopic patterns observed in migratory *Rangifer,* but one *Rangifer* specimen did not meet these expectations. It is therefore possible that the pattern found at Jonzac may have been due to sampling bias. The analysis of Pech IV and RDM was composed of a total of six *Rangifer* specimens deposited during MIS 4 at Pech IV and RDM, and four *Rangifer* specimens deposited during MIS 5a-c at both sites; however, only one of the *Rangifer* specimens sampled (RDM J18-1379 from Level 4) had associated first, second and third molars.

The ability to sequence all molars allows mobility patterns to be reconstructed for the first year and a half of a reindeer’s life. Sampling individual teeth is useful as it provides some information about mobility, but the information is limited to movements made within the first few months of the animal's life. While analyses at Jonzac and Pech IV and RDM have gone a long way in improving our knowledge about the mobility patterns of Pleistocene herbivores in France, more studies across multiple sites and including more geographic diversity should be completed to fully address the observed discrepancies.

Mobility comparisons among Pleistocene *Bison* for southwestern France

Britton and coworkers (2011) also analyzed radiogenic strontium isotope ratios from the second and third molars of a *Bison* recovered from Jonzac. Results from this analysis showed that there was little variation in radiogenic strontium isotope values across enamel layers, suggesting that the *Bison* remained within one geological region during tooth development. The mobility pattern inferred from the *Bison* at Jonzac is consistent with the findings of a study on the paleomobility behavior of *Bison* from southeastern Ukraine (Julien et al., 2012), and with the current study. Overall, the *Bison* analyzed from RDM and Pech IV show fairly little variation in radiogenic strontium isotope ratios across enamel layers (Fig. 5.4), although one *Bison* specimen from Pech IV does appear to have moved from a more radiogenic region such as the Massif Central or the Pyrénées into an area with lower ratios.

Analyses of *Bison* mobility from RDM, Pech IV, and Jonzac have interesting implications for the Neandertals who would have hunted them. If *Bison* truly were living within restricted regions (as reflected in the low isotopic variation in their teeth), that means that they were behaving more like *Bison* living in high productivity environments such as woodland *Bison*, and they would have been present for Neandertals to hunt year round. *Bison* are large herbivores that would have been a valuable resource, and if present close to Neandertal cave sites year round, may have limited the need for Neandertals to undertake long distance movements to hunt other animals.

CHAPTER 7: CONCLUSIONS

In this study, it was hypothesized that if climatic shifts affected the local ecology of Neandertal habitats in southwestern France, those shifts would have imposed patterned mobility changes in large herbivores living in the Aquitaine Basin, which in turn would have caused Neandertals to become nutritionally stressed. Specifically, it was predicted that if cold climatic cycles caused environments in the Dordogne Valley to change from boreal forest environments to open tundra, large herbivores would have responded by changing their movement patterns from non-migratory during warmer time periods to long distance round trip migrants during glacial cycles. The increased mobility patterns of Neandertal prey species would likely have caused Neandertals to travel more to intercept migratory herds. The effects of prey species movements away from Neandertal local environments, and increase in Neandertal mobility would have contributed to a shortage of more easily-obtained calories available to Neandertals. In response, Neandertals would have hyper processed nutrients from carcasses.

Results from this study showed that Neandertals did processes bones more thoroughly during cold climates than they did during warm climates. Neandertals were fracturing bones for the removal of bone marrow through time, but in colder climates Neandertals were percussing bones more. The intensity with which Neandertals were percussing bones was not only for extraction of marrow, but also for bone grease, stored within spongy bone and epiphyseal ends. It was also found that bones with a relatively small amount of marrow showed signs of processing. Neandertals did not only focus their efforts on extracting within-bone nutrients, but they also appear to have cut all meat from the bone. The frequency of cut marks on skeletal elements was greater in levels deposited during cold climates. Thus, evidence from the zooarchaeological portion of this study supports the hypothesis that Neandertals experienced nutritional stress during the sampled cold climate cycles.

Results from the radiogenic strontium isotope analysis do not support the hypothesis that herbivores became more migratory during cold climate cycles. There is no indication of consistent changes in mobility between fauna from warm versus cold levels at either RDM or Pech IV. This result suggests that either climate changes within the Dordogne Valley of France did not track global climate changes as reflected in the marine isotope stages and Dansgaard-Oeschger events, or that the behavior of these Pleistocene herbivores were not particularly sensitive to such environmental shifts.

The inferred non-migratory movements of large herbivores (particularly of *Rangifer* and *Bison*) at Pech IV and RDM suggest that animals in this region were behaving like woodland species. This result is consistent with environmental reconstructions, which propose that southwestern France was characterized by mosaic habitats of woodlands and boreal forests even during glacial cycles, although environments may have differed within the Aquitaine Basin (e.g., Sánchez Goñi et al., 2008; Bruxelles and Jarry, 2011). Analyses conducted at Jonzac (northwestern Aquitaine Basin) suggest that *Rangifer* in this area may have been migratory (Britton et al., 2011). This behavior may indicate that the environment in this region was more open than areas further south. However, the inferred low mobility of *Bison* analyzed from RDM, Pech IV and Jonzac suggests that they would have been present for Neandertals to hunt year round. The variation in the radiogenic strontium isotope ratios of *Cervus*, *Equus* and *Rangifer* suggest that they were moving across more radiogenically distinct geological substrates than *Bison*, although the distances they traveled cannot be inferred. What can be said for certain is that *Rangifer* at Pech IV, RDM and Jonzac were not moving into mountain ranges.

Importantly, the results from this analysis demonstrate that not all Pleistocene *Rangifer* were following long distance round trip migrations, and this information will be useful for researchers attempting to reconstruct Neandertal behaviors across the landscape. The fact that most of the animals analyzed in this study appear to have been staying within the sedimentary basins of France indicates that Neandertals would not have needed to travel to the surrounding mountainous regions to hunt, and their mobility patterns would not have needed to change between warm and cold climatic cycles. It therefore seems likely that Neandertal mobility patterns were similar to hunter-gatherers who hunt many different species of herbivores in boreal forest environments. These hunter-gatherers move their camps within the boreal forests more than five times/year, traversing an average of 285 km/year. Skeletal element transport data from the zooarchaeological analysis provides indirect supporting evidence that Neandertals were not traveling more during cold climates. Skeletal element abundance is consistent through climatic oscillations. Distance is one factor that can alter decisions about which bones are taken back to a central place for processing. Thus, two lines of evidence from this dissertation suggest Neandertals may have practiced residential mobility, moving their campsites within the Dordogne Valley or the Aquataine Basin to places where resources were found. Neandertals were likely living in small family groups, similar to hunter-gatherers who inhabit boreal forest environments and employ hunting economies focused on multiple species of terrestrial animals (e.g., Naskapi, Montagnais, Eastern Cree, and the Attikamek) (Speck and Eiseley, 1942; Smith, 1983; Dods, 1998; Binford, 2001).

If the migratory behaviors of Neandertal prey species did not change during cold climate cycles, then an alternate explanation must be found for why Neandertals were experiencing nutritional stress in cold climates. The most likely reason is that the Dordogne Valley was a refuge area during cold climate cycles, but areas surrounding the Dordogne were not as protected from climatic fluctuations. Recently Bruxelles and Jarry (2011) found that environmental conditions just south of the Dordogne Valley were often abandoned by hominids during cold climate cycles. They suggest that environmental deterioration would have meant that habitable areas were restricted to narrow river valleys within the greater Aquitaine Basin. Additionally, pollen records show that Northwestern France was sparsely to non-vegetated during glacial cycles (Fletcher et al., 2010). If this is the case, the onset of glacial events may have also reduced the productivity of the Dordogne Valley, but a suitable environment surrounding the Valley may not have existed, in which case herbivores would not have had a place to migrate. Reduced productivity would have diminished herbivore populations and this would have placed nutritional stress on hunters.

Evidence that the local environment was changing can be found in species abundance data collected in this dissertation. While it is important to stress that within the Aquitaine Basin each species of deer was present throughout climatic cycles, their abundance within the environment changed. *Rangifer* were more abundant during glacial cycles. This abundance of *Rangifer* has often caused Paleolithic archaeologist to envision vast herds of *Rangifer* moving through the Pleistocene landscape, but results from this analysis suggest that this was not the case for *Rangifer* in southwestern France. *Rangifer* possess a keen ability to digest lichens and nutrient poor foods (Jefferies et al., 1994). Thus, it is not surprising that their relative abundance to other animals increased when environmental shifts reduced the availability of easy to digest plant foods. However, the fact that *Rangifer* relative abundance changed does not mean that the population size of *Rangifer* increased. Additionally, if higher quality resources were not available in other locations, then *Rangifer* would not have had cause to undertake long distance round trip migrations. Thus, deterioration of environments surrounding the Dordogne Valley and a reduction in the productivity of the valley itself would have lead to a relative increase in *Rangifer* compared to other animals; however, the reduction in environmental productivity was not severe enough to cause other deer species to go extinct. The contraction of habitable environments would have caused herbivores within the Dordogne Valley to continue to behave similar to woodland species today.

The combined use of quantitative zooarchaeological methods with radiogenic strontium isotope analysis enabled very specific questions to be asked about how climate change affected both Neandertals and the animals they hunted. Results from this analysis support the general hypotheses that cold climates stressed Neandertal populations (Finlayson and Giles Pacheco, 2000; Finlayson et al., 2001, 2002; Finlayson, 2004; Stewart et al., 2004; Finlayson and Carrion, 2008). This study found that during glacial cycles, Neandertals experienced nutritional stress, most likely resulting from decreasing prey populations. However, decrease in prey abundance was not caused by herbivores increasing their mobility behaviors. Herbivores within the Dordogne Valley behaved like woodland species in both warm and cold climates and would have been available for Neandertals to hunt year round. Hunter-gatherers that hunt non-migratory terrestrial mammals tend to be less mobile themselves, moving with small family groups within regional territories. This finding could be used to support recent genetic models proposed by Premo and Hublin (2009) that low genetic diversity found among Neandertals may be explained by low mobility rates between groups (Premo and Hublin, 2009). Barton et al., (2011) have also recently proposed that the distances over which hominid populations traveled may be directly related to population sizes and extinction. Decreased mobility among human populations may also play an important role in restricting the flow of ideas between groups, creating a roadblock for the development of cultural complexity (Powell et al., 2009). The results from this analysis have provided detailed information about Neandertal ecology and behaviors through time and temperature changes, and these new insights should be used to inform models that seek to explain issues relating to Neandertal cultural complexity and the eventual extinction of Neandertals.

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APPENDIX A

ArcVeiw GIS images of high survivial bones from Roc de Marsal and Pech IV

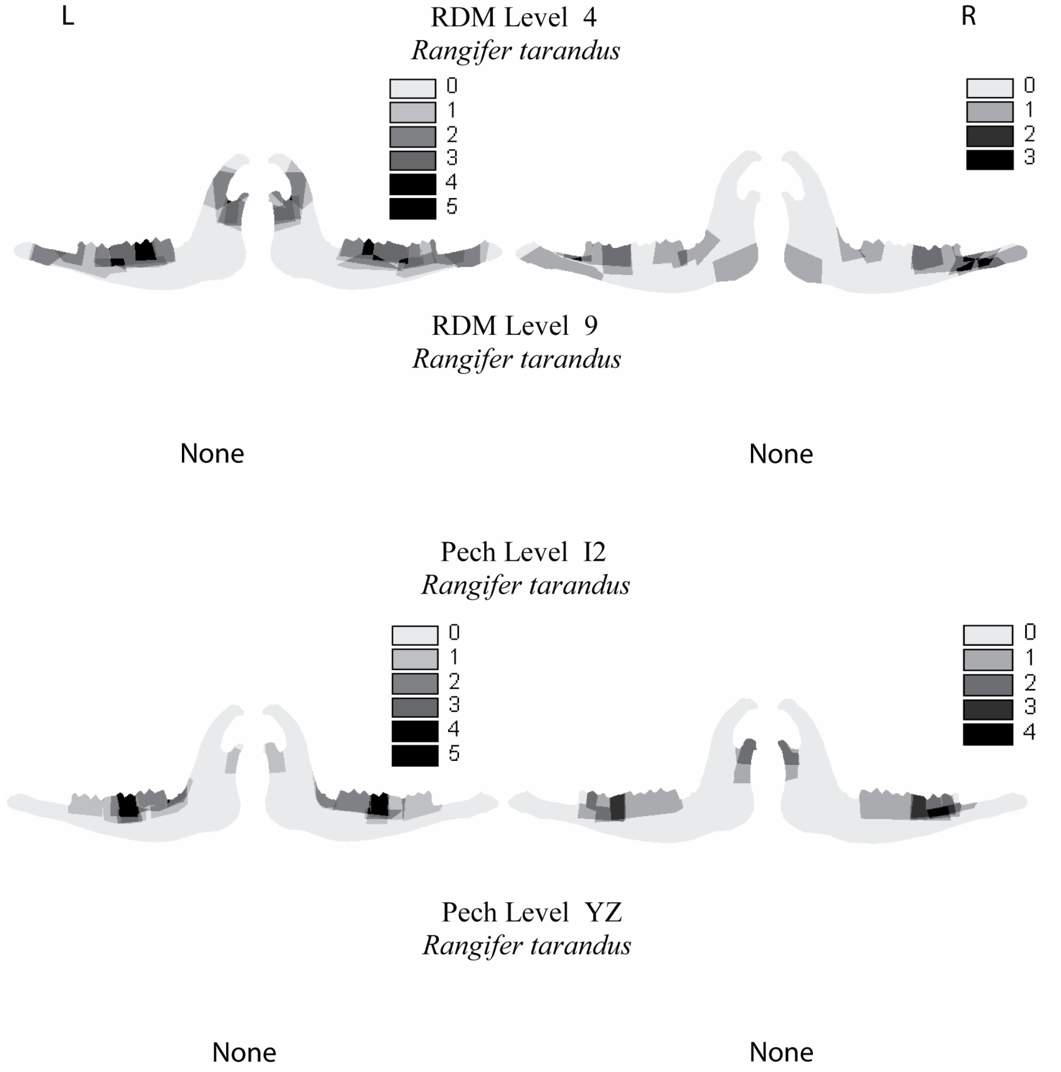
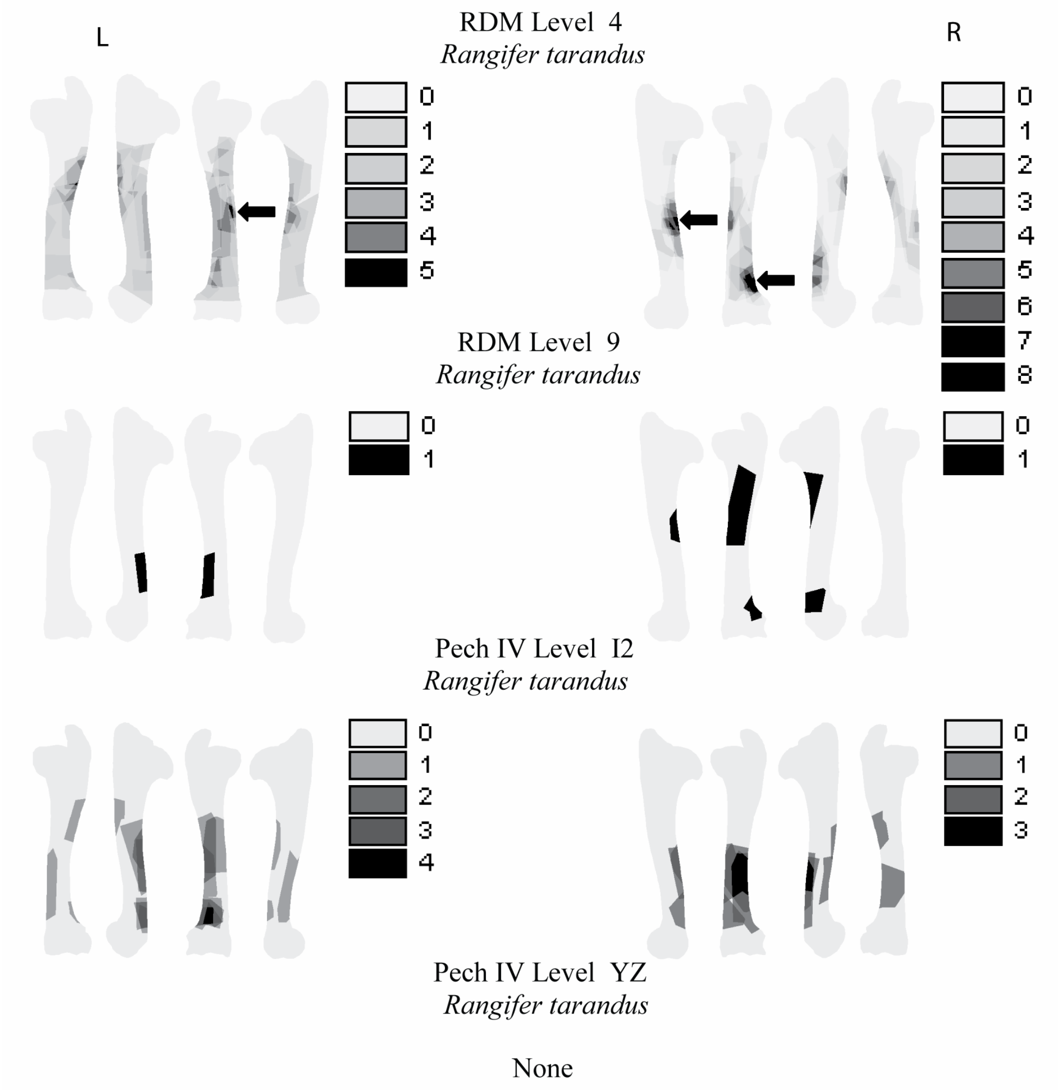


Fig. A1. Left and right reindeer mandibular fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See caption under Figure 11a for explanation.



RDM Level 4
Rangifer tarandus

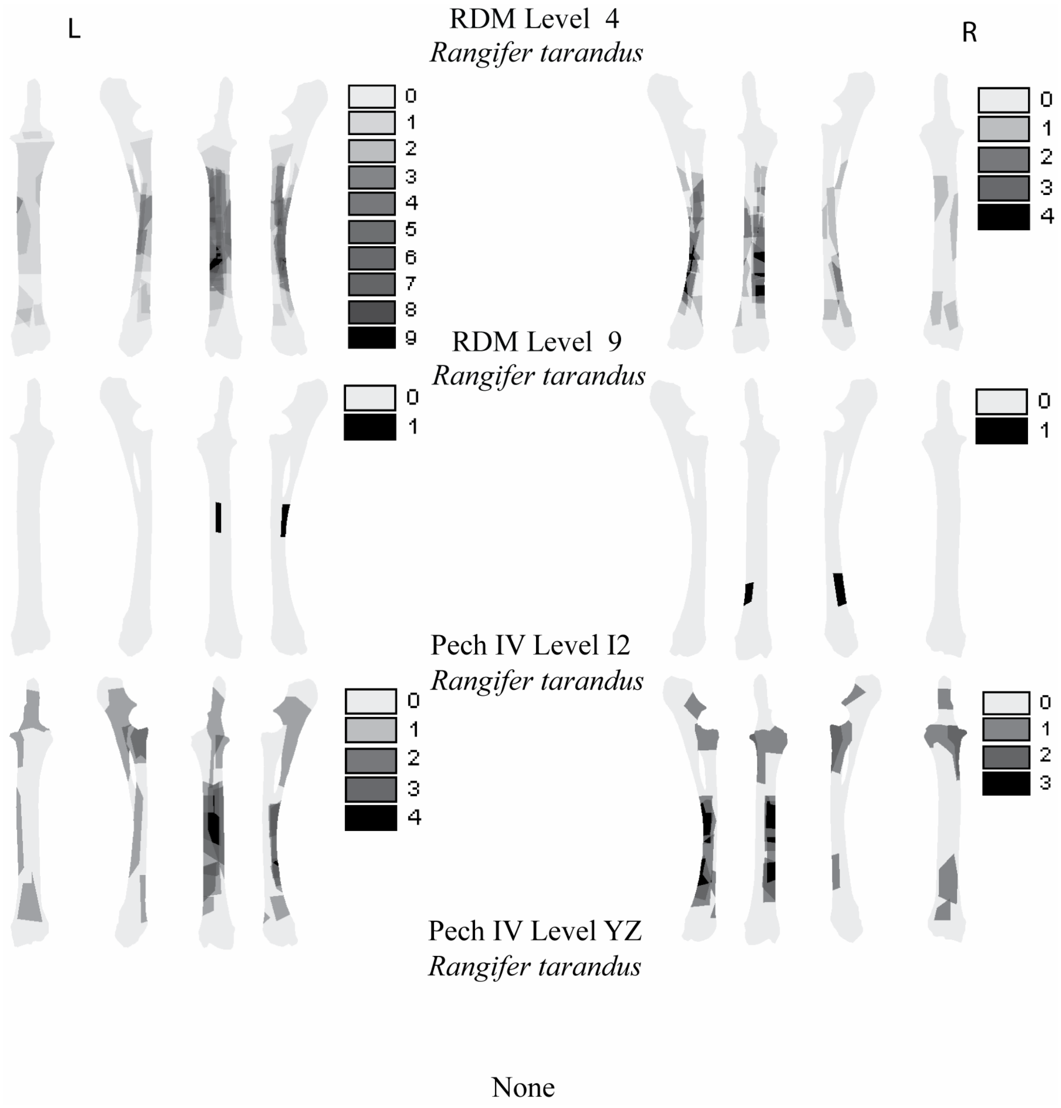
RDM Level 9
Rangifer tarandus

Pech IV Level I2
Rangifer tarandus

Pech IV Level YZ
Rangifer tarandus

None

Fig. A2. Left and right reindeer humeral fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. Black arrows are used to highlight the highest number of overlaps when the area of overlap is small and hard to see. See the caption under Figure 11a for further explanation.



RDM Level 4
Rangifer tarandus

RDM Level 9
Rangifer tarandus

Pech IV Level I2
Rangifer tarandus

Pech IV Level YZ
Rangifer tarandus

None

Fig. A3. Left and right reindeer radioulnar fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

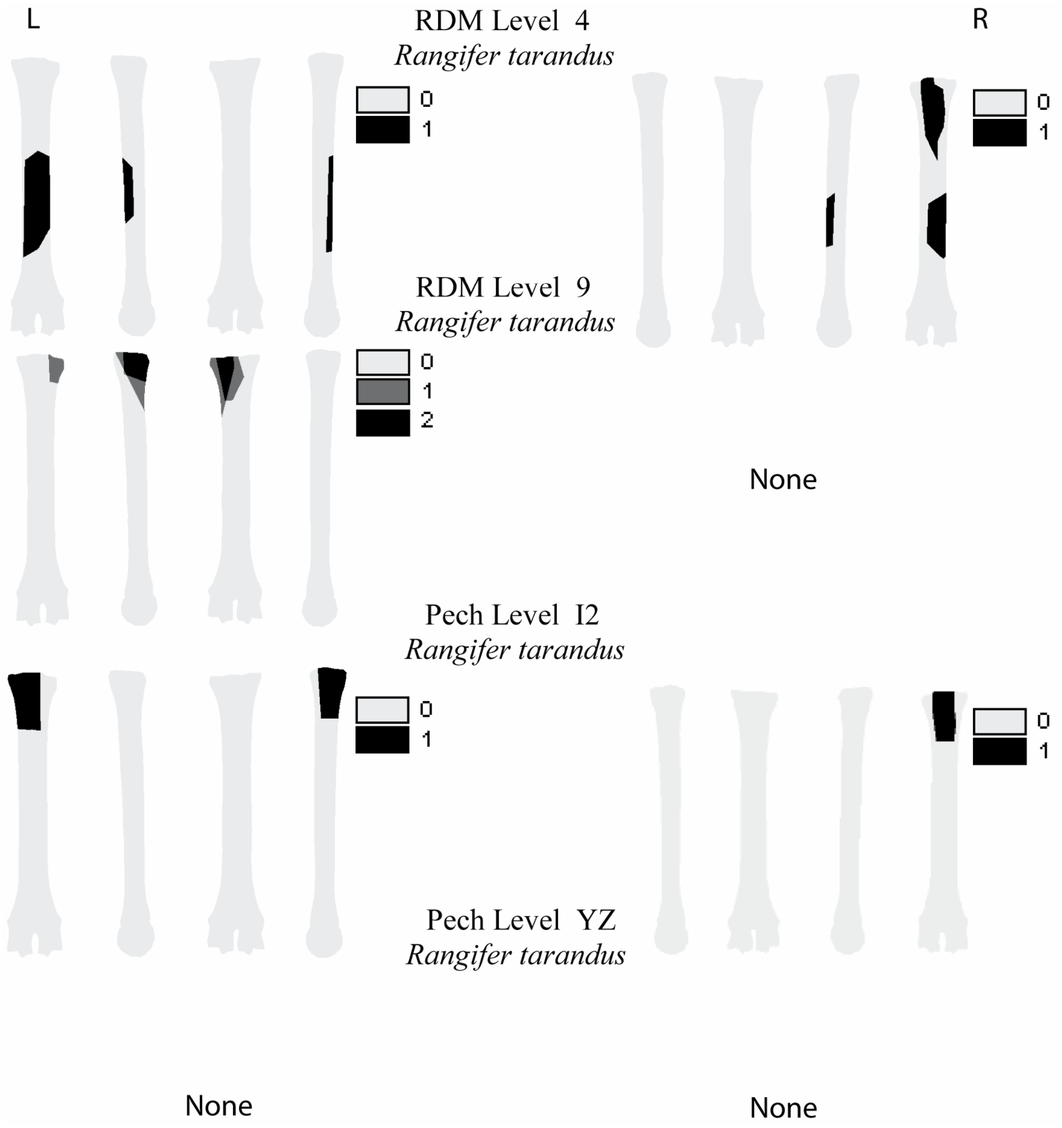


Fig. A4. Left and right reindeer metacarpal fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

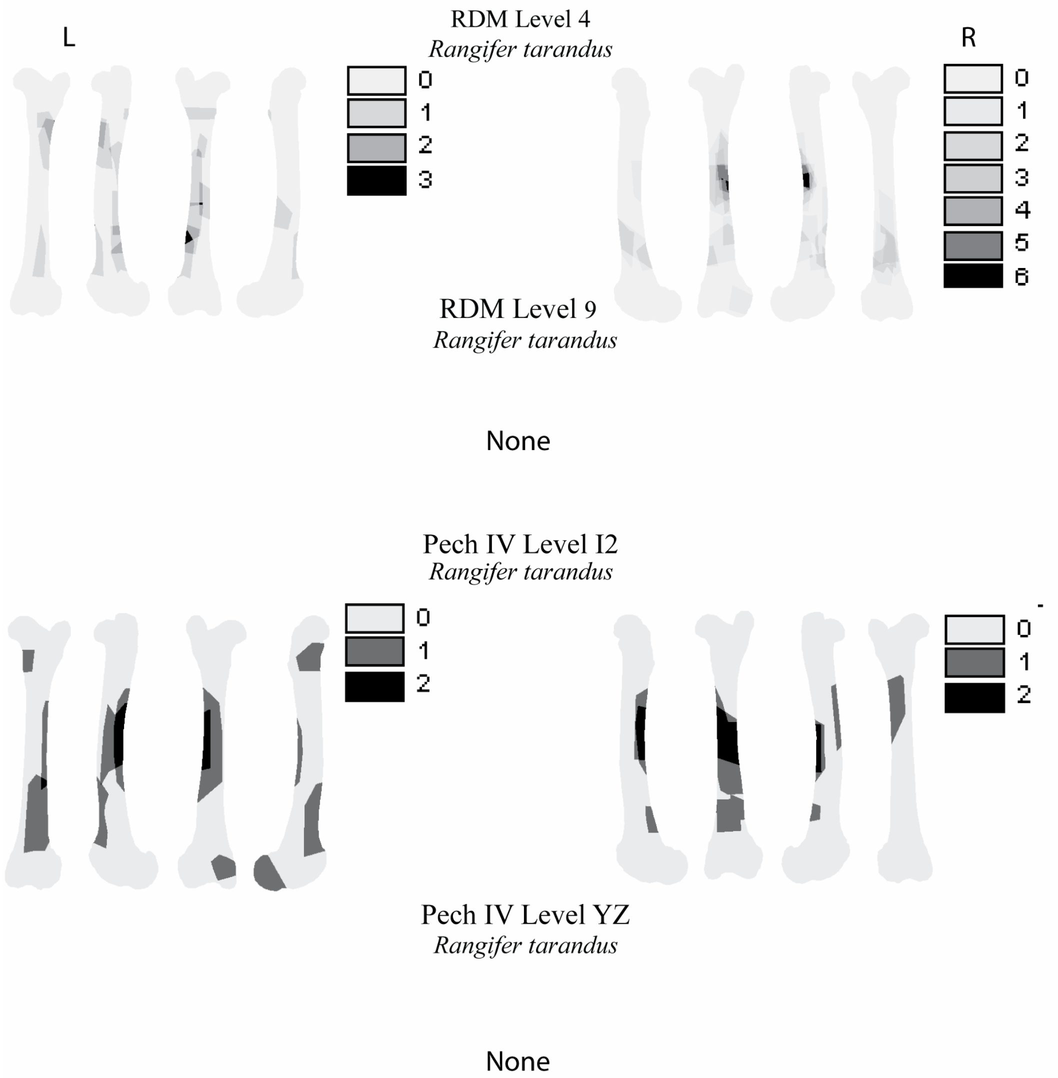
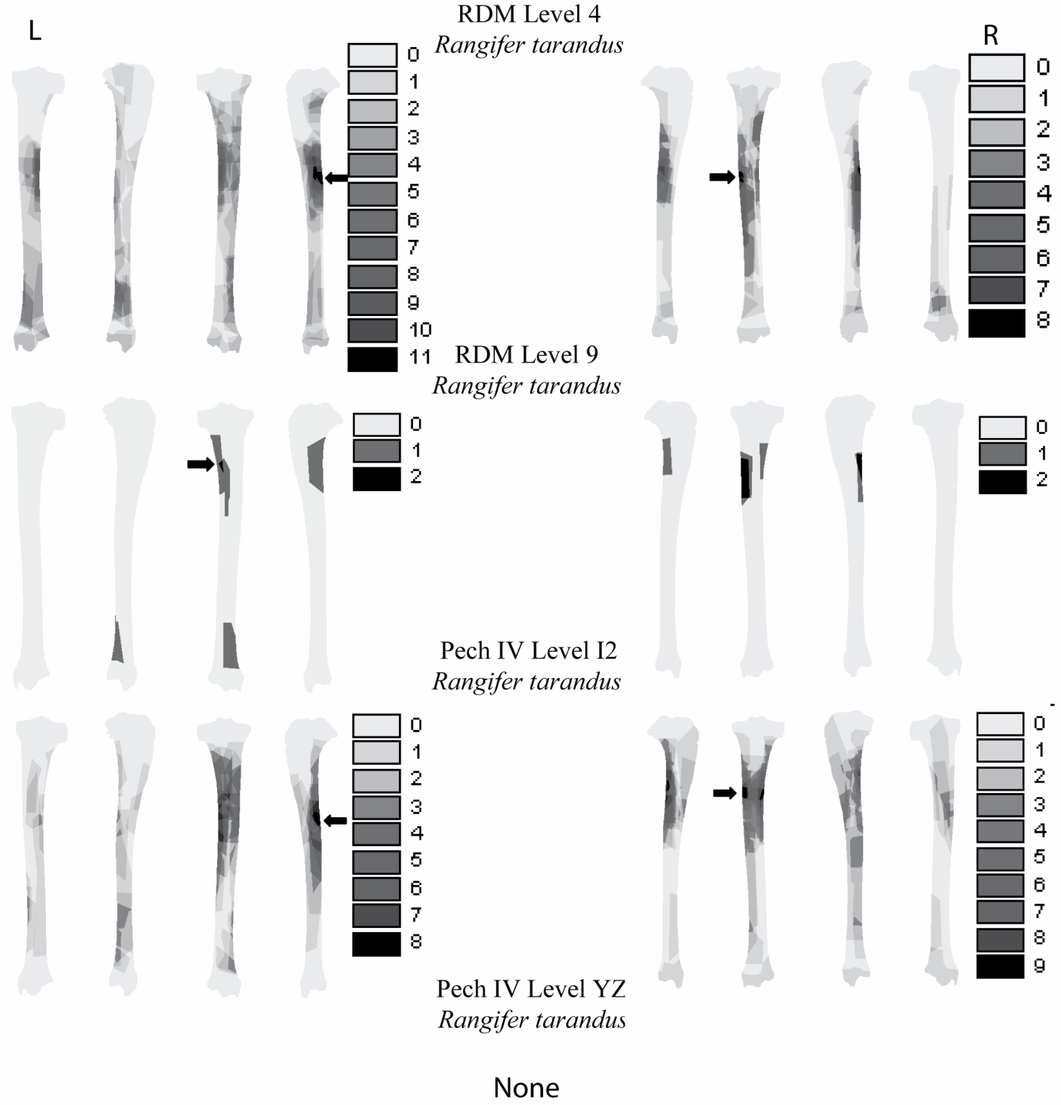


Fig. A5. Left and right reindeer femoral fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.


RDM Level 4
Rangifer tarandus

RDM Level 9
Rangifer tarandus

Pech IV Level I2
Rangifer tarandus

Pech IV Level YZ
Rangifer tarandus

Fig. A6. Left and right reindeer tibial fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. Black arrows are used to highlight the highest number of overlaps when the area of overlap is small and hard to see. See the caption under Figure 11a for further explanation.

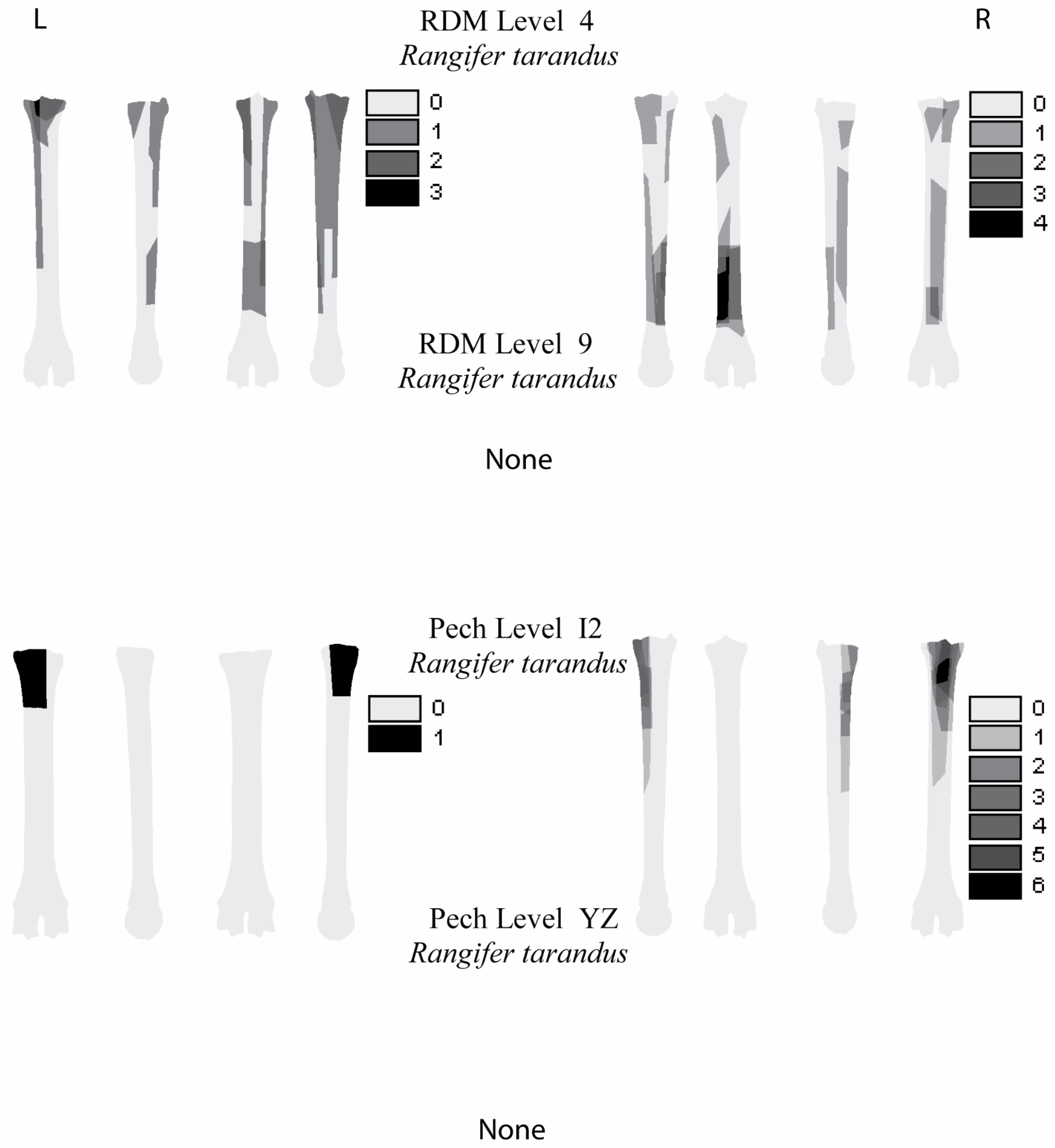


Fig. A7. Left and right reindeer metatarsal fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

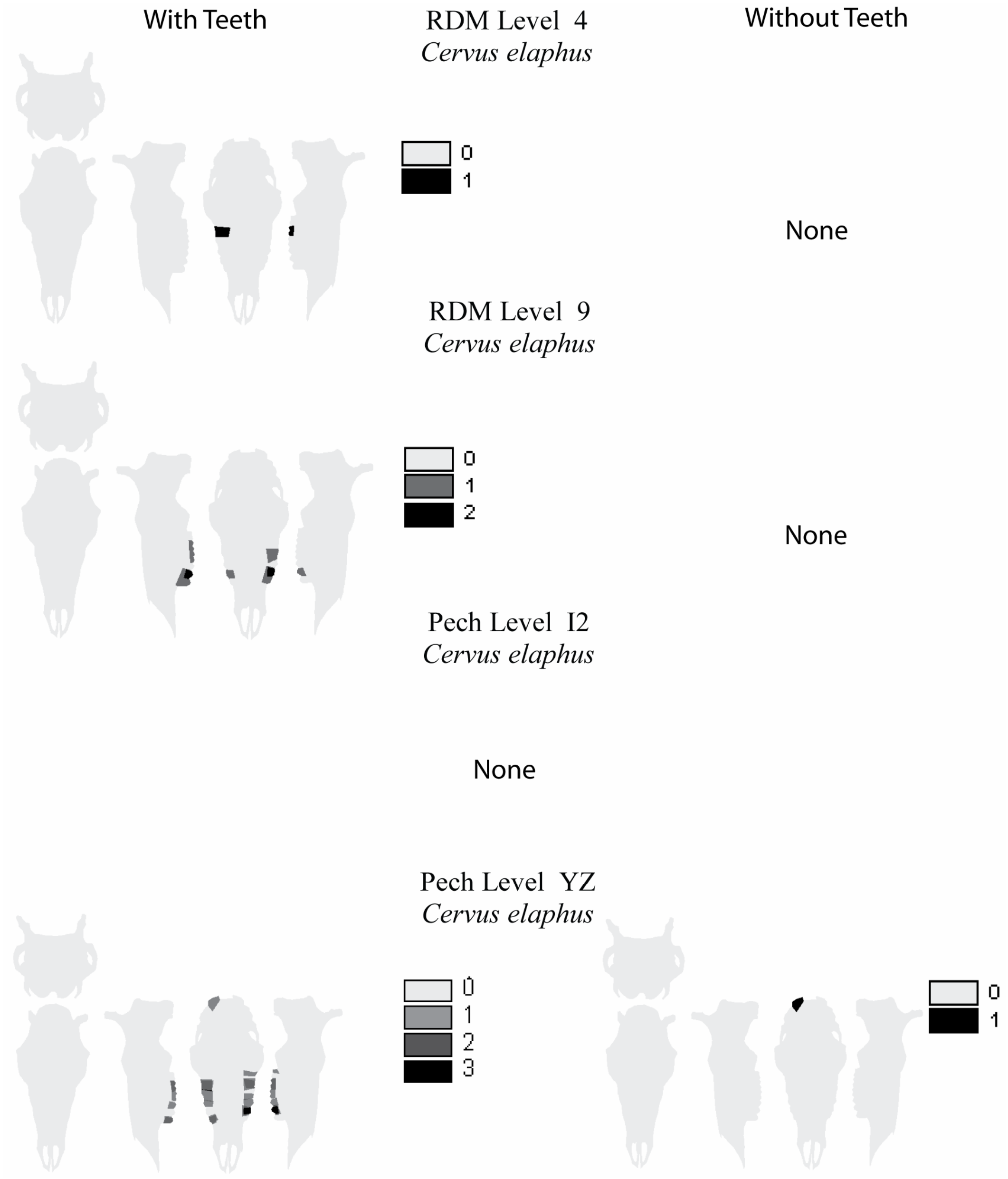
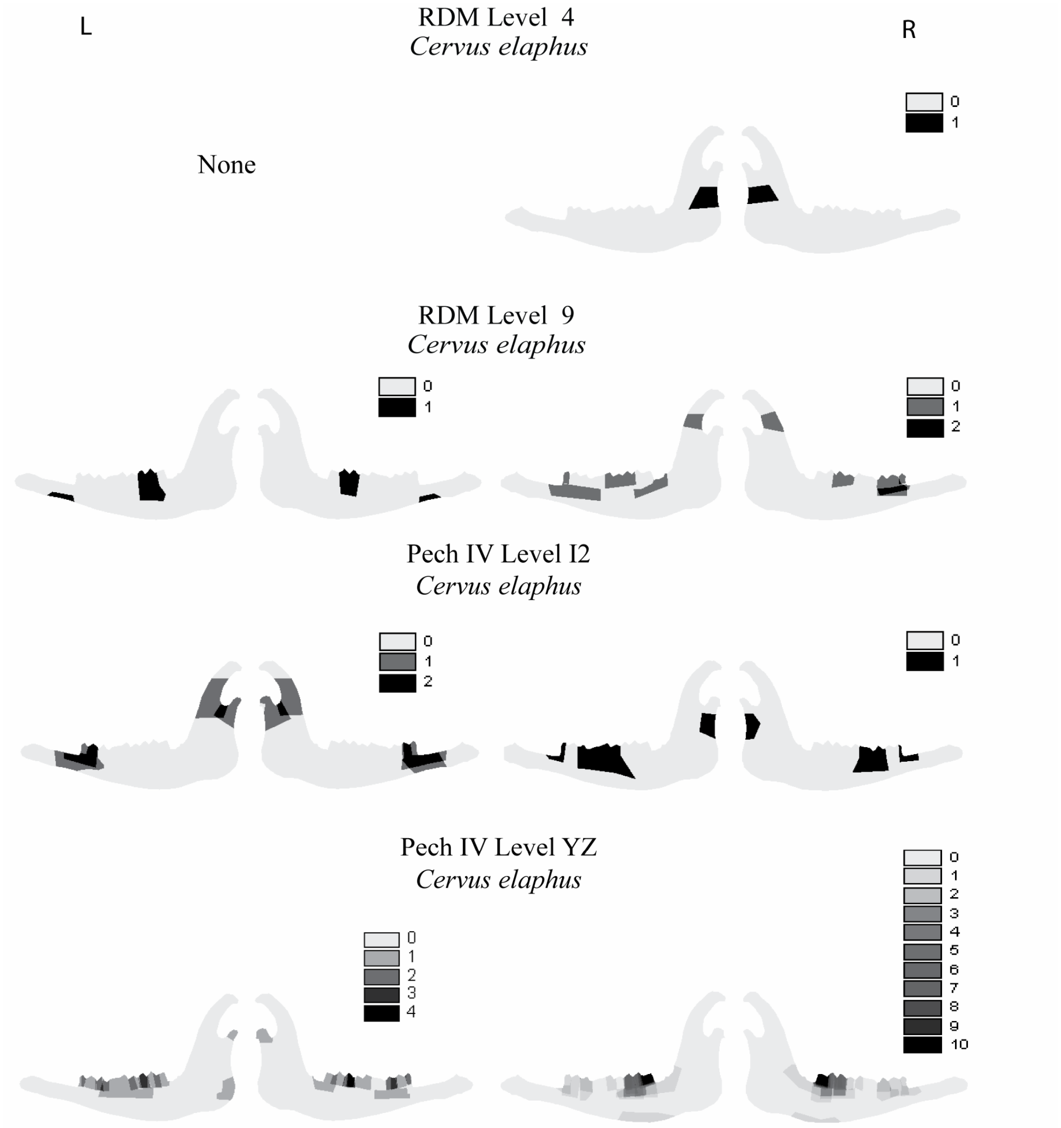


Fig. A7. Cranial remains of red deer analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.



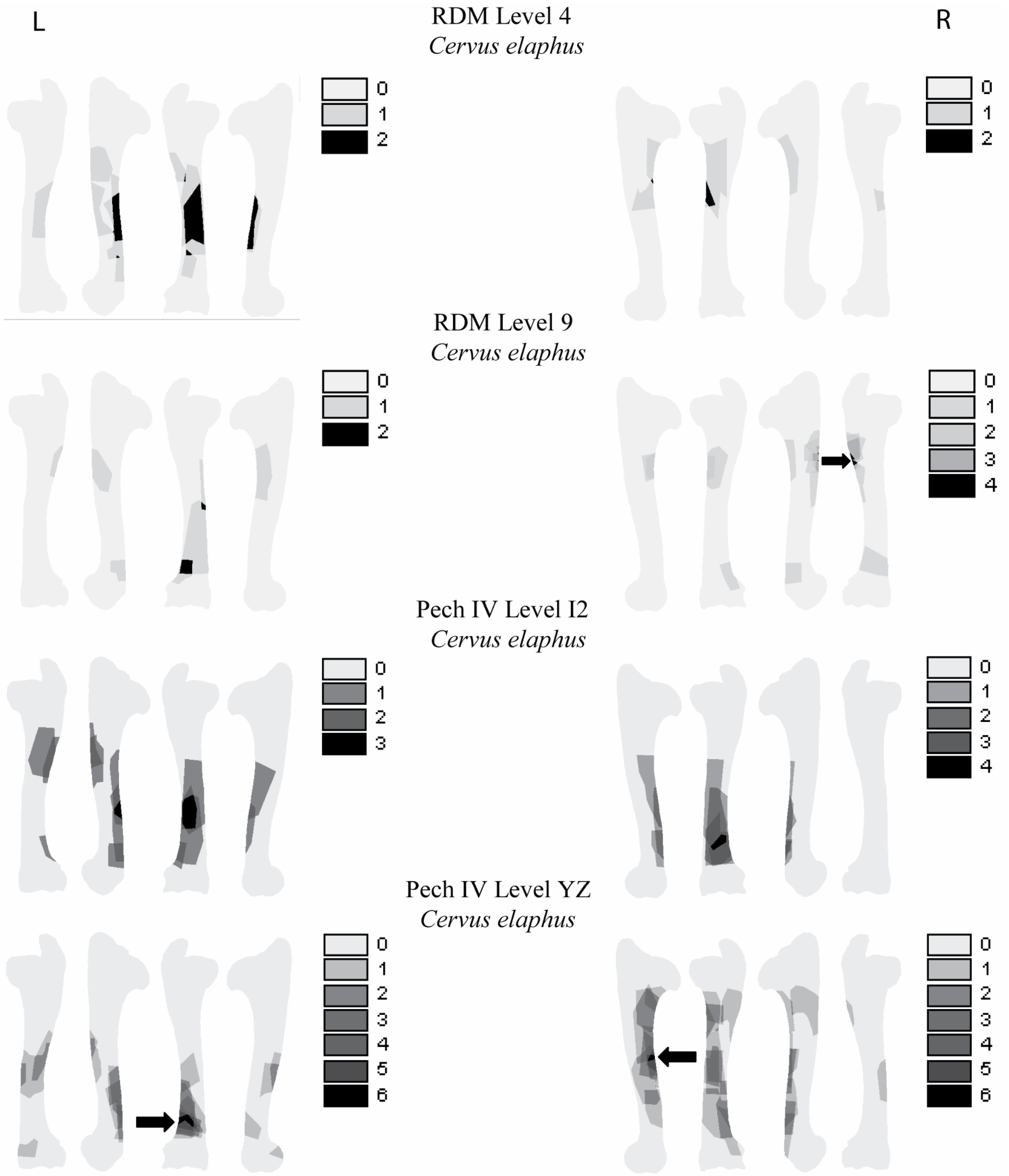
RDM Level 4
Cervus elaphus

RDM Level 9
Cervus elaphus

Pech IV Level I2
Cervus elaphus

Pech IV Level YZ
Cervus elaphus

Fig. A8. Left and right red deer mandibular fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

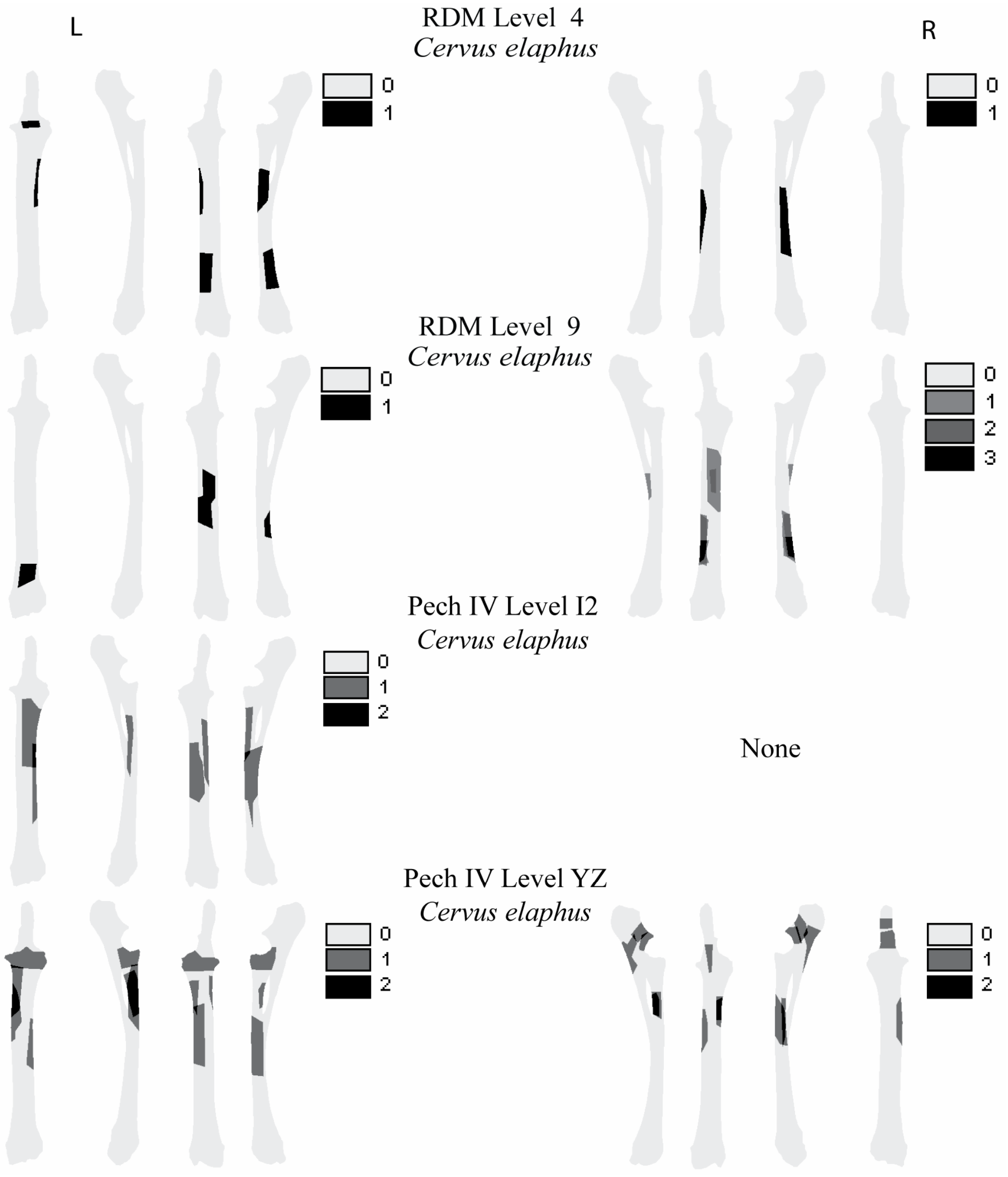

RDM Level 4
Cervus elaphus

RDM Level 9
Cervus elaphus

Pech IV Level I2
Cervus elaphus

Pech IV Level YZ
Cervus elaphus

Fig. A9. Left and right red deer humeral fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. Black arrows are used to highlight the highest number of overlaps when the area of overlap is small and hard to see. See the caption under Figure 11a for further explanation.



RDM Level 4
Cervus elaphus

RDM Level 9
Cervus elaphus

Pech IV Level I2
Cervus elaphus

Pech IV Level YZ
Cervus elaphus

Fig. A10. Left and right red deer radioulnar fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

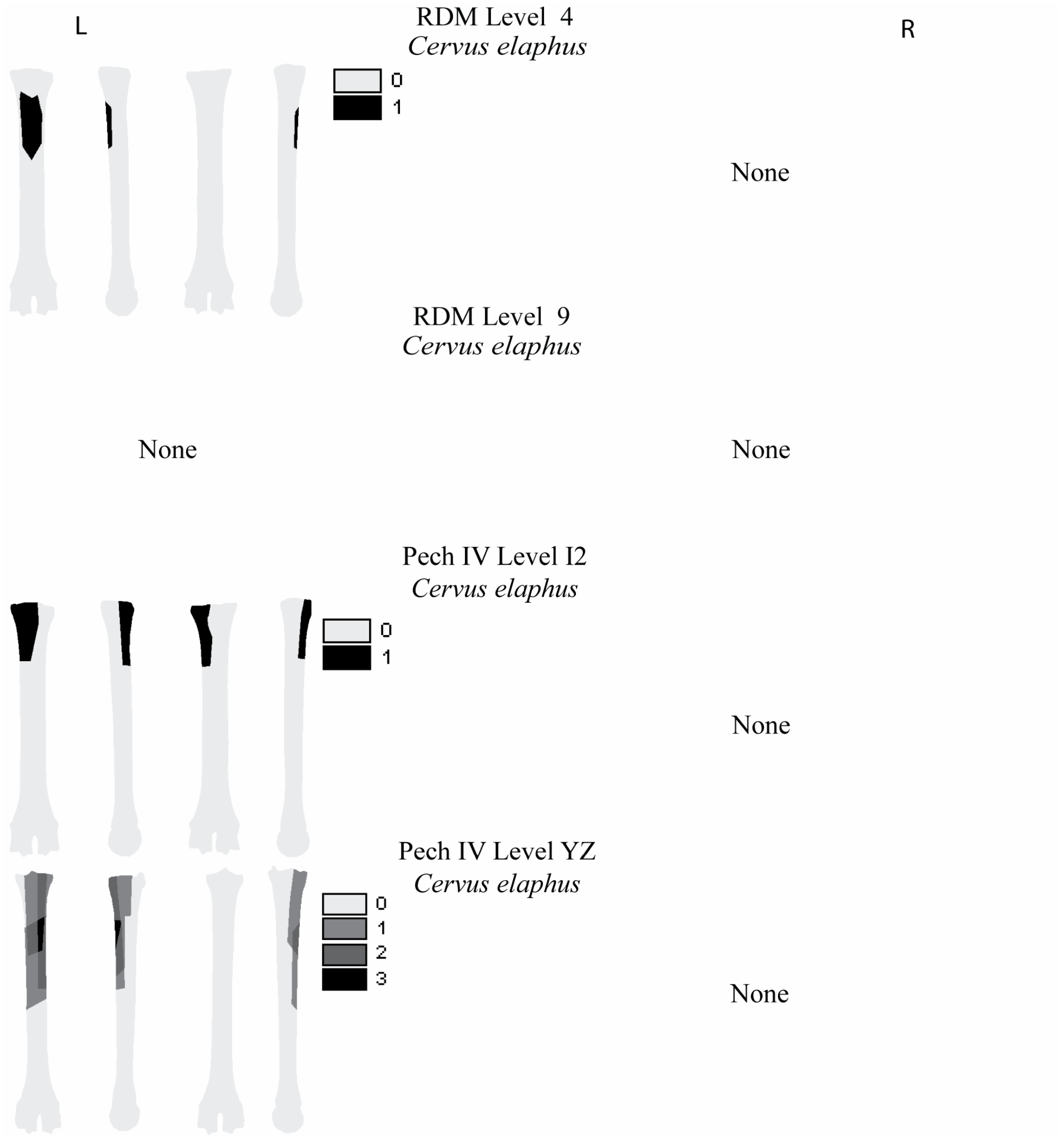


Fig. A11. Left and right red deer metcarpal fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

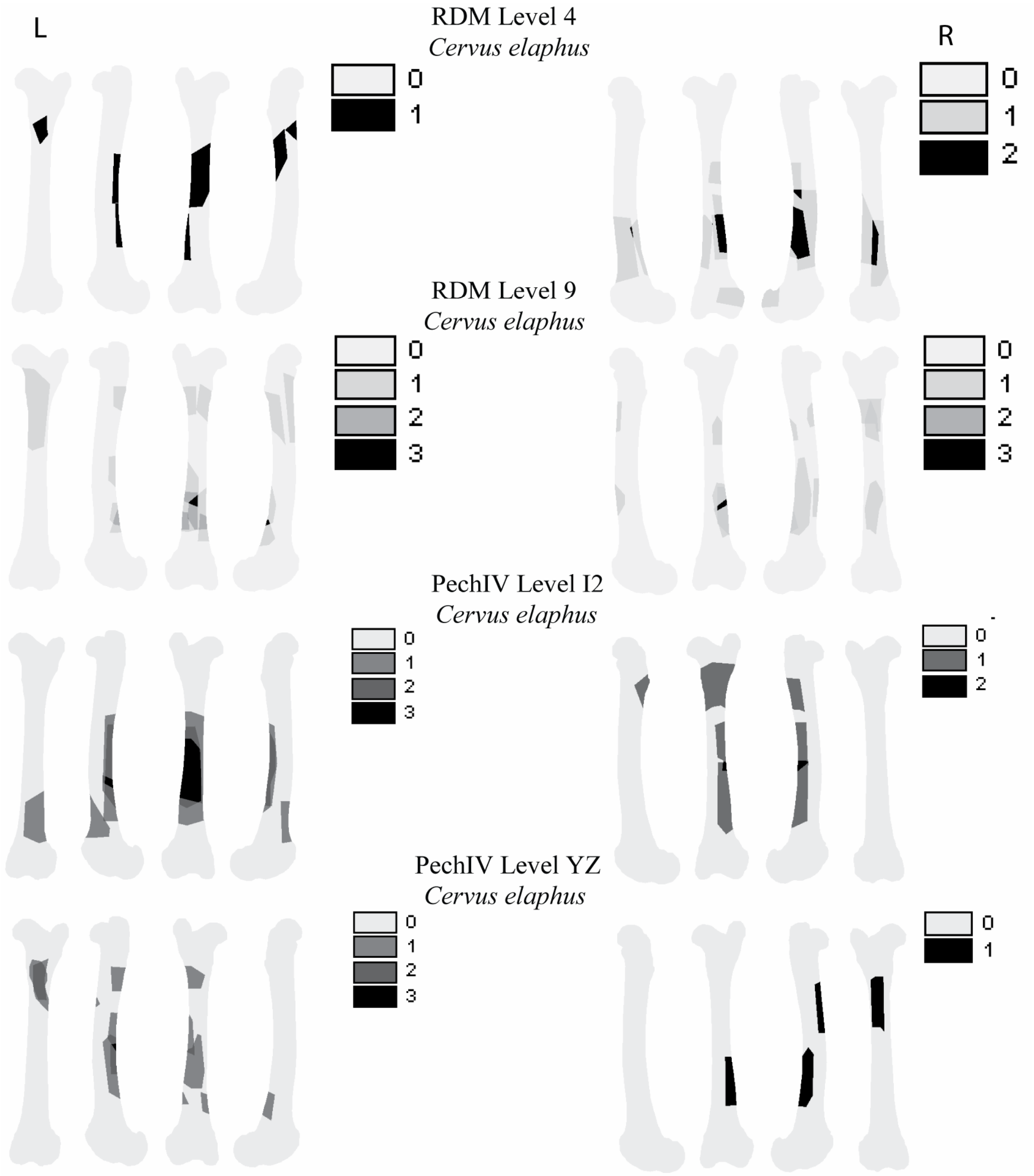


Fig. A12. Left and right red deer femoral fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

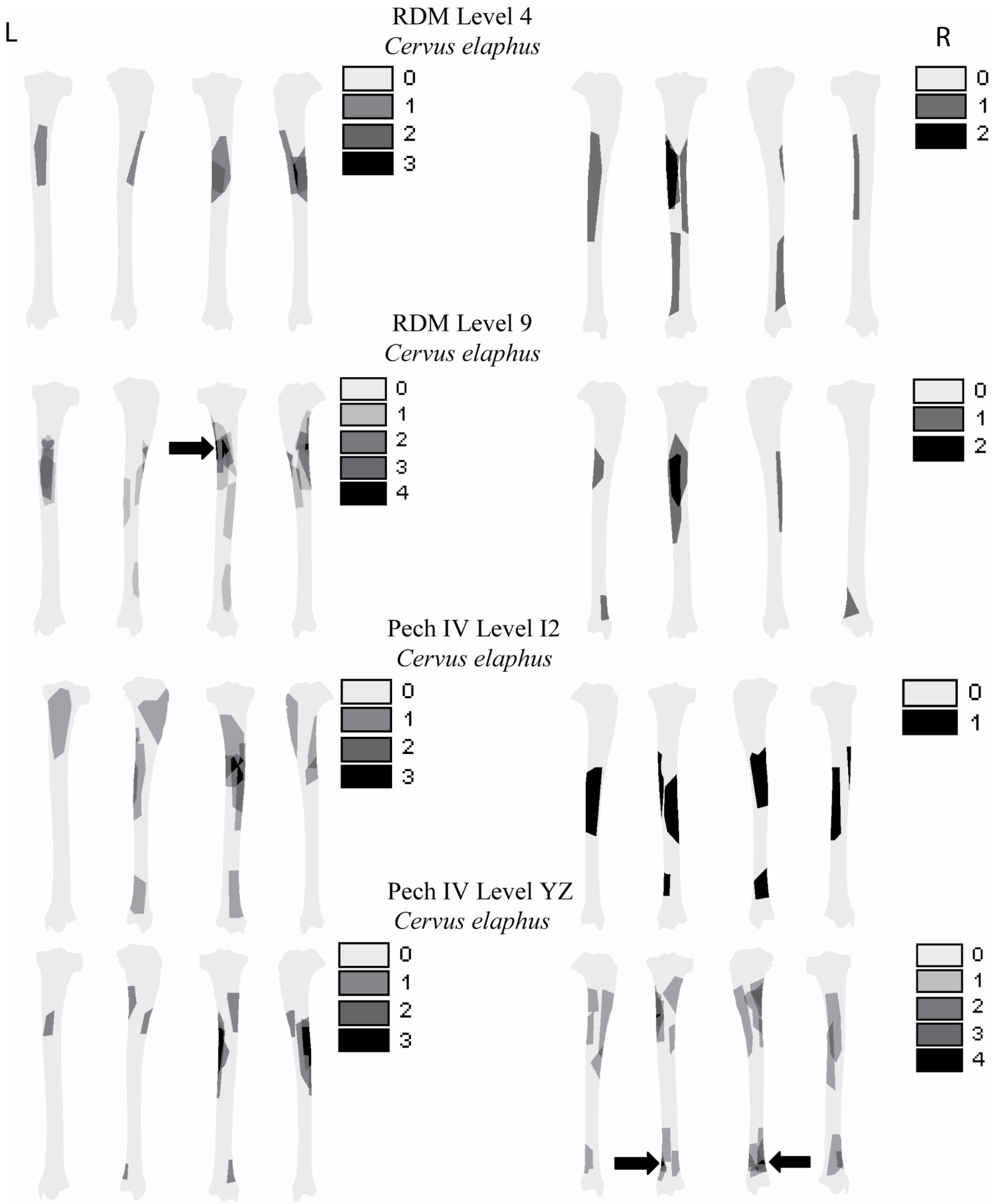


Fig. A13. Left and right red deer tibial fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. Black arrows are used to highlight the highest number of overlaps when the area of overlap is small and hard to see. See the caption under Figure 11a for further explanation.

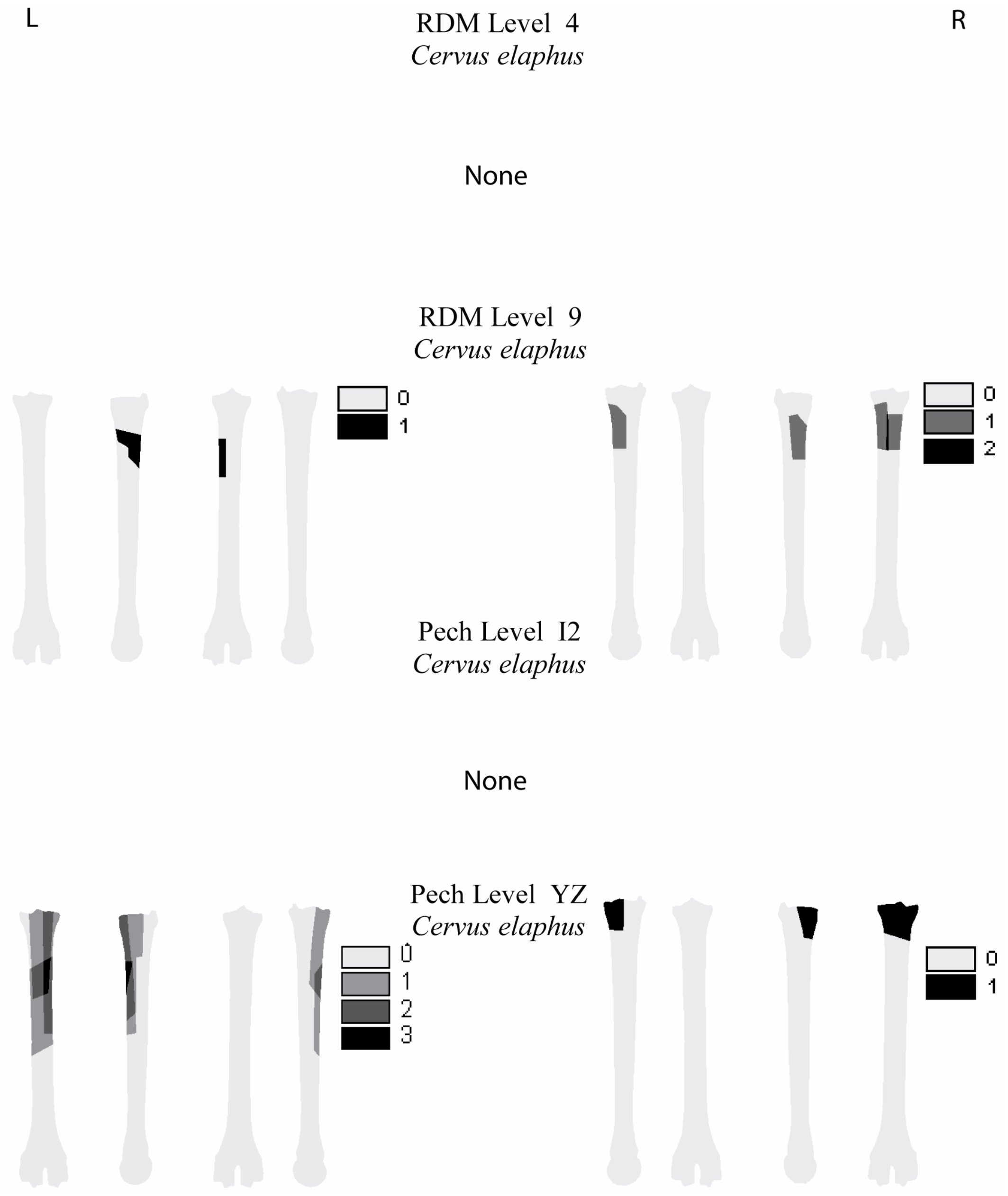


Fig. A14. Left and right red deer metatarsal fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

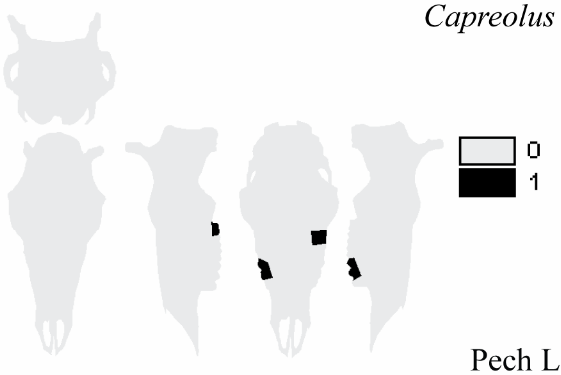
With Teeth

RDM Level 4
Capreolus capreolus

Without Teeth

None

RDM Level 9
Capreolus capreolus



None

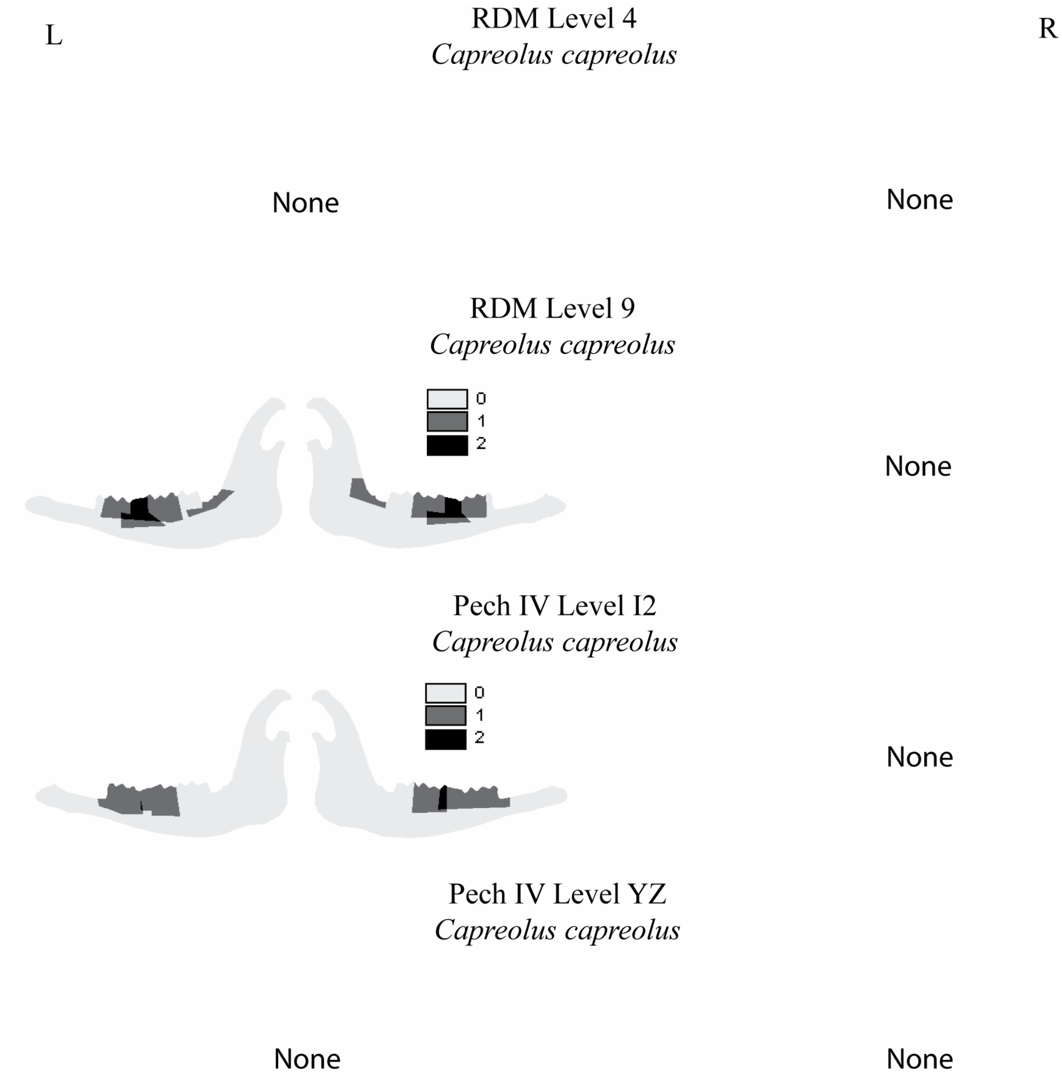
Pech Level I2
Capreolus capreolus

None

Pech Level YZ
Capreolus capreolus

None

Fig. A15. Cranial remains of roe deer analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.



RDM Level 4
Capreolus capreolus

RDM Level 9
Capreolus capreolus

Pech IV Level I2
Capreolus capreolus

Pech IV Level YZ
Capreolus capreolus

Fig. A16. Left and right roe deer mandibular fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

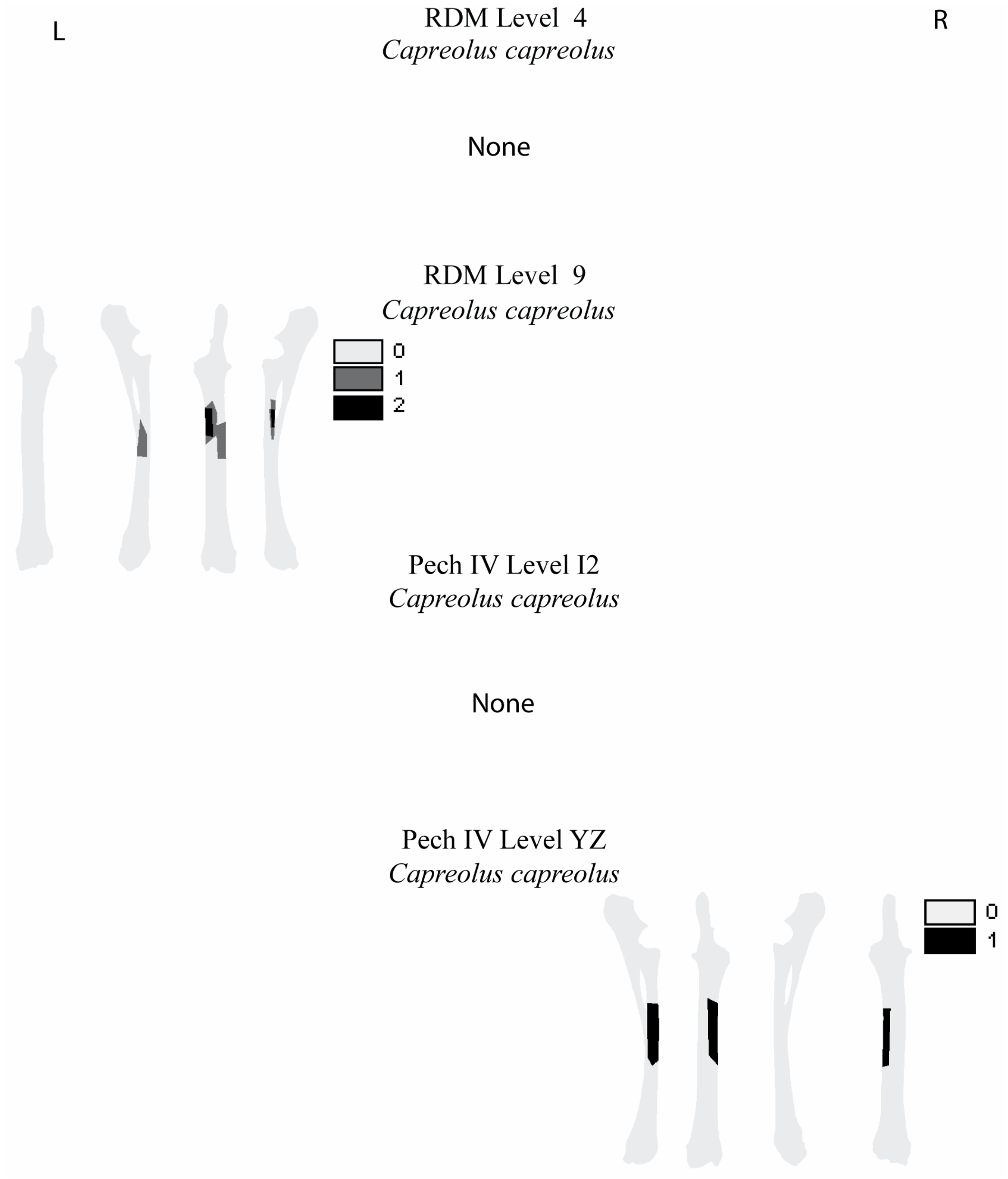


Figure A17. Left and right roe deer radioulnar fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

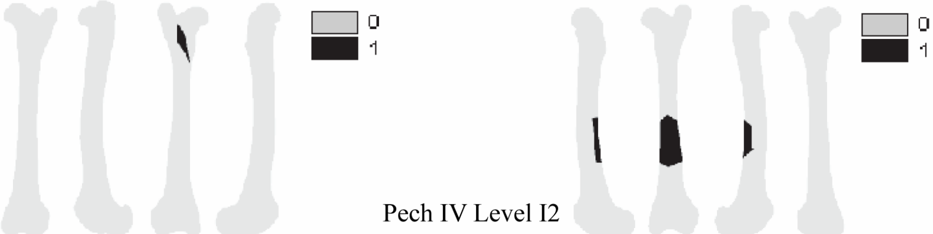
L

RDM Level 4
Capreolus capreolus

R

None

RDM Level 9
Capreolus capreolus

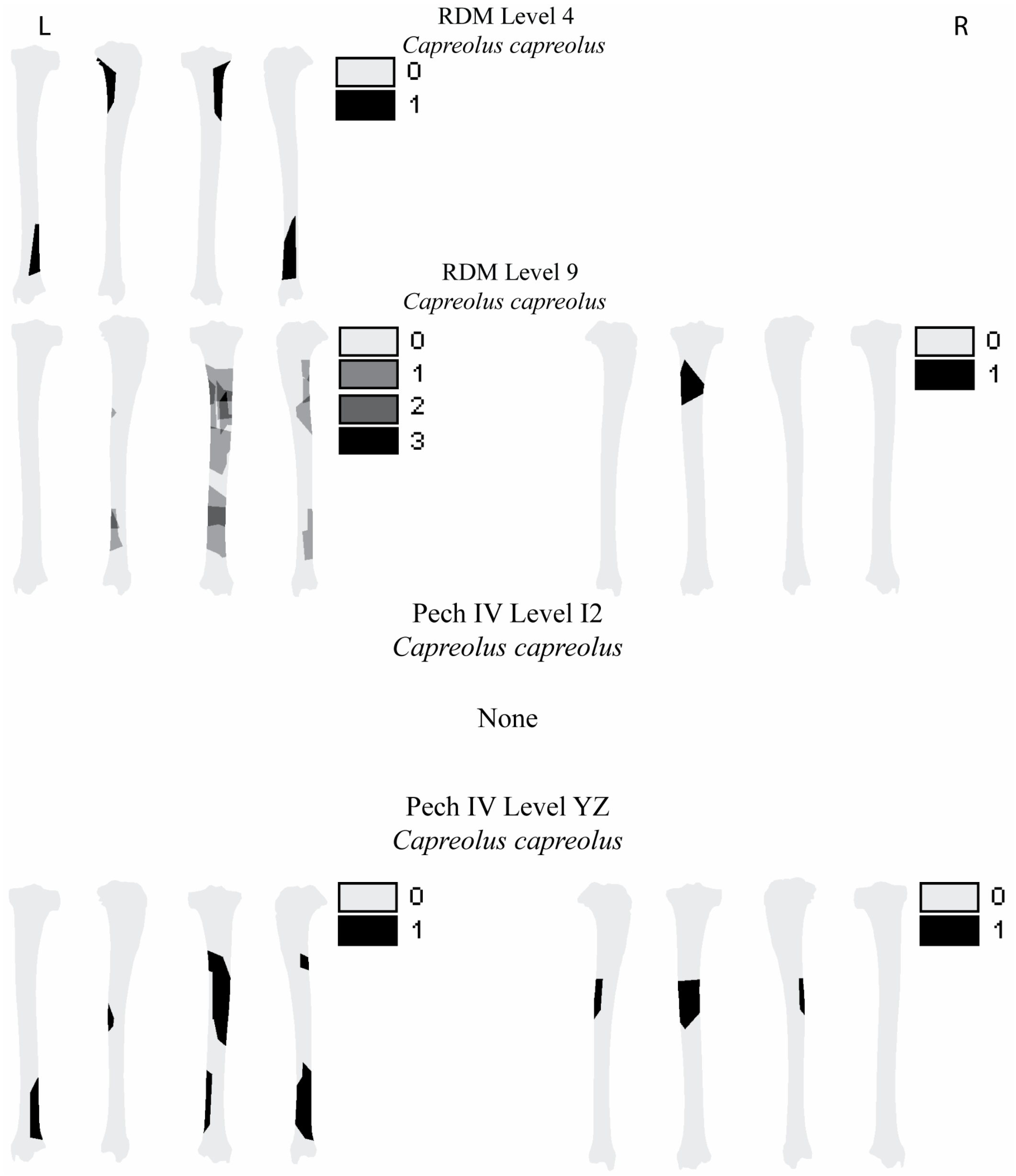


Pech IV Level I2
Capreolus capreolus

None

Pech IV Level YZ
Capreolus capreolus

Fig. A18. Left and right roe deer femoral fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.



RDM Level 4
Capreolus capreolus

RDM Level 9
Capreolus capreolus

Pech IV Level I2
Capreolus capreolus

None

Pech IV Level YZ
Capreolus capreolus

Fig. A19. Left and right roe deer tibial fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

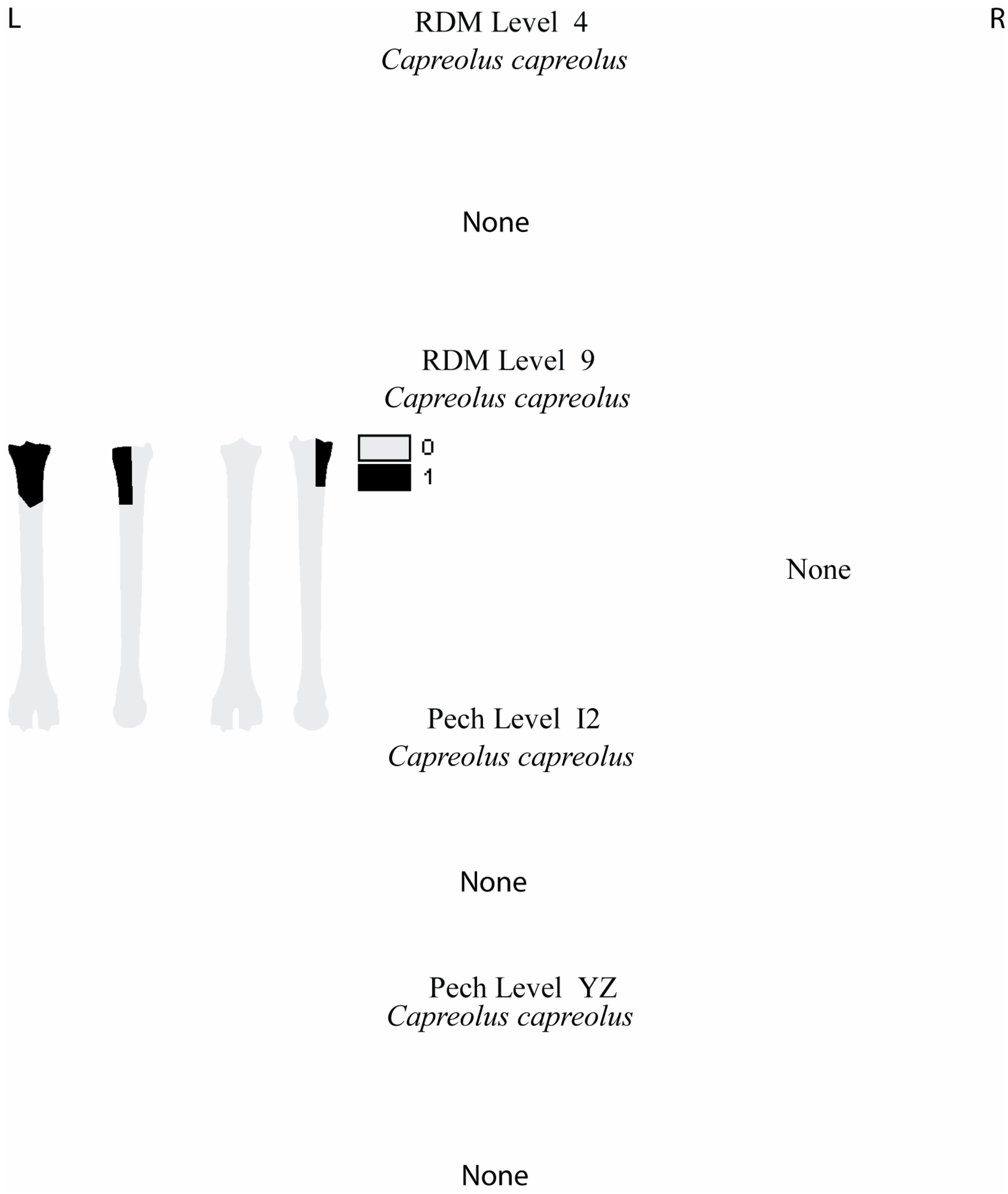


Fig. A20. Left and right roe deer metatarsal fragments analyzed from Roc de Marsal and Bordes' excavation of Pech de l'Azé IV. See the caption under Figure 11a for further explanation.

APPENDIX B

Surface modification marks mapped onto ArcView GIS templates for high survival skeletal elements

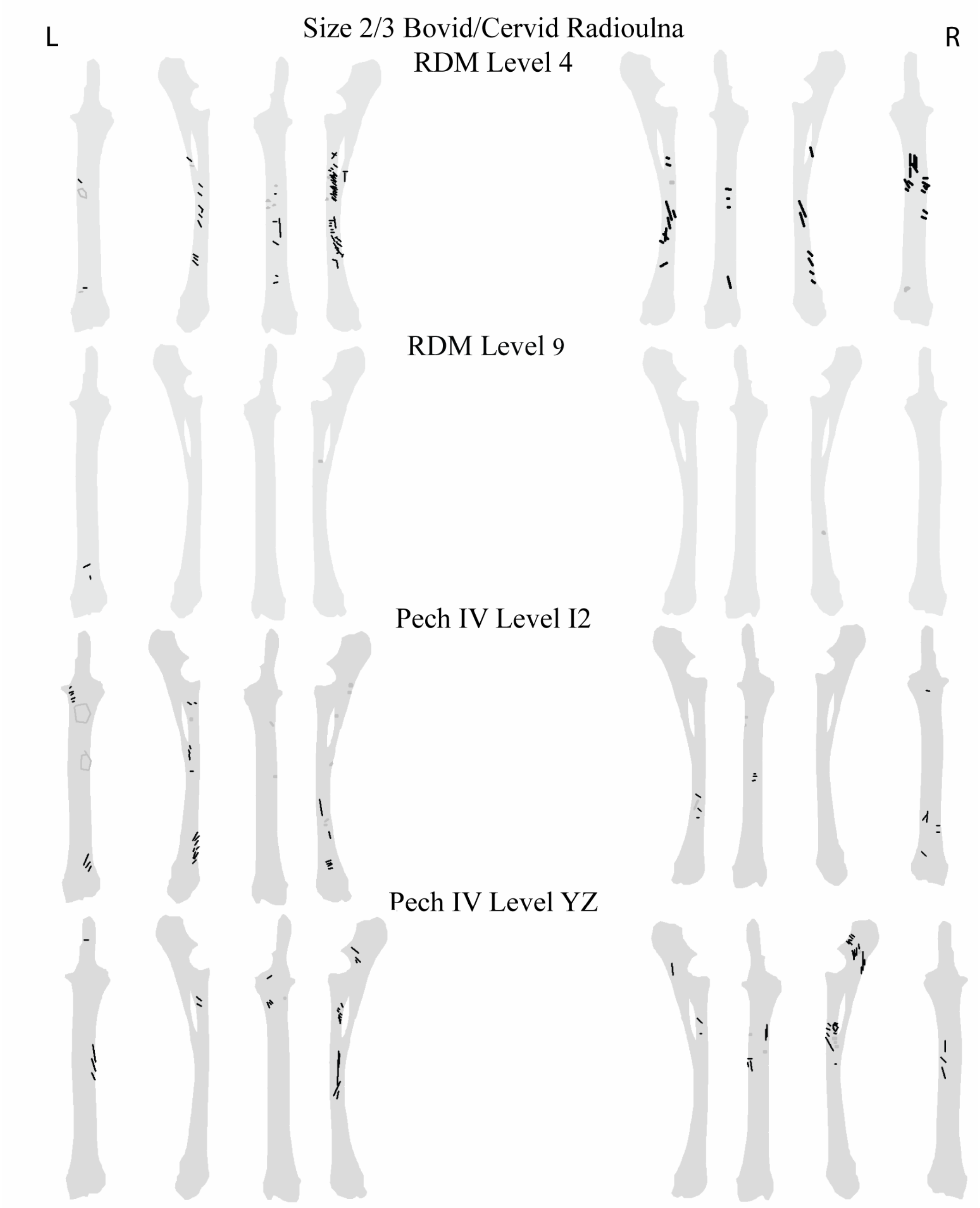


Fig. B1. Templates of the medial, lateral, anterior and posterior views of a cervid radioulna. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

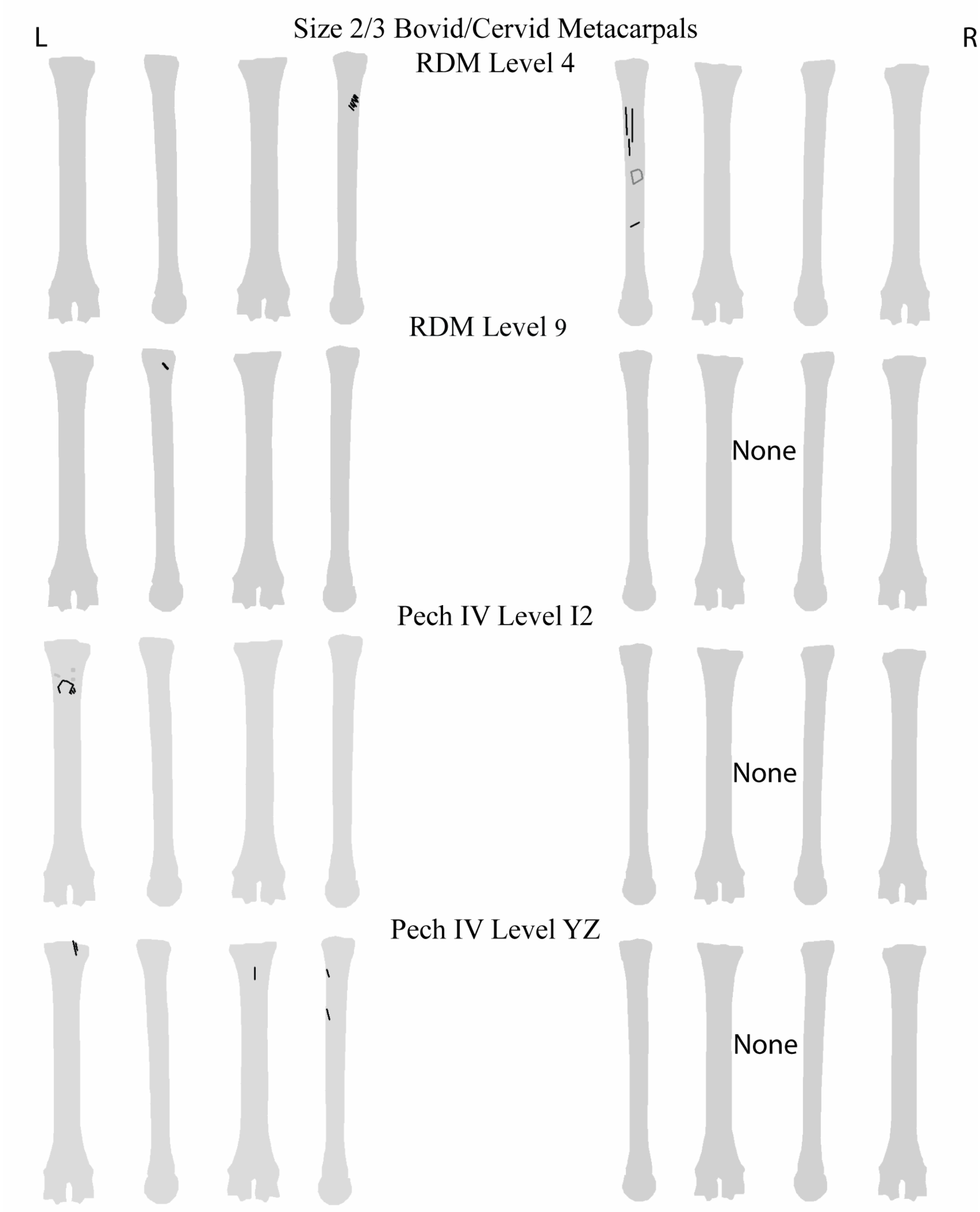


Fig. B2. Templates of the medial, lateral, anterior and posterior views of a cervid metacarpal. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

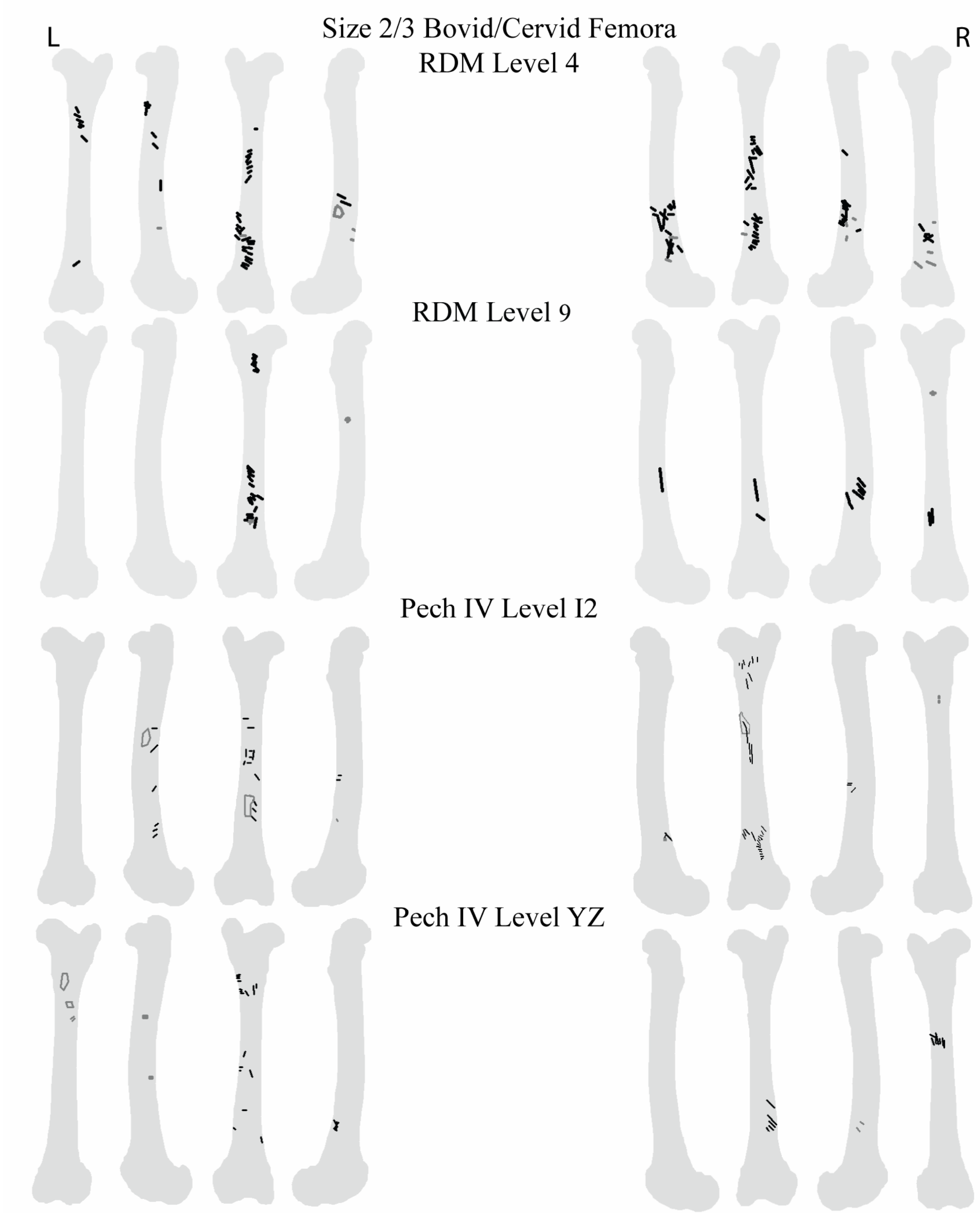


Fig. B3. Templates of the medial, lateral, anterior and posterior views of a cervid femur. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

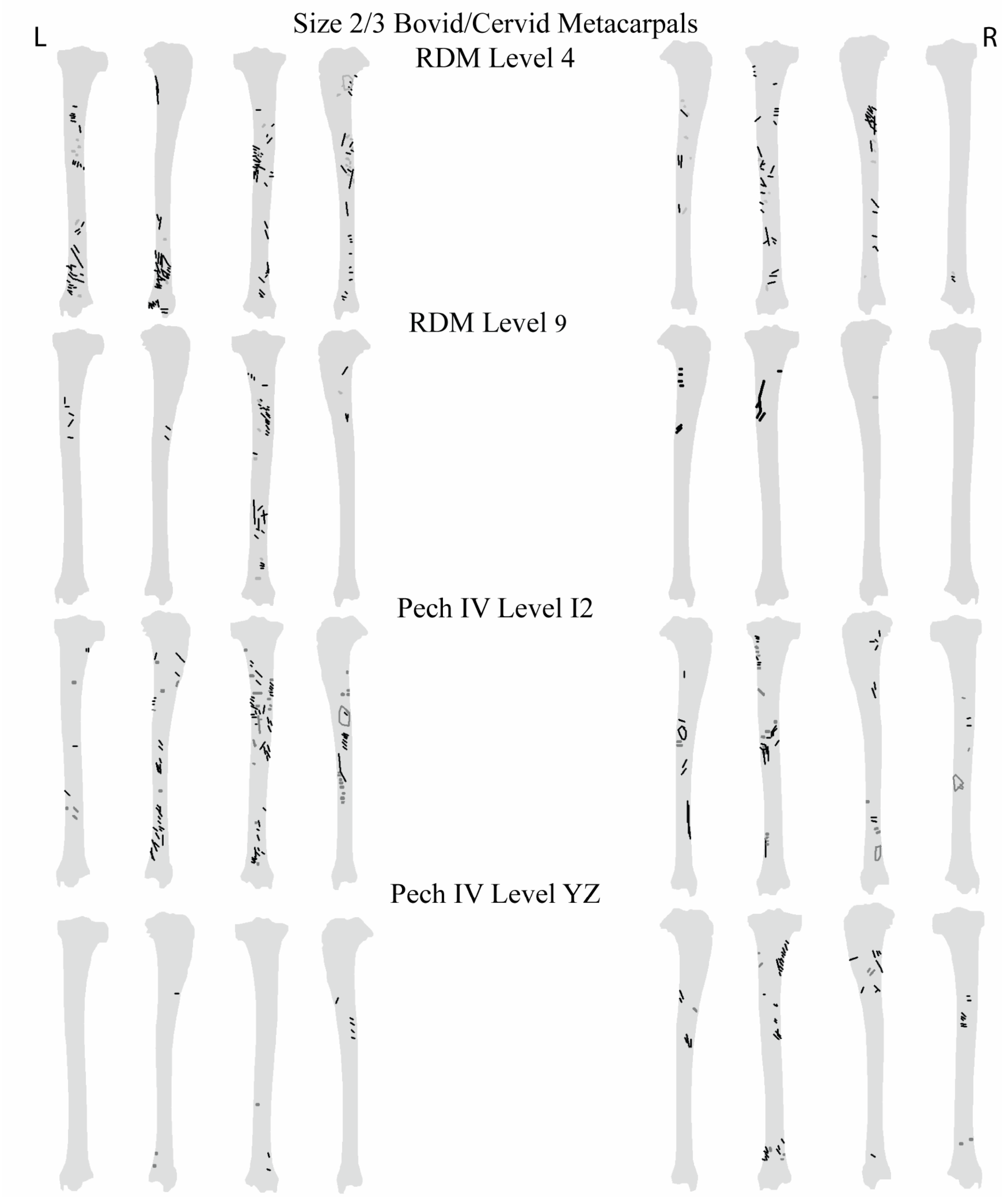


Fig. B4. Templates of the medial, lateral, anterior and posterior views of a cervid tibia. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

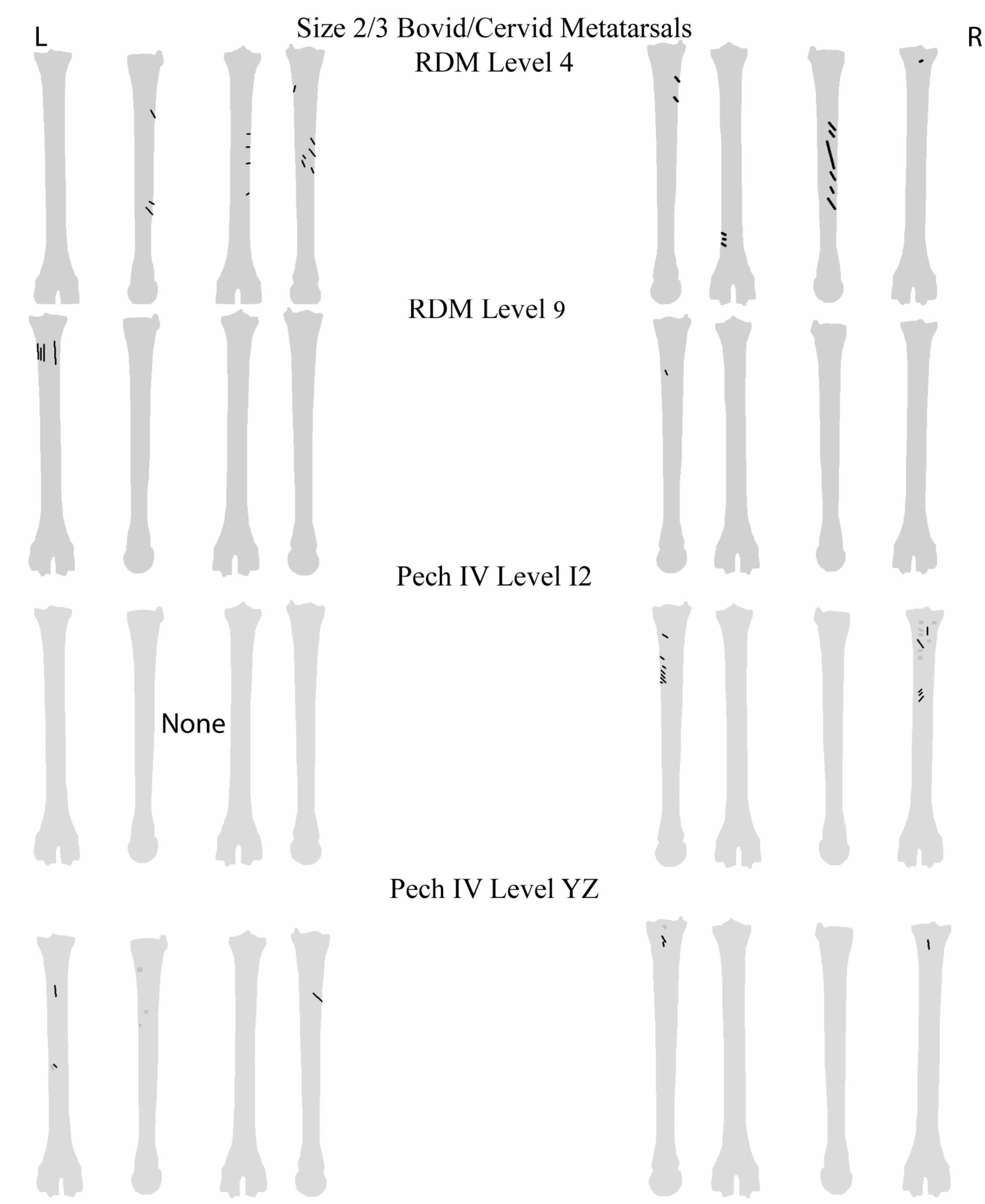
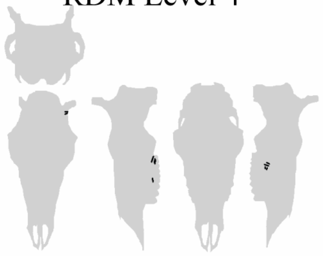


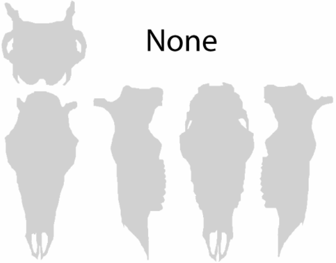
Fig. B5. Templates of the medial, lateral, anterior and posterior views of a cervid metatarsal. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

Size 2/3 Bovid/Cervid Cranial Fragments

RDM Level 4

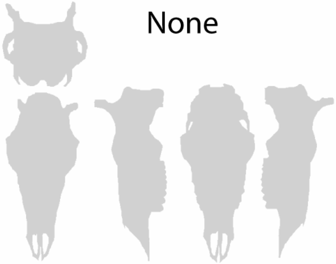


RDM Level 9



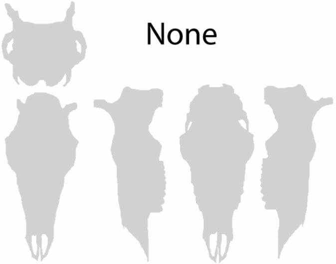
None

Pech IV Level I2



None

Pech IV Level YZ



None

Fig. B6. Templates of the superior, inferior, posterior and left lateral and right lateral views of a cervid skull. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey.

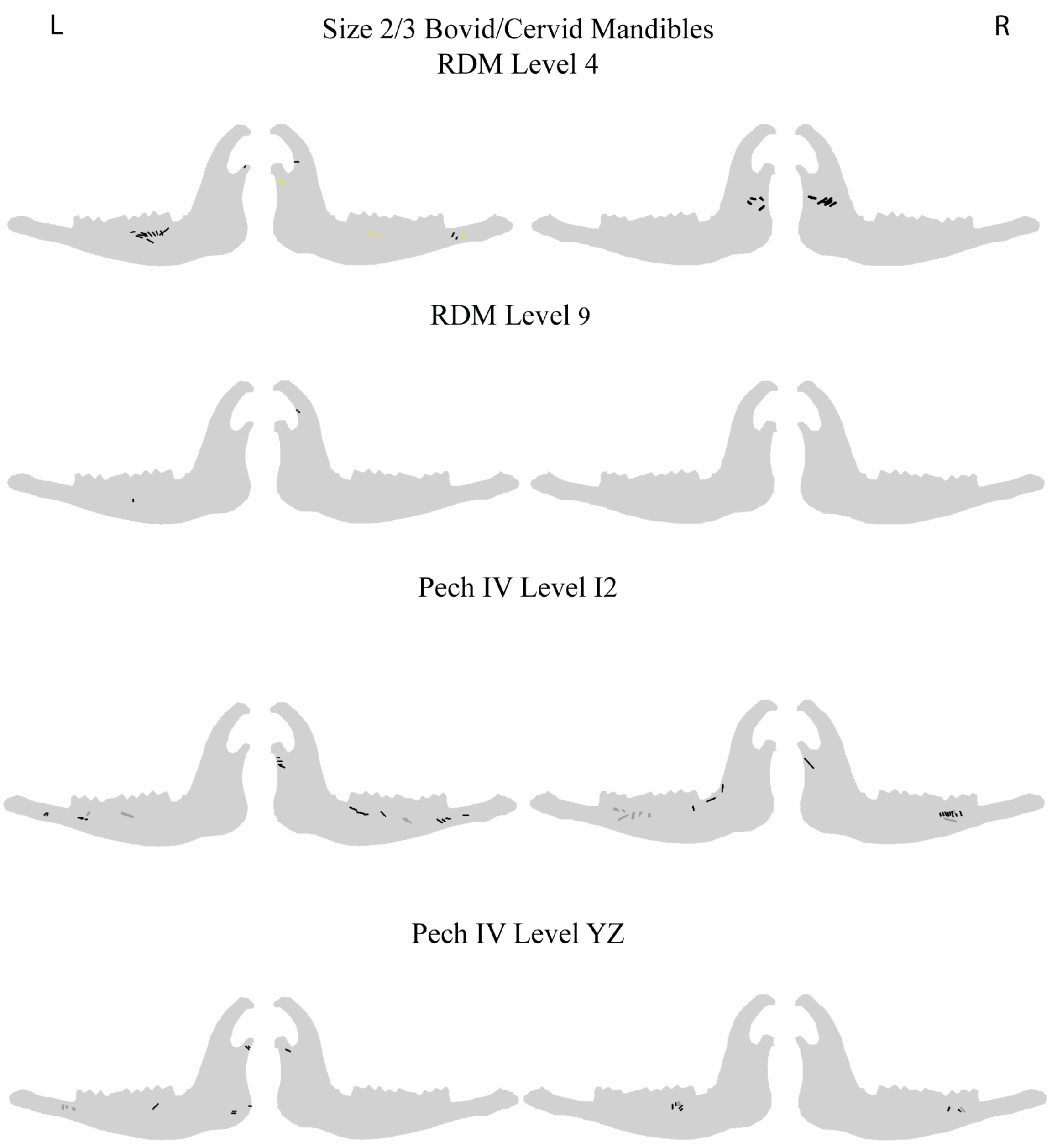


Fig. B7. Templates of buccal and lingual views of a cervid mandible. Cut marks observed on size 2/3 cervids are drawn on to each template in black. Percussion marks are drawn in dark grey or yellow.