LATE PLEISTOCENE POPULATION INTERACTION IN WESTERN EUROPE AND MODERN HUMAN ORIGINS: NEW INSIGHTS BASED ON THE FAUNAL REMAINS FROM SAINT-CÉSAIRE, SOUTHWESTERN FRANCE

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anthropology)
in The University of Michigan
2004

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DEDICATION

A Norman Clermont

pour une soif de connaître et un rire hors du commun,

parce qu'il m'a appris à apprendre

ACKNOWLEDGMENTS

This study is the result of a long, partly American, partly French, journey. Funding for this research was provided by the National Science Foundation, the Social Sciences and Humanities Research Council of Canada, and the Fonds des Chercheurs et Aide à la Recherche.

In Michigan, I benefited from the help of many individuals. Among these, I first want to thank Robert Whallon, my advisor, for his patience, support, and inspiration. Bob contributed to many of the ideas presented in this work. He also introduced me to several of his French friends, many of whom became mine as well. For all this, I can never thank him enough.

I also owe a great deal to John Speth who showed ways to sharpen the ideas and strengthen the arguments. Our many discussions on Saint-Césaire, Kebara, and many other topics fine-tuned my approach to the problem of modern human origins. John O'Shea has been a thoughtful teacher and his comments improved the propositions discussed here. Many thanks to Daniel Fisher who has had many valuable insights in taphonomy and fauna. His views helped broaden the scope of this analysis. I would like to express my appreciation to Jacques Jaubert who generously shared his knowledge of the Middle Paleolithic with me. I had many discussions with Milford Wolpoff, which contributed to my research in a significant way. I would also like to thank Bill Farrand, Kent Flannery, Joyce Marcus, Graciela Cabana, Leland Davis, Carla Sinopoli, and Loring Brace for their help and advice.

During the writing process, I had the opportunity to spend a month at the Hebrew University in Jerusalem. Discussions with Naama Goren-Inbar, Rivka Rabinovich, and Erella Hovers taught me a great deal about the Levantine Paleolithic. In addition to the many suggestions they made, Anna Belfer-Cohen and Liora Horwitz spent considerable time commenting on earlier drafts of this work. These efforts are extremely appreciated.

I am indebted to Frank Miller from the Canadian Wildlife Service and Eigil Reimers from the University of Oslo, Department of Biology for sharing information on caribou and reindeer biology. Frank has been especially helpful in pointing out weaknesses in the methods and assumptions used by archaeologists to interpret seasonality.

En France, ce projet s'est crystallisé alors que je complétais mon DEA à l'Université de Paris-X, Nanterre. Catherine Perlès et Anne Delagnes furent d'un support extraordinaire. Je les remercie pour leurs encouragements prodigués dans un environnement qui s'est avéré particulièrement stimulant. Jacques Pelegrin a joué un rôle considerable dans ma formation. Sa générosité, à laquelle se mêle une grande honnêteté, furent, et sont toujours, une source d'inspiration. Françoise Audouze et Jim Enloe m'ont accueilli chaleureusement à Verberie. Je tiens à les remercier pour leurs judicieux conseils. Jim a également contribué à éclaircir plusieurs points nébuleux quant à l'interprétation des restes dentaires. J'aimerais également exprimer toute ma gratitude à Jean-Philip Brugal pour son soutien, son amitié et pour avoir clarifié certains problèmes de méthodologie. Par ces critiques, mais surtout par ses encouragements, Liliane Meignen a contribué à la bonne marche de ce projet. Je tiens de plus à remercier Paola Villa pour ses commentaires et questions. Les heures passées en laboratoire en sa compagnie furent

particulièrement formatrices et ont permis d'affiner ma lecture du matériel. Merci à Jean-François Baratin et au Service Régional de l'Archéologie (Poitou-Charente) pour avoir permis le financement de l'archivage et du conditionnement du matériel.

A Bordeaux, j'ai bénéficié d'un accueil plus que chaleureux à l'Institut de Préhistoire et de Géologie du Quaternaire où l'étude du materiel s'est déroulé. Je voudrais remercier en particulier Jean-Philippe Rigaud, Françoise Delpech et Jean-Pierre Texier pour m'avoir reçu dans leur laboratoire. Dominique Armand et Jean-Luc Guadelli m'ont dirigé dans l'apprentissage de la faune et de ses subtilités autant taphonomiques que taxonomiques et j'aimerais les remercier en ce sens. Geneviève Rauber et Michèle Charuel ont grandement facilité mon séjour par leur bonne humeur et leur aide. Jean-Baptiste Mallye, François Lacrampe-Cuyaubère, William Rendu et, en particulier, Nicolay Sirakov (fils) et Tsenka Tsanova ont participé d'une facon ou d'une autre à la réalisation de cette étude. Je les remercie de tout coeur. En plus de leur amitié, j'ai grandement profité de nombreuses discussions entretenues avec Cédric Beauval, Véronique Laroulandie, François Lacrampe-Cuyaubère, Hélène Rougier, Fanny Bocquentin, David Péressinoto, Jean-George Ferrié, Jean-Christophe Castel, Marian VanHaeren, Sandrine Costamagno, Nicolas Teyssandier, David Cochard, Marie Soressi, Arnaud Lenoble et Jean-Guillaume Bordes. Celles-ci m'ont permis de mieux cerner certains problèmes liés à l'interprétation des assemblages paléolithiques. J'aimerais également souligner les contributions de Jacques Jaubert, Jean-Michel Geneste, Jehanne Féblot-Augustins, Francesco d'Errico, Jean-Claude Marquet, Jean-Luc Guadelli, Patrick Michel, Pierre-Yves Demars, Bernard Vandermeersch, Michel Lenoir et Olivier Le Gall qui ont permis de compléter des informations manquantes. Un merci tout particulier à Bruno Maureille pour son enthousiasme et ses suggestions.

Bien que travaillant sur des problématiques bien différentes, je tiens à exprimer toute ma reconnaissance à Pierre Pétrequin pour ses encouragements et des échanges particulièrement stimulants. De plus, je tiens à souligner l'extrême gentillesse de François Lévêque qui s'est toujours montré d'une grande disponibilité et d'une patience indémontable. Les informations qu'il m'a fournies sur Saint-Césaire furent capitales quant à l'accomplissement de cette recherche. Je ne pourrais jamais assez remercier Cédric Beauval pour son aide. Sans lui, cette étude aurait été bien différente. J'aimerais également souligner à quel point je suis redevable à ma famille qui m'a toujours soutenu et encouragé au milieu de tous ces déménagements. Enfin, Laure, tout simplement parce que sans toi, tout cela perdrait de son sens.

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CHAPTER 1

INTRODUCTION TO THE RESEARCH PROBLEM

The material remains uncovered in archaeological sites are not direct observations of the phenomena of interest, but rather are the results of those phenomena. It is the task of the archaeologist to encode information and patterns into the static objects based on his knowledge of observable phenomena considered relevant for giving meaning to the archaeological traces (Binford 1977). In this perspective, observable phenomena are used as an analogical bridge that allows one to retrodict the past. As a matter of fact, any statement in archaeology, as in any science, can only be uniformitarian in nature, even though this may result in a simplification of the reality (Shea 1982). Therefore, past cultural behaviors are best interpreted and understood by linking them to current observable phenomena. Paleolithic research has drawn extensively on these principles. This approach provides the framework from which one of the oldest debates in anthropology is examined: the origins of modern humans.

There is a consensus that the Neandertals were the only population present in the Mousterian of Western Europe (Vandermeersch 1989; Hublin 1988). This population produced various Levallois-based industries, although several variants, including discoid, Quina, and laminar reduction sequences are also known (Bordes 1984; Boëda 1989, 1990, 1993; Révillion 1995; Bourguignon 1997). Occupation of this region during the Upper Paleolithic is attributed universally to modern human populations. Laminar reduction sequences, portable art, and elaborated bone tool technology are features associated with these groups (Sonneville-Bordes 1960; Mellars 1989a). In contrast, there is a lack of consensus with respect to the nature of the occupation during the transition from the Middle to the Upper Paleolithic. For some scholars, the transition is characterized by the replacement of local populations by incoming modern human migrants (e.g., Stringer and Andrews 1988; Vandermeersch 1989; Mellars 1989a, 1989b, 1996; Demars and Hublin 1989; Trinkaus 1986; Duarte *et al.* 1999; Bar-Yosef 2002). These authors generally consider the Neandertals to differ biologically from modern humans, some considering these two groups as different species, but more commonly, as two different subspecies (or semispecies to use a concept widespread in evolutionary biology). This view, however, has been contested by others who argue that Neandertals were connected with early modern humans through gene flow and contributed to the gene pool of subsequent populations (Brace 1964, 1979; Thorne and Wolpoff 1981; Smith 1982; Wolpoff *et al.* 1984; Frayer *et al.* 1993; Wolpoff 1999). This unresolved debate concerning modern human origins is the focus of this study.

The present analysis tests the "Neandertal Replacement model," and more specifically, seeks to reassess the assumption of a migration of early modern humans into Western Europe at the Middle to Upper Paleolithic boundary. This model differs from several other archaeological hypotheses, however, as it implies the coexistence and interaction of two human species or subspecies, a situation that has no close analogue today. The test detailed here focuses on ecology and adopts an evolutionary perspective, approaches whose respective strengths are found in the existence of universals of prey dynamics and a large body of observations on species interaction and evolution (e.g., Mayr 1982; Stephens and Krebs 1986; Smith and Winterhalder 1992; Futuyma 1997). Because Neandertals and early modern humans are extinct populations, hypotheses about population interaction and evolution in the late Pleistocene must be based on indirect sources of information. Even molecular studies are limited in this way and use observations drawn from living groups or static remains, for instance, fossil DNA, in order to produce inferences about the genetic makeup of these past populations.

Several tests of the Neandertal replacement model have been proposed, mostly based on skeletal remains (e.g., Stringer 1974, 1982; Stringer and Andrews 1988; Braüer 1981; Wolpoff *et al.* 1984; Wolpoff 1989, 1999; Hublin 1990; Rak 1990; Frayer *et al.* 1993), but also on genetic evidence (e.g., Cann *et al.* 1987; Vigilant *et al.* 1991; Stoneking *et al.* 1992; Horai *et al.* 1995; Tischkoff *et al.* 1996; Krings *et al.* 1997, 1999, 2000; Ovchinnikov *et al.* 2000; Schmitz *et al.* 2002; Yu *et al.* 2002; Caramelli *et al.* 2003). Generally, the limitations of these tests lie in our understanding of the cultural and biological correlates associated with the process of speciation.

Little comparable effort has been made in archaeology, although some have investigated biocultural changes during the Middle to Upper Paleolithic transition (Mellars 1989a, 1996; White 1982; Binford 1982, 1989; Whallon 1989; Straus 1997; Lieberman and Shea 1994; D'Errico *et al.* 1998; Gamble 1999; Bar-Yosef 2002). However, few of these archaeological studies have tried to test the core assumptions underlying the Neandertal replacement model.

This study is a first step in this direction. Propositions are formulated about the consequences of a modern human incursion into Western Europe and, more specifically, in southwestern France during the Middle to Upper Paleolithic transition. The data used for this test are not based on the skeletal characteristics or the genome of late Pleistocene human populations, but are instead derived from the material traces of their behaviors. The archaeological test incorporates information generated by ecologists and anthropologists on the demographic stability of small forager populations over time and draws on recent studies of resource exploitation by temperate climate foragers.

It is argued that late Pleistocene populations were kept close to the carrying capacity of the environment in Western Europe and were vulnerable to fluctuations in resource abundance, in particular during the snow-covered season. If the hypothesis of a modern human incursion into Eurasia during the Middle to Upper Paleolithic is true, it can be suggested that this demographic growth increased local populations far beyond carrying capacity and led to chronic resource depression. Therefore, it is suggested that Neandertals and early modern humans adapted to these stresses in predictable ways in order to cope with resource scarcity.

These predictable responses or expectations, all related to fauna and therefore potentially visible in the archaeological record, are linked to maximization of carcass utilization, changes in the transport of low and high utility parts, of high- and low-ranked taxa, marrow exploitation of low utility parts, and the importance of scavenging. These archaeological expectations are tested using eight faunal assemblages from Saint-Césaire (Charente-Maritime), a site in southwestern France that spans the period of the transition from the Middle to the Upper Paleolithic. It is important to note that even though the discussion focuses here on Western Europe, this archaeological model might be applicable to other regions as well.

The history and development of the Neandertal replacement model is presented in Chapter 2, as well as problems associated with its application to the archaeological record. The theoretical underpinnings of the archaeological implications derived from this model are laid out in Chapter 3. Chapter 4 describes the faunal assemblages from Saint-Césaire used to test the Neandertal replacement model. In addition to problems related to identification biases, a detailed taphonomic study of these assemblages is provided in Chapter 5. The biological cycle of the major species identified at Saint-Césaire is summarized in Chapter 6 and their skeletal correlates are examined in order to determine seasonality of prey procurement. Evidence of resource depression is investigated in the Saint-Césaire occupations in Chapter 7. This set of data is then compared with two other sequences documenting the Middle to Upper Paleolithic transition (Chapter 8). Lastly, in the final chapter, the results are discussed in the perspective of current debates about late Pleistocene population interaction in Western Europe.

CHAPTER 2

THE REPLACEMENT MODEL AND ITS HISTORICAL ROOTS

The Middle to Upper Paleolithic transition (roughly between 40,000 and 32,000 BP) represents a critical period in modern human origins in Western Europe. Important biological and cultural changes are recorded during this short time period. Most notable are the emergence and spread of art and elaborated bone technology, the widespread diffusion of laminar reduction sequences, the diversification of stone tool morphology, and the increase of raw material transfers (Gamble 1999; Mellars 1996; White 1982; Kozlowski 1990; Féblot-Augustins 1993). Although the evidence of cultural change is not generally questioned, the skeletal evidence is more ambiguous and hinges on the way in which the disappearance of archaic skeletal features is interpreted.

In general, Neandertals exhibit a number of archaic features, for instance, postcranial robusticity, the lack of chin, large frontal sinuses, arched brow-ridges, taurodontism, and expanded anterior loading. In addition, this population tends to show a combination of derived features: a retromolar space, occipital bunning, hyperarctic body proportions, short and wide phalanges, a dorsal axillary groove on the scapula, and a particular morphology of the occipitomastoid and pubic areas, which despite their respective variation would distinguish them from modern humans (Trinkaus 1986; Rak 1990). Differences in growth patterns between Neandertals and modern humans have also been suggested (Churchill 1998).

It is often argued that this set of biological traits disappeared from Eurasia at the onset of the Early Upper Paleolithic as a consequence of the replacement of the Neandertals by modern humans (Stringer and Andrews 1988; Mellars 1989a, 1996; Demars and Hublin 1989; D'Errico *et al.* 1998; Bar-Yosef 2002). The question then is, how can these changes be interpreted? Under what circumstances were they induced? How different were the Neandertals and the early modern humans? Did the Neandertals really go extinct? If yes, what selective advantages were possessed by the incoming modern humans? More specifically, this study will address the following related issue: *was there a demic expansion of modern humans into Western Europe during the Middle to Upper Paleolithic transition as commonly argued?*

Two models, based primarily on biological evidence, have emerged in the last two decades in an attempt to address the problem of the origins of modern humans. The "Neandertal Replacement Model" or "Late Pleistocene Out-of-Africa Model," states that a new biological species emerged in Africa at least by 150,000 BP (White *et al.* 2003), and spread into Europe to replace the Neandertals (Stringer and Gamble 1993; Klein 2003; Stringer and Andrews 1988; Vandermeersch 1989; Kozlowski 2000; Demars and Hublin 1989). For the sake of clarity, this model will be referred to as the *Neandertal Replacement model* or, simply, the *replacement model* throughout the text.

In reaction, a second model, known as the "Multiregional model," has been put forward by Wolpoff, Thorne, and others (Thorne and Wolpoff 1981; Wolpoff 1999). This model, reviewed in greater detail below, argues for cultural continuity and gene flow between regional populations during most of the Pleistocene.

These questions have puzzled generations of scholars and have generated innumerable books and papers, which have appeared at an exponential rate in the last two decades. It is not the purpose of this analysis to review all the contributions made. Instead, the study of several key propositions will lay out some of the main problems relative to the interpretation of the transition from the Middle to Upper Paleolithic and suggest possible avenues for resolving the debate. An emphasis is put on the Châtelperronian and the Early Aurignacian, two archaeological complexes that are directly relevant to the sites and questions at the core of this study. The historical roots of the replacement model and its development during the twentieth century are also discussed in detail, as it might be productive to pinpoint the bases of some of the assumptions underlying this model. However, it is worth stressing that this historical review is not exhaustive, nor does it emphasize all the nuances of the many perspectives and arguments discussed below. Nonetheless, this overview provides what appears to be a useful representation of the intellectual context from which the replacement model emerged.

The discovery of the deep time of human evolution

The simultaneous publication by Darwin and Wallace (Darwin and Wallace 1859; Darwin 1859) of the theory of natural selection created seismic reactions in England (Ruse 1979). For the first time in the history of science, divine intervention was no longer necessary to explain species diversity. For this reason, the theory of evolution by means of natural selection was very much disputed (Bowler 1983). A vital element in the elaboration of the theory of natural selection was the idea of the “deep time” of the earth put forward by Lyell (Ruse 1979). The same year that *On the Origin of Species* appeared, 1859, a commission of renowned English scientists confirmed the association of human tools with extinct fauna at Abbeville, accepting by this very fact, the notion of an “antediluvian man” long defended by Boucher de Perthes. These synchronous efforts contributed to extend the idea of deep time to humans, implicit in Darwin’s book (e.g., Huxley 1863; Haeckel 1877). The same year, Broca founded the *Société d’Anthropologie de Paris*, a forum for debates on human diversity and origins. These three ingredients set the pace for the investigation of the origins of modern humans.

In its early development, Paleolithic archaeology played essentially the double role of documenting “cultures” and building chronologies, using paleontology and geology as templates (Lartet and Christy 1865-1875; de Mortillet 1883, 1903). Gabriel de Mortillet (1883) systematized the use of artifacts as index fossils. This proposed classification contributed to the establishment of a relatively robust chronology for the Paleolithic that represented a notable improvement over the not-so-strongly patterned faunal chronology of Lartet and Christy (1865-1875). Following the impetus of these scholars, a long tradition of research was launched in France, which produced a very detailed chronology, especially fine-tuned for the Upper Paleolithic.

Early excavations sometimes led to the discovery of human skeletal remains, many of which are now interpreted as Neandertals. These remains, at the time studied by paleontologists and doctors, created much excitement due to the strangeness of some of the forms uncovered. However, the training of these professionals was not perfectly suited to address the variability uncovered. Specialists were clearly needed. Inspired by scholars like Schaaffhausen, Broca, de Quatrefages, Huxley, and Dubois, biological anthropology developed as a discipline to make sense of these skeletal remains by specifying their affinities with living humans.

Small sample size and uncertainties in chronological attribution restricted the reach of early interpretations about the evolution of modern humans. At the beginning of the twentieth century, after several decades of excavations, the number of human remains attributed with any degree of certainty to the Paleolithic was very small and the chronology of several important technocomplexes was still extremely sketchy.

Some of these early finds are especially noteworthy. In 1908 and 1909, the discovery of several Neandertal burials associated with Mousterian artifacts at Le Moustier, La Ferrassie, La Chapelle-aux-Saints, and, a few years later, at La Quina, secured the status of the Neandertals as a past hominid population (Boule 1923). These were not the first Neandertals found, however, given that remains of this taxon were previously noted at Engis (1828), Gibraltar (1848), La Naulette (1866), Spy (1886), Krapina (1899-1905), and more importantly, at Feldhofer Cave (1856) in the Neander valley (Boule 1923; Smith 1982). The skeletal remains found at Feldhofer Cave are of paramount importance, as these established for the first time that an archaic form of hominid, presented as a "missing link" between humans and primates, existed in the past (e.g., Huxley 1863).

The uncovering, in 1868, of several burials by road workers at a locality known as "Cro-Magnon" has also been of great importance, as it projected the ancestry of *living* humans into a relatively far past. Louis Lartet (1868), not to be confused with his father Edouard, demonstrated that the Cro-Magnon remains were Paleolithic in age. Sonneville-

Bordes (1959), and Bouchud (1965), refined the chronology of the findings and attributed them to the Aurignacian. However, these remains are now probably associated with the Early Gravettian as suggested by an AMS date of 27,680 ± 270 on a *Littorina* shell associated with the burials (Henry-Gambier 2002). The excavation of several modern human burials near Menton (Verneau 1907; Cartailhac 1907) followed the discovery of the Cro-Magnon remains. In 1881-1882, a large sample of early modern humans, possibly associated with an Early Aurignacian, was uncovered at Mladec (Moravia). Additional human remains were also found in 1903-1904. In the same region, three early modern human burials were excavated at Brno between 1885 and 1927. One of the skeletons was apparently found with an Aurignacian-like industry, whereas the other two were presumably affiliated with the Pavlovian (Jelínek 1969; Smith 1982).

Another find made in 1909, this time at Roc de Combe-Capelle, attracted much interest. The skeletal remains unearthed at this site were supposed to be associated with a Châtelperronian assemblage and considered to be the earliest evidence of modern human presence in the early Upper Paleolithic of Western Europe (Klaatsch and Hauser 1910). These remains, discovered by Otto Hauser, were published as a member of the species *Homo aurignacensis hauseri*. With few exceptions (Sonneville-Bordes 1958, Bordes 1981), the crude stratigraphic descriptions, combined with the bad reputation of Hauser in France, partially motivated by political and nationalistic issues (see Boule 1923:189-190 for an example), raised strong doubts, especially among archaeologists, about its attribution to the Châtelperronian and relevance to the question of modern human origins (Henri-Martin 1961; Leroi-Gourhan 1965; Delporte 1970; Lévêque and Vandermeersch 1980, 1981; Vandermeersch 1984, see comments after Thoma 1978). The skull, thought to have been partially destroyed during the Second World War (Harrold 1981), was recently rediscovered at the Berlin Museum (Hoffman and Wegner 2002).

Early hypotheses on modern human origins

G. de Mortillet was a free spirit and an extremely opinionated person (Pautrat 1993). His aim in studying human evolution was to counter religious dogmas and old prejudices in order to build a new science (de Mortillet 1883). As an anticlerical positivist strongly committed to the idea of evolution, de Mortillet applied his *a priori* conception of biological and cultural changes to the archaeological records. Two themes are prevalent in his work: evolution is *gradual* and composed of several minute steps, grading from the crudest to the finest archaeological assemblages, and is driven by an internal stride toward *progress* (Pautrat 1993). However, his linear evolutionary scheme was somewhat inflexible. Despite this attitude, de Mortillet's contribution has been fundamental to the development of Paleolithic research.

For de Mortillet, the human path followed a slow, gradual evolution. Talking specifically about the Neandertals, he (1883:249; translation by the author) claimed that "the Neandertal race was not directly replaced by another race that came fully constituted to take its place. It evolved locally little by little." Neandertals were also inferred to have developed into Cro-Magnons: "Our first human type is the Neandertal type. This type, essentially autochthonous, slowly modified itself and evolved during the Quaternary into Cro-Magnons" (de Mortillet 1883:628; translation by the author). This proposition, one of the first to emphasize continuity between Neandertals and modern humans, was to be severely challenged by a young Parisian scholar: Marcellin Boule.

Somewhat forgotten today, Marcellin Boule was a key figure that is closely associated with the emergence of paleoanthropology as a discipline. Boule provided the first modern interpretation of Neandertal biology. Contrary to de Mortillet who attributed the Neandertals to the early Pleistocene, Boule showed that they belong to a distinct species, thought to be characteristic of the Middle Pleistocene:

> the cranium from La Chapelle-aux-Saints shows all the characters, sometimes exaggerated, of the skullcaps of Neandertal and Spy, which means that these different osseous pieces, found at distant locations in Western Europe, but from identical or very close geological levels, certainly belong to a single morphological type (Boule 1908:524; translation by the author).

Today, virtually all scholars consider the Neandertals to be the only hominid taxon present in the Mousterian of Europe (e.g., Vandermeersch 1989; Hublin 1988). This conviction, however, was far from being the mainstream opinion for most of the twentieth century. Boule advanced the hypothesis, possibly against de Mortillet, of the existence of a *Pre-sapiens* phylum during the Middle Pleistocene of this region. This Pre-sapiens phylum was thought to have given rise to the Cro-Magnons, while the phylum represented by the Neandertals was said to be an evolutionary dead-end. Because of the very wide influence that Boule formerly had, it is of interest to examine closely his claims.

In a monograph written in collaboration with Piveteau, Boule described the cultural and cognitive capacities of the Neandertals:

> The simplicity and uniformity of his lithic toolkits and the probable absence of any esthetic or moral preoccupation is in agreement with the brutal aspect of this heavy and vigorous body, of this osseous head with robust jaws of bestial aspect in which are still expressed the predominance of purely vegetative functions over cerebral functions. He probably only had a rudimentary language.
>
> *Homo Neanderthalensis* differs from all actual humans, even the most inferior ones; he represents an extinct species, characterizing a true degree in the evolution of human form. Perhaps evolving from *Homo Heidelbergensis*, he cannot be seen as an ancestor of *Homo sapiens*, of which he was the contemporary. It is an archaic species in the Mousterian period that appears to be a less evolved type compared to the direct ancestors of *Homo sapiens*; he was, compared to them, what are today the so-called inferior races in relation to the superior ones (Boule and Piveteau 1935:839; translation by the author).

Interestingly enough, these claims are not very different from Boule's earlier statements (e.g., Boule 1908:525, 1923:240), which suggests that his opinions did not change much over his career concerning these issues.

Boule also studied the skeletal remains of Cro-Magnon. In doing so, he followed Paul Broca (1868) who brilliantly analyzed these skeletons. Boule affirmed that the Cro-Magnons belonged to a single species composed of a number of sub-populations. With them, asserts Boule (1923:250), the biological evolution of humans is put to an end, which shifts, according to him, the study of modern human origins from the zoological to the anthropological and ethnographic spheres.

The “Cro-Magnon race” was considered by Boule and his contemporaries to represent the type population for early modern humans. Other populations were also described. Verneau (1913) studied human bones from the Grimaldi caves (Italy) near Menton where several Upper Paleolithic burials were found. Based on the observation of “Negroid” features on some of the remains, he suggested the existence of a distinct early modern human group called the “Grimaldi race.” Additionally, a third group, the “Chancelade race,” was proposed, based on a skeleton found in a Magdalenian context. This population, thought to be characterized, like the Neandertals, by a prehensile toe, was presumed to be related to modern Eskimos (Boule 1923). Importantly, the Grimaldi group, the earliest modern human population according to Boule, was inferred to have migrated from Africa to Europe (Boule 1923). It is also important to take note that the same author considered the individuals of Predmost and Brno to be Cro-Magnon variants. In spite of this diversity, all of these individuals were said to belong to a single homogeneous species.

Some of Boule’s interpretations raise scorn today. However, Boule was highly respected at his time, and well-established contemporaries and successors (e.g., Keith; Verneau; McCown; Howells) adopted several of his claims without much discussion. Yet, why did Boule adopt such an unenthusiastic view about the Neandertals? Part of it seems to be a reaction against the *in situ* evolutionary scheme of G. de Mortillet: “the history of the first human groups cannot have the aspect of a continuous and steady evolution, rather, it is constituted of the intermittent contributions of successive migrations of distant provenience, from the huge Asian and African territories about which we have only rare and vague information.” (Boule 1923:*X*; translation by the author). There are many reasons to believe that H. Breuil (discussed below) played a considerable role in Boule's adoption of this assumption.

The Piltdown hoax also reinforced Boule's negative attitude about the evolutionary role of Neandertals. The Piltdown skull, "found" in England, was composed of a cranium of modern appearance associated with a simian mandible, a mixture of traits often thought to represent an early stage of human evolution.

Although he questioned the association between the jaw and the skull, Boule accepted in his early papers the authenticity and old age of the skullcap and attributed it to an early form of modern human. In this perspective, he advanced the view that modern humans were of great antiquity, possibly of Pliocene or Miocene age: "A day will come where we will discover, in a terrain much older than Piltdown, a hominid of short height, with an almost erect posture, and a cerebral case relatively really large compared to its total body volume, but inferior in absolute terms to those of modern hominids" (Boule 1923:176; translation by the author; see also Boule 1908:525). In 1953, Oakley and his collaborators, however, showed that these remains, supposedly found in an early Pleistocene stratum were in fact the product of a forgery that falsely associated a recent human skull with an adolescent orangutan mandible (Oakley and Groves 1970; Gee 1996; Clermont 1992).

Because of this purported long chronology, the Neandertals and *Homo erectus* appeared to Boule geologically too young and too "primitive" to be ancestral forms of modern human. He therefore conjectured that they were evolutionary dead-ends. This position was sharpened by the belief that Neandertals coexisted with the presumably very different Cro-Magnons: "the Cro-Magnons, which seem to have suddenly replaced the

Neandertals in our country, had to exist somewhere before, except if we accept a mutation so important and so sudden that the idea becomes absurd (Boule 1923:245; translation by the author).” The idea of a coexistence of these populations was crucial to Boule’s argument. This assumption was possible because Boule (1908:525) collapsed, deliberately or not, the Neandertals and the Grimaldi group into a single time block, despite the fact that Cartailhac (1907) showed that the latter were associated with the Aurignacian (they are now known to be even younger, and are attributed by Mussi [1990] to the Gravettian or the Epigravettian). This misinterpretation of the archaeological sequence, later corrected (Boule 1923:276), was used by Boule to support the contention that the Neandertals were contemporaneous with early modern humans. In other words, with this interpretation, the Neandertals suddenly coexisted in Europe with modern humans.

In sum, Boule argued for a much longer evolutionary history for humans than the one suggested by the morphology of the Neandertals. This led him to downplay the anatomical and cultural features of this population. Brace (1964) has suggested that Boule was anti-evolutionary and has characterized him as a catastrophist, strongly influenced by Cuvier. A more satisfactory term would be that he was a transformist, but probably not a Darwinist (see Tort 1995 for nuances between these terms), as Boule made inferences about past hominid forms that are clearly evolutionary. In fact, Boule seems to have been more strongly influenced by Albert Gaudry, a well-known transformist who nevertheless believed in a divine power (Gaudant 1991), and by de Quatrefages and Hamy, rather than by Cuvier’s ideas. The reason why Boule rejected most fossils uncovered in his time as related to modern humans is that very few of them fitted the long chronology and the specific anatomical evolution that he envisioned. Boule was simply waiting for the unearthing of a different and older form of early modern human than the Neandertals.

It is interesting to note that, at the opposite end of the spectrum, Hrdlicka (1927) proposed that the Neandertals were the ancestors of modern humans. This proposition, however, did not raise much enthusiasm when it was first formulated (Brace 1964).

In 1939, McCown and Keith published a synthesis of the human remains from the Mount Carmel area (Israel), which had very important implications for the debate on modern human origins. These authors analyzed several Mousterian skeletons from the sites of Skhul and Tabun. The unsuspected variability uncovered within their sample led them to reject Hrdlicka's idea of a Neandertal stage of evolution:

> As our investigations proceeded we encountered so many characters which linked the Skhul to the Tabun type that we were ultimately obliged to presume that we had before us the remains of a single people, the Skhul and the Tabun types being but the extremes of the same series. Yet the range in form, from that represented by Skhul IV (male) to Tabun I (female), is unexpectedly great. The Tabun type possesses many features which link it to the Neanderthal type of Europe while the extreme Skhul type passes towards a Neanthropic form such as that found at Cromagnon (McCown and Keith 1939:13).

This continuum in skeletal characters was interpreted as an argument against the possibility of hybridization between two biologically distinct populations. In fact, instead of stressing diachronic continuity, as did Hrdlicka, McCown and Keith emphasized geographical continuity. Noting in Europe a geographical continuum between the French Neandertals to the west and the more modern-looking Neandertal forms to the east (e.g., Krapina), McCown and Keith argued for the existence of a similar continuum in Western Asia. For them, this geographical continuum was taken as a demonstration that the Mount Carmel population had been a transitional form of modern human for which the origins were to be found in Eastern Asia:

> Our belief is that at Mount Carmel we have reached a transitional zone which leads from one ancient area of racial differentiation (the Neanderthal or Palaeoanthropic) to another ancient area lying farther to the east, a Neanthropic area where the proto-Caucasian (or proto-Cromagnon) type of man was being evolved. The evidence is now convincing that in mid-Pleistocene times the inhabitants of Europe—of the continent at least—were all Neanderthal in type, but we have seen that the type becomes modified as we proceed from west to east and that in Palestine [the Mount Carmel area] we find a transitional type leading towards the Neanthropic type. It seems logical to us to assume that when the wide tracts of westerns Asia of mid-Pleistocene times are entered we shall find ourselves in the homeland of the proto-Caucasian. Eastern Asia we regard as the evolutionary cradle of the Proto-Mongols. Our theory therefore assumes that the Mount Carmel people *are not the actual* ancestors of the Cromagnons but Neanderthaloid collaterals or cousins of the ancestors of that type. We expect that the fossil remains of the *real* proto-Cromagnons will be discovered still farther to the east. (McCown and Keith 1939:17, emphasis added).

In their view, the fate of the Mount Carmel population was not too different from the one envisioned for the European Neandertals: a modern human form would have evolved in Eastern Asia and spread to the west replacing the European Neandertal and the Levantine “Neandertaloid” populations.

Breuil, Peyrony, Garrod, and large-scale migration models

The Châtelperronian was long thought to be one of the earliest cultural manifestations of modern humans. The first reference to the Châtelperronian as an early Upper Paleolithic episode was made by Henri Breuil (1907, 1911, 1913) after his visit to the Grotte des Fées located near the village of Châtelperron. With the help of Emile Cartailhac, Breuil classified the Châtelperronian as an early part of the Aurignacian in the so-called *bataille aurignacienne* that opposed him to Gabriel and Adrien de Mortillet (1903) who believed that the Aurignacian was more recent than the Solutrean based on its "progress" (see Breuil 1909, 1911, and Cartailhac 1907 for an overview of this debate). Breuil (1912) proposed a linear succession for the Early Upper Paleolithic starting with the Châtelperronian (Early Aurignacian in his terminology), followed by the Aurignacian (Middle Aurignacian), and the Gravettian (Late Aurignacian), a sequence now known to be correct (D'Errico *et al.* 1998).

Although his first papers stressed continuity (e.g., Breuil 1909), Breuil was convinced that large-scale migrations were the rule rather than the exception in the Paleolithic. Breuil and Lantier (1951:180), for instance, argued that the origin of the Châtelperronian was to be found in Asia Minor, an hypothesis also favored by Capitan (1922), while the Aurignacian was claimed to derive from the northern steppes of China. Another illustration of Breuil's search for migrations is his attempt to locate the origin of the Solutrean in North Africa, Eastern Europe (Hungary and the Balkans), and the Madrid area (Breuil and Lantier 1951). Clearly, there was little place for *in situ* evolution in Breuil's approach. For him, the Middle to Upper Paleolithic transition corresponded to "a substitution, probably violent, of the Paleanthropic humans by Neanthropic humans, completely destroyed by the visitors (…), the Neanthropes seem nowhere to have evolved from the known Paleoanthropes, neither in the race or civilization" (Breuil and Lantier 1951:161; translation by the author).

Although he adhered to this conceptual framework, Peyrony (1933, 1934, 1936, 1946) modified considerably Breuil's linear cultural sequence. Noting striking similarities between Châtelperron points and Gravette points, Peyrony (1933) suggested that the Châtelperronian (the Lower Perigordian in his terminology) evolved directly into the Gravettian (Upper Perigordian). This conclusion is important, as this industrial connection was believed to indicate that modern humans were the authors of the Châtelperronian. The Middle Perigordian (Perigordian II and III) was presumed to represent an intermediate step in this evolution. This Perigordian phylum was seen as distinct, but contemporaneous, with the Aurignacian phylum constituted of the Aurignacian I through V defined at La Ferrassie and Laugerie-Haute (Peyrony 1934). These findings gave rise to the hypothesis of *a partial parallelism* of the Perigordian and Aurignacian phyla and were interpreted to signal the coexistence of two different populations of modern humans in Western Europe. In the thirties, this proposition was not unreasonable given the arguments made by Boule and others on the inferred coexistence of several species and "races" of modern humans during the Early Upper Paleolithic.

Like Breuil (1912), Peyrony (1933) argued that the Aurignacians were oriental Cro-Magnon migrants. In contrast, the Châtelperronians were described as evolved Mousterians that "retreated" to some sites like Bos del Ser (southwestern France), following the arrival of the Cro-Magnons (Peyrony 1933:556). Peyrony associated the Châtelperronian with the anatomically modern Combe-Capelle group, which was thought to have supplanted the local Neandertal populations. Peyrony made interesting propositions about the similarities he observed between Châtelperronian and Aurignacian bone tools, which prompted him to ask whether "the men from La Ferrassie did not have contacts with the first Cro-Magnons who arrived in the Vézère valley, and whether these contacts would not have been a cause for the relatively rapid transformation of the toolkit" (Peyrony 1934:42; translation by the author).

D. Garrod also drew extensively on migrations to explain changes in archaeological industries in the Upper Paleolithic of Western Europe. She suggested that this region was a geographical dead-end in which waves of migrants ended their courses:

> the blade cultures, after all, have an immensely wide distribution, and it is unlikely that the key to their development is to be found in southern France. If we take more distant regions into account it becomes clear that the French sequence is the result of successive immigrations, superimposed, perhaps, on a certain amount of local variation and development in place (Garrod 1938:19).

Based on this assumption, she envisioned three different sources for the Châtelperronian: the Lower Capsian of North Africa, the Lower Kenyan Aurignacian, and the Early Upper Paleolithic of Palestine, but failed to find a center of origin. Garrod (1938:24) derived the Aurignacian, like most of her contemporaries, from a distinct oriental "stock."

Important advances were also being made in biological anthropology. While Bordes reassessed the complexity of the Mousterian (see below), C. Arambourg (1955) established that the Neandertals stood and walked upright like living humans, far different from the apish description proposed by Boule. Nonetheless, some old conceptions persisted. Vallois (1949, 1954), for instance, claimed that the skeletal remains from Fontéchevade, Swanscombe, and Steinheim were part of a modern human phylum that coexisted with Neandertals, in agreement with the Pre-Sapiens hypothesis defended by Boule and Bordes. All these remains, however, pre-date the classic Neandertals. In order to account for the chronological gap between these supposedly early modern humans and those of the Upper Paleolithic, Vallois hypothesized that modern humans were either few in number during the Mousterian, explaining their absence in the later Mousterian of Western Europe, or were occupying Asia. From there, where they were "pressed back" (Vallois 1954:18), modern humans would have migrated to Western Europe in the Early Upper Paleolithic.

With few exceptions, the propositions seen so far have stressed the extinction of the Neandertals. However, Hrdlicka found a strong ally in F. Weidenreich. Based on an inferred continuity in the skeletal material of Asia, Weidenreich asserted that all of the populations that lived after the appearance of *Homo erectus* were variants of a single species:

> I believe that all primate forms recognized as hominids–no matter whether they lived in the past or live today–represent morphologically a unity when compared with other primate forms, and that they can be regarded as *one specie*s. I arrived at this conclusion by an elaborated anatomical analysis of all particular features, from Pithecanthropus

> robustus up to modern man of today. *If all hominid types and their variations, regardless of time and space, are taken into consideration, their arrangement in a continuous evolutionary line, leading from the most primitive state to the most advanced, does not meet with any difficulty. Neither any gaps nor deviations are recognizable.* This statement holds good for the entire skeleton, in particular for skull and dentition, and concerns this part not only as a whole, but also their minor structures and special patterns (Weidenreich 1947:189; original emphasis).

Importantly, Weidenreich agreed with McCown and Keith (1939) that the fossil sample from the Levant is intermediate in form between Neandertals and early modern humans. The mechanism ensuring continuity is described:

> All this points to an already world-wide distribution of early phases which transmuted into more advanced types by vertical differentiation, while they split into geographical groups by horizontal differentiation. Both processes may have been accelerated or retarded at certain times and in certain places (…) One can speculate about their causes. They might have been due to general environmental conditions, yet the state of the population as regards its density or scarcity, migration, interbreeding and extermination certainly played a decisive role (Weidenreich 1947:202).

Although gene flow is not particularly emphasized in the text, except for occasional references to “crossing” and “interbreeding,” a figure on p. 201 of the same paper is explicit about its role in the evolution of modern humans. Clearly, Weidenreich’s reticulate model includes most of the ingredients and concepts of what will later become known as the “Multiregional” model (Wolpoff and Caspari 1996).

W. W. Howells, one of the strongest promoters of the "Pre-sapiens" hypothesis, defended a more traditional perspective. For him, the Neandertals represent a distinct species that evolved in relative isolation (Howells 1942, 1978). This population was said to be extinct, although it is stressed that Neandertals were culturally complex, which is a significant departure from Boule. The replacement of the Neandertals was attributed to a possible dispossession of game by modern humans supposed to have been "quicker and more athletic, if not necessarily more powerful" (Howells 1942:193). Several of these qualities, however, are now believed to better characterize the Neandertals (Trinkaus 1986).

Contrary to the preceding authors, F. C. Howell expressed strong doubts about the Pre-sapiens hypothesis. Using a functional approach, Howell explained the peculiarities of the Neandertal anatomy as reflecting the arctic conditions in which they lived and their relative isolation from neighboring populations:

> it is not inconceivable, and indeed appears highly probable, that isolation of western representatives of the early Neanderthal gradient for several tens of thousands of years in a rather limited area, and subjection to the rigors of an extreme arctic environment, would account for the appearance of the classic Neanderthal population. Under this environment, selection would be severe, chance for genetic drift at an optimum, and opportunities for migration reduced to a minimum. These multiple factors brought about a distinctive race of mankind occupying this area during Würm I (Howell 1951:407-409).

For Howell, the Late Pleistocene glaciers created a barrier that prevented gene flow between the classic Neandertals and their neighbors, leading the former to drift away from the *sapien*s line. More recently, this hypothesis has been redeveloped by Hublin (1988).

Despite Weidenreich's attempt to demonstrate population continuity through time, later studies generally agreed that early modern humans replaced the Neandertals and, perhaps, the archaic populations of Australasia (e.g., Howells 1976). This consensus was, however, to be seriously challenged. Echoing Howell, Brace (1964, 1979) attacked the Pre-sapiens hypothesis and stressed the incompleteness of the specimens. Also, he argued that the belief that the Neandertals were replaced due to a "specialized" morphology was unsupported and prejudiced. Instead, Brace suggested, following Hrdlicka (1927), a "Neandertal stage" of evolution, prelude to the emergence of modern humans. This proposition was important because it stressed regional continuity and functional adaptation, two ingredients that later became incorporated in the multiregional model. The evolutionary mechanism proposed by Brace for explaining the morphological changes observed between his evolutionary stages focuses on:

> changes in brain size are related to the supposed selective advantage conferred by cerebral increase, while progressive reduction of the dentition and hence the entire facial skeleton is related to the suspension of the advantage in possessing a large face which occurred as a result of increasingly effective cultural adaptation –particularly refinements in cutting tools in the latter part of human cultural and physical evolution (Brace 1964:19).

These polemic propositions were severely challenged (e.g., Le Gros Clark 1964; von Koenigswald 1964), although they have been well received and promoted by others (e.g., Coon 1964; Howell 1964; Brose and Wolpoff 1971). Afterward, the Pre-sapiens hypothesis began to lose ground, pressing former supporters to abandon this position (Howells 1978; Vandermeersch 1978). Indeed, as noted by Vandermeersch (1978), it was increasingly difficult to conclude that there has been a parallel and independent biological evolution of Neandertals and modern humans in Western Europe without admitting the possibility of hybridization.

The sixties also saw the publication of the first results from the excavations at the Grotte du Renne at Arcy-sur-Cure (Leroi-Gourhan 1958, 1965; Leroi-Gourhan and Leroi-Gourhan 1964; Movius 1969). Three Châtelperronian levels were uncovered at this site. Art items, bone tools, and hut features were all observed in these occupations, demonstrating what was then an unsuspected complexity for the Châtelperronian. Some human teeth were also found (Leroi-Gourhan 1958). These provided a lot of information at that time, given that they were the only human remains indubitably associated with a Châtelperronian assemblage. Leroi-Gourhan (1958, 1965) emphasized the archaic (Neandertal) character of these remains.

François Bordes, Peyrony's pupil, spent a considerable portion of his career working on the Mousterian facies. His contribution is extremely important because it pointed out the complexity of the stone tool industries made by the Neandertals. In addition, the suggestion he made that the Neandertals might have used ocher for body decoration forced his contemporaries to reappraise Neandertal cognitive abilities (Bordes 1952).

Bordes' general views on biological and cultural evolution in the late Pleistocene are especially clear in a volume that he edited after a symposium on human origins held in Paris (Bordes 1972a, 1972b). In his review of the papers, Bordes (1972b) concluded that modern humans and Neandertals coexisted, as did Mousterian and Upper Paleolithic industries. This was taken as an indication, largely based on the Levantine data, that no *a priori* link could be made between hominid types and industries, an important modification of his earlier thoughts on the subject (e.g., Bordes 1961). Furthermore, the evolution of modern humans is described as polycentric (it involved several regions) and characterized by strong heterochrony (modern human features evolved at different rates in different regions). According to Bordes (1972a), certain Neandertal populations evolved into modern humans, while others went extinct. For instance, the so-called "classical" Neandertals associated with the Quina, Ferrassie, Typical, and Denticulate facies of the French Mousterian were said to have been replaced. On the other hand, he suspected some hybridization to have occurred in the Middle East between Neandertals and modern humans, as suggested by the variability of the human remains from the Mount Carmel area.

Generally, Bordes stressed evidence for local evolution, thereby countering the hyper-diffusionism of Breuil and Garrod: "the 'elsewhere' from where the western Upper Paleolithic groups would have come decreases steadily with the accumulation of recent discoveries. Of course, we also observe in Asia a shift from the Middle to the Upper Paleolithic, but this Upper Paleolithic is not ours and could not, in general, be seen as its ancestor" (Bordes 1984:218; translation by the author).

Yet Bordes was also a diffusionist, even though he used this concept far more parsimoniously and on a much smaller scale than his predecessors did. For instance, he and his wife, Denise de Sonneville-Bordes, borrowed from Peyrony the hypothesis that the Châtelperronian and the Aurignacian were contemporaneous. The discovery of purported inter-stratification of these technocomplexes at Le Piage (Champagne and Espitalié 1967), Roc de Combe (Bordes and Labrot 1967), and Cueva de El Pendo (Bordes 1984), greatly contributed to the popularization of this interpretation.

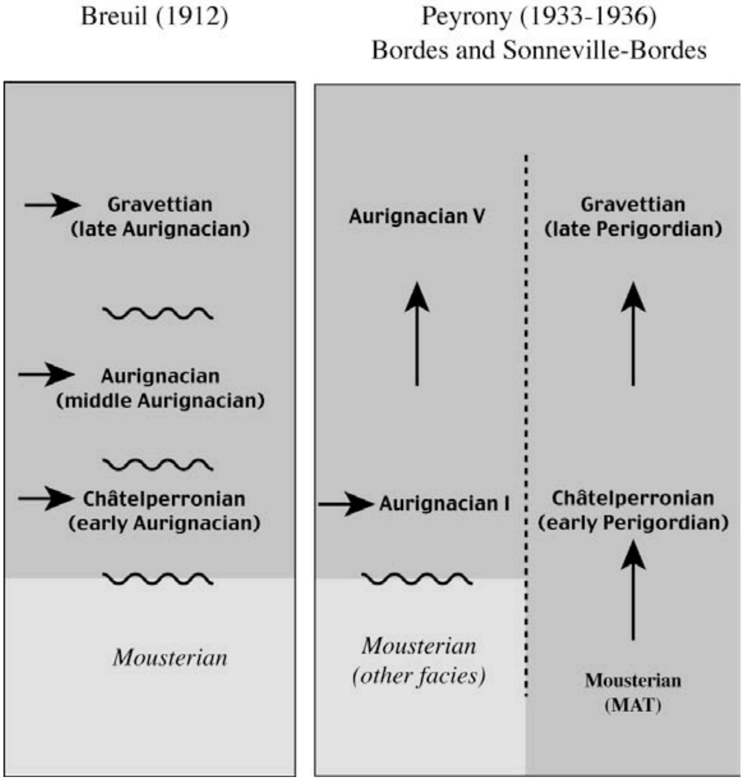

Figure 1. Simplified representation of the evolution of the interpretation of the Middle to Upper Paleolithic transition by Breuil, Peyrony, and Bordes and Sonneville-Bordes. Horizontal arrows indicate migration. Vertical arrows denote filiation. Waves represent replacement events.

Like Peyrony, Bordes (1961, 1981, 1984) stressed that the Châtelperronian was produced by modern humans, based on the "complexity" of its industry and the skeletal material found at Roc de Combe-Capelle. Because he believed that the Mousterian of Acheulean Tradition was the forerunner of the Châtelperronian, Bordes contended that *both* industries were made by modern humans. As a result, Bordes (1961:808) urged physical anthropologists to adopt the Pre-sapiens hypothesis, as this cultural connection meant to him that modern humans were already present in Western Europe before the beginning of the Upper Paleolithic. The development of Peyrony's and Bordes' ideas is summarized in Figure 1 and compared with the interpretations put forward by Breuil.

For more than five decades, the only significant modification to the partial parallelism hypothesis of Peyrony was the suppression of the Middle Perigordian by Sonneville-Bordes (1955, 1958). Indeed, Peyrony's Perigordian II was found to be Aurignacian and is now referred to as the Aurignacian 0 (on this issue, see Bordes 2000, 2002, 2003). In addition, the Perigordian III was shown to postdate the Perigordian V, and, therefore, to be more recent than suggested by Peyrony (see discussion in Harrold 1981). Although Peyrony appeared to have change his opinion about some of these issues in his last papers (Bordes 1984), Bordes adhered to the view that two modern human phyla, a Perigordian and an Aurignacian ones, coexisted in the Early Upper Paleolithic of France.

Following Breuil and Boule, Bordes (1972a:215) asserted, with little supporting evidence, that the Aurignacian emerged in Western Asia or Eastern Europe from a non-specialized form of Neandertal. In his view, the Aurignacians, the "oriental" modern humans, migrated to France with a "well-developed culture" and replaced the "occidental" modern humans associated with the MAT and the Châtelperronian (Bordes 1961:808). However, Bordes failed to locate the geographical source of this migration. Aurignacians were believed to be immigrants because "in contrast to the Perigordians, it does not seem possible to see the Aurignacians as natives" (Bordes and Labrot 1967:27, translation by the author).

More theoretically oriented, Laplace (1966, 1970) suggested that the Aurignacian was the result of the evolution of an undifferentiated *synthétotype* in the "sub-evolved" Châtelperronian. For Laplace, the beginning of the Early Upper Paleolithic was characterized by a "basal polymorphism," which coincided with a notable acceleration in the rate of change. Division within this synthétotype resulted in considerable variability, which he said fueled the parallel development of the Châtelperronian and the Aurignacian. Laplace (1970) claimed that the Middle to Upper Paleolithic transition was triggered by the invention of the blade concept. In this perspective, he suggested that climatic oscillations "probably played a significant role in the onset of the leptolithic [laminar] mutation" (Laplace1970:159; translation by the author). This conceptual framework was, however, severely criticized by Bordes (1963).

Some years later, S. Binford (1972) attempted to explain the Châtelperronian phenomenon. Inspired by the "functional" argument proposed for the Mousterian (Binford and Binford 1966), she suggested that the Châtelperronian was a variant of the Aurignacian. A similar argument was later made by Ashton (1983). Because of numerous problems, however, these propositions met with very little success.

In 1969, J. Jelínek published an important synthesis on the skeletal material of Central and Eastern Europe. His study led him to conclude that the Balkan Neandertals displayed considerable morphological variability. Based on this observation, he argued that the Neandertals represented a variant of modern humans, *Homo sapiens neandertalensis*. These conclusions are important in the debate as they were seen as providing support to the hypothesis of regional continuity:

> the appearance of *H. sapiens sapiens* in Central and Eastern Europe (and perhaps in other regions as well, as future finds may show) need not be explained in terms of a sudden migration from East to West, but rather in terms of local evolution in populations having basic morphological characteristics in common but differing in the intensity and frequency of others—a situation that would have permitted relatively rapid morphological change (Jelínek 1969:492).

It is worth noting that Jelínek (1969:499) extended these conclusions to the classical Neandertals of Western Europe.

Vlcek (1970) adhered to the hypothesis that two distinct hominid types occupied Europe in the Early Upper Paleolithic. According to this author, remains from Cro-Magnon, Mladec and the Grotte des Enfants (one of the Grimaldi caves) typify the first group, the Cro-Magnons. This population is distinguished from a second taxon, the Brno group, characterized by the skeletal remains of Brno 2, Sivtavka, and Combe-Capelle. These groups were not considered "closed," however, as Vlcek suggested that gene flow between them could be detected in the polytypic population of Predmostí. Importantly, like Jelínek, Vlcek argued that the modern human Brno type evolved locally from Neandertals, based on evidence of transitional forms at Krapina and other Central European sites.

These hominid taxa were sometimes criticized as being arbitrary. Riquet (1970) rejected this argument, arguing that the anatomical differences observed between Neandertals and modern humans are too significant to be explained by sampling or by an arbitrary subdivision of a polytypic population. In opposition, Patte (1955, 1959) believed that there was no clear genetic barrier between the two populations and suggested that some Neandertal genes were passed down to early modern humans. A similar conclusion was reached by Genet-Varcin (1970, 1978).

The publication by Vandermeersch (1981) of a large number of human remains from Qafzeh (Israel) contributed significantly to the debate. The human remains uncovered at this site are morphologically similar to the specimens from Skhul (McKown and Keith 1939). In general, these have been described as showing affinities with the Cro-Magnons (Howells 1959; Vandermeersch 1978). Generally thought to date to the end of the Mousterian (Brace 1964; Brose and Wolpoff 1971; Jelinek 1982; Trinkaus 1986), the Qafzeh remains were suspected by others to have a much older age (Vandermeersch 1981). This suspicion has been confirmed by dates in the 90-120 ky range (Valladas *et al.* 1988; Bar-Yosef 1988). The great antiquity of these early modern humans had very important repercussions, as these were in total contradiction with the expectations of the gradualist model promoted by Hrdlicka (1927), Brace (1964), Brose and Wolpoff (1971), Jelinek (1982), and Trinkaus (1986). Indeed, according to this new chronology, the early modern humans from Skhul and Qafzeh would have been more or less contemporaneous with the Neandertal of Tabun level C. More problematic is the fact that these early modern humans would be considerably older than the Neandertal from Kebara dated at ca. 60 ky (Schwarcz *et al.* 1989). The presence of Neandertals in the late Mousterian of the Levant has also been confirmed at Amud (Valladas *et al.* 1999). While multiregionalists now explain these patterns by a center-and-edge effect (Thorne and Wolpoff 1981; Wolpoff 1999), proponents of the replacement model argue for territorial changes between Neandertals and modern humans (Lieberman and Shea 1994; Shea

1998). The reality of these taxonomic categories in the Levant have, however, been recently challenged (Arensburg and Belfer-Cohen 1998).

New hypotheses on a Neandertal replacement

The Saint-Césaire discovery as a paradigm shift

While some important late Pleistocene skeletal remains were excavated in the last decades in Central Europe (Vindija), the Levant (Qafzeh, Kebara), Australia (Lake Mungo), and Africa (Klasies River Mouth, Herto), few new important late Pleistocene human remains have been found in Western Europe during the same time period. However, there are some notable exceptions. In July 1979, a Neandertal skeleton associated with a Châtelperronian industry was uncovered at Saint-Césaire, suggesting that the former is the author of the assemblage (Lévêque and Vandermeersch 1980; Vandermeersch 1984). Although Lévêque and Vandermeersch argued that the association of the skeleton with the assemblage was clear and unambiguous, these claims were severely attacked by F. Bordes (1981) who was rather inclined, as we have seen, to attribute this industry to modern humans. Bordes argued, among other things, that the Neandertal found at Saint-Césaire might have been brought to the site as a prey. He also stressed the possibility that the remains belonged to an “atavistic” individual (a modern human individual marked by the “resurgence” or archaic characters). The association found at Saint-Césaire was thought to have been confirmed by a Neandertal temporal bone found in the Châtelperronian of Grotte du Renne at Arcy-sur-Cure (Hublin *et al.*

1996). However, recent work has raised problems concerning its stratigraphic provenience (Connet 2002).

In this respect, Saint-Césaire can be viewed as having caused a paradigm shift. This is because this discovery changed the identity of the first modern humans in Western Europe, from Châtelperronians to Early Aurignacians, therefore forcing a reappraisal of the cognitive abilities and complexity of these respective populations.

On one hand, the Saint-Césaire discovery supported replacement hypotheses, as a single population, a more parsimonious explanation, was presumed to have lived in Western Europe before the Upper Paleolithic, a scheme that shows a better fit with the data than the tenuous Pre-sapiens hypothesis supported by Boule, Bordes, Howells, and Vallois. More importantly, it made the hypothesis of a smooth anatomical evolution between the Middle and the Upper Paleolithic more difficult to support in this region (Smith 1982; Vandermeersch 1984).

On the other hand, the Saint-Césaire find had a very important drawback for the promoters of the replacement model. It was not too difficult before the discovery of the Saint-Césaire Neandertal burial to highlight behavioral differences between the Middle Paleolithic and the Upper Paleolithic, which were presumed to have been made by, respectively, Neandertals and modern humans. For instance, the presence of art and the spread of laminar reduction sequences were generally directly associated with the modern human expansion. After the Saint-Césaire discovery, however, it became considerably more difficult to argue for major cultural changes between the Châtelperronian and the Early Aurignacian, as these show a similar range of cultural features with respect to lithic, bone tool production, and symbolic expression, and to envision that these changes coincided with a biological shift towards "modern" features. For most, the reaction was simply to stress, implicitly or explicitly, that the Châtelperronian Neandertals were not as culturally complex as the early modern humans (e.g., Stringer and Gamble 1993; Bar-Yosef 1994; Demars and Hublin 1989; Mellars 1989a, 1996, 1999; White 2002).

Besides refuting the notion that modern humans produced the Châtelperronian, Saint-Césaire improved our understanding of space-time systematics for the Early Upper Paleolithic. Up to the eighties, the hypothesis of a partial parallelism between the Perigordian and the Aurignacian was embraced almost universally (e.g., Pradel 1966; Laville *et al.* 1980; Harrold 1981), even though it had been criticized by Garrod (1938), Lynch (1966), Laplace (1970), and S. Binford (1972). We now know that the similarities noted by Peyrony between the Châtelperronian and the Gravettian, the beginning and the end of his Perigordian phylum, are most simply explained by convergence. The association of Neandertals with the Châtelperronian did not fit well conceptually with the partial parallelism hypothesis, as this model assumes that the Perigordian and the Aurignacian phyla were both produced by *modern* humans. In other words, if we follow the logic of Peyrony and Bordes, Saint-Césaire would imply that the Neandertals were the authors of the Gravettian! This is because the Châtelperronian is said to be the "root" of the Perigordian phylum, which ended with the Gravettian. This problem, in addition to the numerous radiometric dates for the Abri Pataud sequence, which showed a gap of several millennia between the beginning and the end of the Perigordian phylum, and the lack of transitional industries between the Châtelperronian and the Gravettian, led most scholars, including de Sonneville-Bordes (1989), to abandon the partial parallelism hypothesis.

The eighties and the re-formulation of replacement and continuity hypotheses

As we have seen, the Neandertal replacement model has a long history in paleoanthropology. First proposed by Boule and Breuil, replacement hypotheses were extremely influential during the first half of the twentieth century. After a relative eclipse from the sixties to the early eighties, which corresponded to the popularity of gradualist models of human evolution (e.g., Brace 1964; Brose and Wolpoff 1971), the replacement model is now more popular than ever (Stringer 1974, 1989; Stringer and Gamble 1993; Hublin 1988; Demars 1996; Mellars 1996; Van Peer 1998; Gamble 1999). Clearly, the renewed popularity of this model has been strongly influenced by the emergence of mtDNA studies (reviewed in the next section).

Based on a synthesis of the skeletal, genetic, and archaeological evidence then available, Stringer and Andrews (1988) concluded that there is a relatively recent common ancestral population for modern humans. According to them, Europe and Australasia show sharp anatomical discontinuities between archaic populations and early modern humans. In this perspective, it is asserted that early modern humans arose in Africa, perhaps as early as 150 kya ago (White *et al.* 2003), and then spread to Eurasia to replace the local populations. Importantly, population replacement is presumed in this model to have been complete and without significant interbreeding. The empirical predictions of the replacement hypothesis are explicitly presented:

> The model of a recent African origin, on the contrary, predicts different patterns of variation comparing African populations and those from elsewhere. Variation should be greatest within African populations (based on their earlier divergence, and assuming predominantly neutral genetic change), and they should be sharply distinguished in gene frequencies from non-African populations. Transitional fossils would not occur outside the African area of origin, and population replacement would represent the mode of establishment of *Homo sapiens* in other areas. The earliest record of *Homo sapiens* fossils should occur in the continent of origin of the species (Africa), and the youngest records at the peripheries of the radiation. Population relationships in Europe, Asia, and Australasia would approximate those of the Holocene only in the later Pleistocene (Stringer and Andrews 1988:1264).

Stringer and Andrews interpret the fact that archaeological "colonization" events coincide with molecular divergence dates as strong support for this scenario. Furthermore, these authors argued that the presence of derived features in Neandertals, especially arctic body proportions, is an indication of their replacement (early modern humans tend to be characterized by more tropical body proportions). Nonetheless, it is important to emphasize that the lack of anatomical continuity in Western Europe and the inferred cultural and behavioral discontinuities between the Châtelperronian and the Aurignacian are considered by most as the best line of evidence supporting the replacement model.

Stringer and Andrews (1988) defined modern humans as having a gracile skeleton, and a relatively voluminous, short, high, and domed cranium. The supraorbital torus and external cranial buttressing are reduced considerably, if not absent, the dentition and supporting architecture are also reduced, the face is orthognathous, and a mental eminence is present on the mandible. To this list, can be added tropical body proportions and changes in hand and foot morphology (Trinkaus 1986). The definition presented by Stringer and Andrew has, however, been severely criticized, as it would exclude living Australian aborigines from modern humans (Wolpoff 1999).

Dissatisfied by this understanding of human variation, a "Multiregional Model" was proposed in reaction to these propositions (Thorne and Wolpoff 1981, Smith 1982; Wolpoff *et al.* 1984; Wolpoff 1989, 1999; Frayer *et al.* 1993; Wolpoff and Caspari 1996). Gene flow is seen in this model as the principal mechanism that contributed to the maintenance of unity between African and Eurasian populations throughout the middle and late Pleistocene:

> Multiregional Model posits that humans evolved as an interconnected polytypic species from a single origin in Africa some 2 myr ago. The small population effects during initial colonizations as humans expanded out of Africa helped establish regional differences, some of which were subsequently maintained through isolation-by-distance and adaptive variation. Advantageous changes spread widely because of genic exchanges across the interconnected network of populations (Wolpoff 1999:543).

For many, this model has received its strongest support from Central Europe and Asia. Building on the work of Jelínek (1969), Smith (1982) highlighted evidence for phenetic continuity in Central Europe based on specimens from Mladec, Vindija, Brno, and Predmosti. Furthermore, this author noted that few regions seem to exhibit clade features. However, Smith *et al.* (1989) also argued that modern humans emerged first in Africa but contended that there is little evidence for replacement. Therefore, the spread of anatomical features from Africa to Europe and Australasia is said not to result from a modern human radiation, but is rather explained by an “assimilation model, since it involves assimilation of new elements into existing gene pools or, in some cases perhaps, old elements into new gene pools” (Smith *et al.* 1989:62).

Tropical body proportions are often cited as one of the best lines of evidence in support of the replacement model. However, Frayer *et al.* (1993) have pointed out that the Bergman-Allen rule should have prevailed in Western Europe, and individuals with tropical body proportions should have been selected out in the course of the Upper Paleolithic. On the other hand, the multiregional model provides no convincing explanation for these unexpected body proportions. Whatever scenario is adopted, these body proportions cannot be satisfactorily explained with the above models.

To explain the anatomical peculiarities of the Neandertals, Trinkaus (1986) has emphasized functional adaptation and pointed out that the Neandertals would have been very powerful and robust, which he interpreted as a biological compensation for a technology that was not as efficient as the one used by modern humans. These assertions were used as arguments supporting the replacement model (see also Klein 2003). However, these conclusions seem contradicted by the fact that early modern humans are also relatively robust (Vandermeersch 1981). Moreover, modern humans and Neandertals made comparably complex toolkits in the Middle Paleolithic of the Levant (Jelinek 1990; Bar-Yosef and Meignen 1992), an observation that may undermine Trinkaus’ proposition. In addition, the link between toolkit complexity, efficiency, and skeletal robusticity is far from clear.

In addition to these propositions, a “Hybridization Model” has been promoted by some (Braüer 1981, 1989; Trinkaus 1986; Trinkaus *et al.* 2003; Duarte *et al.* 1999;

Eswaran 2002), which emphasizes that gene flow might have been possible between archaic populations and modern human migrants. The discovery of "hybrid" specimens in Portugal and Romania has been presented as evidence for admixture between Neandertals and modern humans (Duarte *et al.* 1999; Trinkaus *et al.* 2003).

The hybridization model should not be interpreted as a variant of the multiregional model, even though these positions only vary with respect to the *amount* of gene flow inferred to have occurred between archaic *sapiens* and modern humans and the degree of isolation said to have characterized the former population. In fact, most hybridization scenarios depart in a very fundamental way from the multiregional model and, for this reason, should not be included with it; they assume, contrary to the continuity hypothesis, that there has been a large-scale modern human expansion out of Africa (Braüer 1981; Duarte *et al.* 1999; Trinkaus *et al.* 2003). Because of this important assumption, the hybridization hypothesis is, in fact, closer to the replacement model than the multiregional model, which stresses regional continuity, even though the latter position does not preclude the possibility of local extinctions and small-scale migrations. Indeed, from this viewpoint, the replacement and hybridization models differ only on the question of how long these populations are said to have been diverging.

The eighties also correspond to the rise of archaeological models for explaining the Middle to Upper Paleolithic transition. Almost all the propositions made in this field were framed within the perspective of the replacement model (e.g., Mellars 1989a, 1989b, 1996; Demars and Hublin 1989; Bar-Yosef 1994; Van Peer 1998; Gamble 1999). It is important to note that, despite their differences, these models usually share the general assumption that the Neandertals were, in one way or another, not as efficient or as culturally complex as were early modern humans. Unfortunately, these propositions rarely state the causes and context linked to the emergence of the modern human selective advantage(s).

Mellars has presented his ideas about the Middle to Upper Paleolithic transition in a series of publications (Mellars 1973, 1989a, 1989b, 1996, 1998, 1999). Persuaded that modern humans replaced the Neandertals, he offered several scenarios to explain their extinction. For instance, he suggested, based on a model proposed by Whallon (1989), that Neandertals were not able to produce a full language. On other occasions, however, Mellars stressed cultural factors and stated that the Neandertals had a generalized economy, in contrast to modern humans groups who focused on large herds of a single species (Mellars 1996, 2004). For him, this specialization implies a more complex organization, being less opportunistic. Yet, narrow species-focused assemblages may just reflect prey availability (Enloe 1993; Costamagno 1999; Burke 2000; Grayson and Delpech 2002). Additionally, a narrow species focus is documented at a number of Mousterian sites, for instance at Wallertheim (Gaudzinski 1995), Combe-Grenal (Chase 1986; Guadelli 1987), Mauran (Farizy *et al.* 1994), La Borde (Jaubert and Brugal 1990), Coudoulous (Jaubert 1999), and Biache-Saint-Vaast (Auguste 1995). Thus, narrow focus does not necessarily imply a more complex organization or confer a selective advantage. Mellars also stressed that Neandertals practiced scavenging to a greater extent than modern humans. However, scavenging is frequent in modern foragers (O'Connell *et al.* 1988), and there is little evidence supporting this hypothesis during the transition (David and Poulain 1990; this study). Moreover, Straus (1990), Lindly and Clark (1990), and Simek and Price (1990) stressed that the cultural evidence commonly used by Mellars (e.g., 1989a) to demonstrate that modern humans were more efficient or better organized than the Neandertals (e.g., specialized hunting; complex burials; use of a wider diversity of tools) are, in fact, more characteristic of the late Upper Paleolithic. Therefore, they argue that these arguments cannot be used to explain the replacement of the Neandertals.

In a recent book, Mellars (1996) refined his model and reconstructed how Neandertals and modern humans might have coexisted in southwestern France. Focusing on economy, he proposed that these populations avoided each other by exploiting different resources:

> One possibility is that the Châtelperronian and early Aurignacian groups were adapted to significantly different foraging and subsistence strategies – with the Aurignacian perhaps focusing mainly on specialized hunting of reindeer herds along major migration trails (such as the valleys of the Dordogne and Vézère) while Châtelperronian groups were adapted to more generalized animal exploitation, perhaps still dependent partially on scavenging rather than on deliberate and strategic hunting of game (Mellars 1996:416).

Demars (1990, 1996) and Pelegrin (1995) also proposed similar avoidance models.

Taking a different perspective, White (1982) commented on cultural changes between the Middle and the Upper Paleolithic. He suggested that these changes were related to a total restructuring of social relations, possibly caused by an increase in population density. Binford (1982a) criticized White’s “social” explanation and instead put the accent on differences in adaptation between Neandertals and modern humans:

> storage contrasts, if they can be demonstrated, appear to me to be symptomatic of a still more provocative contrast between the earlier time ranges and the Upper Paleolithic in its

> "modern man" manifestations. Early adaptations appear to me to be based on tactics which do not require much planning ahead (that is, beyond one or two days); in addition to the absence of storage (assuming for the moment that my impressions are correct) there is an absence of curated technologies (Binford 1976, 1979) and of the tactical use of such resources as salmon, the exploitation of which in large quantities requires the anticipation from one year to the next of spawning runs, etc. Perhaps of similar relevance is early populations' inability to penetrate the Eurasiatic steppe, where both storage and the anticipation of herd movements would seem prerequisite to adaptation. It is my impression that the *ability to anticipate events and conditions not yet experienced* was not one of the strengths of our ancestors prior to the appearance of clear evidence for symboling (…) things which mark the appearance of 'culture' as we know it (Binford 1982:178).

Some of these interesting suggestions are, however, contradicted by the fact that evidence for symboling is associated with Neandertals in the Châtelperronian, a feature argued to have been evolved independently by them (D'Errico *et al.* 1998; Baffier and Julien 1990; Baffier 1999). Binford (1982a; 1989) also emphasized organizational differences between the Middle and the Upper Paleolithic. According to him, Neandertals were foragers, whereas early modern humans are said to have used a collector strategy in which trips are logistically organized.

The hypothesis of Neandertal replacement has also been studied from a quite different perspective. Instead of looking at skeletal features or artifacts, some have suggested that the answer to our questions might be lying inside us. These scholars are molecular biologists.

A new player: molecular biology

The field of molecular biology recorded a florescence of publications and discoveries since the pioneering work of Zuckerkandl and Pauling in the early 1960's on protein divergence (Li and Grauer 1991). One by one, techniques like protein electrophoresis, protein immunology, DNA-DNA hybridization, restriction analyses, and DNA sequencing were added to the panoply of more classical devices permitting the assessment of phylogenetic relationships within and between taxa. A brief summary of molecular evolution theory and of some major contributions to the debate on modern human origins are presented here.

Basic principles about molecular evolution and phylogenetic reconstruction

Nuclear DNA codes most human genes (Avise 1994). However, the coding of information is not restricted to the nucleus of the cell. DNA is also found in mitochondria (mtDNA), organelles located in the cytoplasm that have been extensively used in studying molecular evolution and whose primary function is to produce energy (Avise 1994). mtDNA and nuclear DNA each constitutes a unique genome.

Recent advances now make it possible to extract ancient DNA. However, because only short sequences tend to be preserved in archaeological bones, amplification is usually required (Hofreiter *et al.* 2001). This is made possible with the *Polymerase Chain Reaction* (PCR) technique, which allows one to obtain millions of cloned DNA fragments (Hillis *et al.* 1996). However, contamination of samples by modern DNA is frequent and difficult to detect when dealing with human remains (Hofreiter *et al.* 2001; Pusch and Bachman 2004). Due to its sheer numbers in humans (more than 1,800 copies per cell), mtDNA is more likely to be preserved in archaeological remains than nuclear DNA, which possesses only a few copies per cell (Avise 1994). Our discussion will therefore focus on mtDNA. As we will see, however, mtDNA does not provide a full picture of the molecular evolution of humans and needs to be contrasted with information from other regions and genomes.

In humans, mtDNA consists of a closed circular molecule composed of ~16,569 base pairs, which represents only a small fraction compared to the three billion base pairs found in the nuclear genome (Avise 1994). With few exceptions (Howell *et al.* 1996), individuals are generally homoplasmic, that is, they possess a unique mtDNA sequence repeated in all bones and tissues. mtDNA molecules are generally stable, but on some occasions may vary in size (Avise 1994). Insertion or deletion changes are rare in mtDNA. However, transversions, and especially transitions, both grouped under the term *nucleotide substitution*, are more frequent (Li and Grauer 1991). Research on modern human origins has generally focused on the mtDNA D–loop or *displacement loop*, a non-coding region associated with replication that shows a very high mutation rate, and therefore often is referred to as the *hypervariable* control region (Avise 1994).

Because it does not have or has inefficient repair enzymes to correct for substitutions, mtDNA accumulates mutations at a rate 10 to 20 times faster than nuclear DNA (Avise 1994). This is one reason why mtDNA has attracted the interest of researchers, the second being that mtDNA is, with rare exceptions, strictly maternally inherited. This means that, contrary to nuclear DNA, which reshuffles variation during meiosis, mtDNA does not recombine during maternal transmission, but rather clones itself, therefore reducing the possibility of "blurring" phylogenetic relationships (Li and Grauer 1991). Through time, mtDNA tends to accumulate mutations, some of which become fixed. Thus mtDNA reflects the molecular evolution of female mitochondrial nucleotide sequences (often referred to as "matrilineages" in the literature).

This constellation of characteristics allows direct comparisons of mtDNA sequences between almost any living organisms, the underlying assumption being that the longer the time of divergence, the less the amount of genetic material still in common (Avise 1994). Because advantageous mutations are expected to be extremely rare, molecular biologists assume that most substitutions are neutral or very slightly deleterious, meaning that they have little impact on the organism. This assumption based on the neutral theory of molecular evolution (Kimura 1983) asserts that natural selection essentially serves to "purify" variation by removing deleterious mutations (Futuyma 1997). Because mutations seem to accumulate at a relatively steady rate, the degree of divergence between two homologous nucleotide sequences can be used as a *molecular clock* defined as "a stochastic clock that is dependent, like radioactive decay, on events that occur with constant probabilities" (Ayala 1995:1930). It has been theorized that mutation rates in species with very different life spans would be skewed by a generation-time effect. Rats, for instance, might accumulate mutations at higher rate than humans due to higher generation turnover (Li and Grauer 1991; Li *et al.* 1996). Kumar and Subramanian (2002), and Ohta (1993) have rejected this hypothesis. Another potential problem is that males may show higher mutation rates than females, as the number of cell divisions in sperm production is much higher than the number of cell divisions associated with egg production. This hypothesis is, again, controversial (Ellegren 2002; Makova and Li 2002). However, this problem does not affect mtDNA, from which the bulk of the research on modern human origins has been carried out.

In most studies of modern human origins, it is assumed that the low nucleotide diversity among humans compared to chimpanzees (see Stone *et al.* 2002) is the product of a recent population bottleneck followed by a population expansion (Sherry *et al.* 1994). Usually, the most diverse population, that is, the population with the highest level of allelic heterogozity is considered as the likely source of expansion (Cann *et al.* 1987). Departures from neutrality, which may blur demographic patterns, are generally assessed through Tajima's (1989) *D* statistic. In most cases, an excess of rare allelic variants is interpreted as the result of genetic drift[1] following a severe population bottleneck (see Templeton [1992] and Wall [2000] for a critique of these assumptions).

Despite these difficulties, DNA studies have great potential for clarifying phylogenetic relationships between species, including fossils of past populations like the Neandertals, and represent an exciting complement to more traditional approaches to the problem of modern human origins.

A window on past population dynamics

Brown (1980) performed one of the first molecular analyses focusing on the origins of modern humans. He argued that the variation observed in the mtDNA of living humans indicates that modern populations diverged around 180-360 kya, a scenario that

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[1] Genetic drift is a random change in allele frequencies within a population (Futuyma 1998),

became known as the “Garden of Eden” hypothesis. Following this idea, Cann and her associates proposed in 1987 a second model of modern human origins. This model, labeled the “Eve Theory,” launched a vivid debate in anthropology. These authors stated that modern mtDNA diversity reflects a severe bottleneck in population size around 200 kya and concluded that although: “archaic types of mtDNA could have been lost from the hybridization population, the probability of mtDNA lineages becoming extinct in an expanding population is low. Thus we propose that *Homo erectus* in Asia was replaced without much mixing with the invading *Homo sapiens* from Africa” (Cann *et al.* 1987:35-36).

However, many inconsistencies were noted in this study. Excoffier and Langaney (1989), Maddison *et al.* (1991), and Templeton (1993, 1997) argue that the conclusions were not supported by the presented evidence due to several statistical and topological errors. As an example, Maddison *et al.* (1991) reports finding 10,000 trees five steps shorter than the maximum parsimonious tree proposed by Cann and her colleagues. Nevertheless, several studies have since been published supporting the Eve theory (e.g., Vigilant *et al.* 1991; Stoneking *et al.* 1992; Yu *et al.* 2002; Tischkoff *et al.* 1996; Horai *et al.* 1995; Krings *et al.* 1997; Schmitz *et al*. 2002; Ovchinnikov *et al.* 2000; Höss 2000; Krings *et al*. 2000; Excoffier and Schneider 1999; Excoffier 2002). Problems have been raised about some of the demographic models used in these studies, customarily based on the assumption of perfect random mating (panmixia), said to be a problematic assumption in human populations (Templeton 1993; Nordborg 1998; Wall 2000; Hawks *et al.* 2000). Other problems were also highlighted in relation to the estimation of effective population size, population census size, and the use of nucleotide diversity as a proxy for studying population bottlenecks (Templeton 1993, 1997; Relethford and Jorde 1999; Wall 2000; Hawks *et al.* 2000; Rogers 2001). In addition, important parameters like migration, recombination, hitchhiking, back breeding, gene flow, and background selection are difficult to model accurately (Wall 2000; Wall and Przeworski 2000; Harpending and Rogers 2000; Rosenberg and Nordborg 2002; Harris and Hey 1999).

Spectacular results were presented by Krings *et al.* (1997) who succeeded in extracting and amplifying ancient mtDNA from the eponymous Neandertal specimen. Their conclusions about a Neandertal contribution to the genetic diversity of living populations are unequivocal: "The Neandertal mtDNA sequence thus supports a scenario in which modern humans arose recently in Africa as a distinct species and replaced Neandertals with little or no interbreeding" (Krings *et al.* 1997:27). Krings *et al.* (2000) also amplified the mtDNA of a Neandertal from Vindija, Croatia. Data confirmed their previous conclusions about the negligible role played by Neandertals in the current mtDNA genome. These exciting results inspired other scholars. Ovchinnikov *et al.* (2000) obtained an mtDNA sequence from a young individual, presumably Neandertal, from Mezmaiskaya Cave (Caucasus) dated to approximately 29,000 BP (one of the latest Neandertals known), said to have been associated with Mousterian artifacts (but see Hawks and Wolpoff 2001). The authors found no support for the Multiregional model:

> Phylogenetic analysis places the two Neanderthals from the Caucasus and western Germany together in a clade that is distinct from modern humans, suggesting that their mtDNA types have not contributed to the modern human mtDNA pool. Comparison with modern populations provides no evidence for the multiregional hypothesis of modern human evolution (Ovchinnikov *et al.* 2000:490).

The divergence date proposed by Ovchinnikov *et al.* falls between 106-246 ky, a range of dates considerably younger than the 550 and 690 ky interval suggested by Krings *et al.* (1997). Finally, the mtDNA of a second individual from Feldhofer Cave, named NN1 and maternally unrelated to the other sampled Neandertal from this site, shows that it "falls together with the three previously determined Neandertal DNA sequences to the exclusion of contemporary humans" (Schmitz *et al.* 2002:13346).

In spite of these claims, some molecular biologists proposed that the replacement of archaic *sapiens* populations was not total. Among others, Avise (1994), Hammer *et al.* (1998), Relethford and Jorde (1999), and Underhill *et al.* (2000) have opened the door to a limited gene flow between Neandertals and modern humans.

These interpretations of the fossil DNA data have, however, been challenged. Gutiérrez *et al.* (2002) criticized the fact that these phylogenetic analyses do not take into account the wide variation in substitution rate between sites of the mtDNA D-loop (Heyer *et al.* 2001). Moreover, it is claimed that the model used to assess genetic distances is generally too simplistic. Using Kimura's two parameter model and correcting for variation in substitution rates, Gutiérrez *et al.* (2002:1362) came to the opposite conclusion, that their "results suggest that the Neandertal sequences cannot be considered an outgroup for modern humans." Interestingly, Krings *et al.* (1999) observed that the differences found between Neandertals and modern humans were less than the differences between two out of three chimpanzee subspecies. Indeed, nucleotide diversity is much higher in chimpanzees and bonobos than in humans, a fact that has been interpreted as reflecting longer divergence times, as well as larger population effective sizes for the former taxa (Stone *et al.* 2002). These results suggest to Relethford (2001a) the possibility that Neandertals might have been a subspecies of modern humans.

Challenges to the Eve theory also came from other directions. Recently, mtDNA has been extracted from remains of anatomically modern humans from Lake Mungo, Australia (Adcock *et al.* 2001). Fossil mtDNA from ten different individuals was successfully amplified. Although most individuals cluster with modern humans, one individual of 60 ky of age, LM3, falls *outside* of the actual human clade. This is unexpected. Indeed, following the logic of the Eve theory, these results would mean that early modern humans replaced the early anatomically modern Australians:

> Our data present a serious challenge to interpretation of contemporary human mtDNA variation as supporting the recent out of Africa model. A separate mtDNA lineage in an individual whose morphology is within the contemporary range and who lived in Australia would imply both that anatomically modern humans were among those that were replaced and that part of the replacement occurred in Australia (Adcock *et al.* 2001:541).

These results were said to cast doubts on the Eve theory (Relethford 2001a). Adcock *et al.* (2001:537) also made an important point about the interpretation of DNA variation from the single mtDNA region:

> Different regions of the genome appear to have had different evolutionary histories (7-14), and the idea that the pattern of human evolution can be deduced solely from the pattern of contemporary mitochondrial genome diversity is becoming increasingly untenable (3). There are also indications that the patterns of variation at low-recombining

> regions of the human genome, including the mitochondrial genome, have been affected by the action of selection and do not solely reflect mutation and genetic drift.

Not surprisingly, these conclusions were contested by Cooper *et al.* (2002, but see the reply by Adcock *et al.* 2002). Importantly, Hofreiter *et al.* (2001) suspect contamination of the LM3 sample by a nuclear insertion sequence. Indeed, contamination is a pervasive problem when dealing with human fossil DNA (Pusch and Bachman 2004).

As noted by Avise (1994) and Templeton (1993), the molecular clock should be based on accumulation of neutral mutations, not on shifts of allelic frequencies in ancestral polymorphisms caused by genetic drift, migration or natural selection. A growing number of studies show problems of fit between the neutral theory and genomic data, suggesting that these phenomena may indeed be important causes of patterning in living human DNA (e.g., Tajima 1989; Merriwether *et al.* 1991; Harpending and Rogers 2000; Rogers 2001; Fay *et al.* 2002; Nachman *et al.* 1996). Furthermore, according to Moritz and Hillis (1996), selection would be episodic rather than constant and, therefore, would have greater effect on intraspecific versus interspecific comparisons. In this perspective, Nachman *et al.* (1996) found a higher rate of replacement substitutions to “silent” nucleotide substitutions (a silent substitution is presumed to have little or no impact on protein function) within humans than between species. These authors think that many mitochondrial protein polymorphisms would be slightly deleterious and, therefore, not fixed in evolution. As a result, it is not clear that the large number of differences observed between Neandertals and modern humans testify that the former belonged to a distinct taxonomic group.

Cann *et al.*'s seminal study equated gene tree with species tree. However, instead of adopting a phylogenetic outlook as the Eve theory, a *Coalescence Theory* has been proposed as an alternative (Kingman 1982; Avise 1994; Templeton 1993, 1997; Ayala 1995; Rosenberg and Nordborg 2002). This theory assumes that all genes present in an extant population must have descended from a single gene to which they coalesce. The difference with Cann *et al.*'s model is that each gene or region is presumed to have had a unique story:

> Conclusions about the population tree cannot be drawn simply by looking at the estimated gene tree –different genes might produce different trees- and it is necessary to consider the likelihood of the estimated tree under alternative models. Furthermore, it might not make sense to try to estimate a population tree – the relevant model might involve migration (or horizontal transfer) between populations, population history might not be tree-like, and the rates of migration might be of primary interest (…) The genealogical approach has none of the limitations of the phylogenetic methods and provides a coherent statistical framework in which to consider recombination, migration, selection and other processes (Rosenberg and Nordborg 2002:383).

Templeton (1993, 1997) has been among the first to promote this approach in the study of modern human origins. According to this author, the coalescence of all genetic variation observed in an actual population back to a single maternal ancestor is a stochastic process greatly influenced by genetic drift (Templeton 1993:57). Harpending and Rogers (2000), and Templeton (2002) hypothesize that if the Eve theory is correct, the comparison of all genomic regions, in both mtDNA and nuclear DNA, should give similar coalescence dates, given that older allelic signatures, genetic vestiges of previous populations, should have been "erased" by the Eve bottleneck. In this perspective, there is a growing focus on nuclear DNA, especially on the paternally inherited, mostly non-recombining, Y chromosome, a mechanism of transmission that "mirrors" mtDNA (e.g., Underhill *et al.* 2000; Hammer *et al.* 1998; Semino *et al.* 2000). Evolutionary inferences have also been presented based on nucleotide diversity in X chromosome and autosomes (e.g., Tischkoff *et al.* 1996; Yu *et al.* 2002; Harris and Hey 1999). For these, however, recombination of DNA material during meiosis may obscure evolutionary inferences. In addition, recent studies have been published which compare *single nucleotide polymorphisms* (SNP's; that is, loci that have two or more alleles in a given population) from several different regions in order to get a fuller picture of human evolution (Wakeley *et al.* 2001; Yu *et al.* 2002). The vast majority of these studies found support for the Eve theory.

Comparing haplotype (alleles characteristic of an individual) trees for mtDNA, Y-chromosome, two X-linked regions and six autosomal regions, Templeton found significant differences in coalescence dates between them:

> The GEODIS analyses indicate that the most recent out-of-Africa expansion event was not a replacement event. If it had been, the three significant genetic signatures of the older expansion event (…) and the six significant genetic signatures of older recurrent gene flow (…) would have been wiped away. Although there is considerable error in dating any single inference from only one gene, an out-of-Africa replacement event would require that all nine significant inferences found in all eight bisexually inherited nuclear loci examined would have to be in error simultaneously. Moreover, the dating errors would have to be large in all nine cases and in the same direction. The hypothesis

> of a recent out-of-Africa replacement event is therefore strongly rejected (Templeton 2002:49).

In order to explain the diversity of coalescence dates and the high percentage (90%) of haplotype trees rooted in Africa (see also Takahata *et al.* 2001), Templeton (2002) proposes that at least *two* major population expansions out of Africa occurred after the colonization of Eurasia by *Homo erectus*. For Templeton, the most recent population expansion did not cause a replacement of non-African populations, as some interbreeding is suggested by the older coalescence dates of some genomic regions. Excoffier (2002), however, offers an alternative explanation, which proposes that the regions with old coalescence dates may, in fact, be under strong selection or misdated. As an example of the former, Ayala (1995) showed that the DRB1 gene, associated with the human leukocyte antigen (HLA) complex, points to a coalescence date of 60 million years ago, that is before the divergence of the New World and Old World monkeys! However, contrary to most studies reported here, the DRB1 gene is found in a coding region, and thus should not be expected to be neutral. Finally, Cann (2002) and Macaulay (2002) express skepticism about the method used in Templeton's study.

The rapid growth of molecular anthropology highlights the youth of a field that has been extremely influential in the debate on modern human origins. This influence has been, to some extent, disproportionate, as many controversial propositions are in fact based on assumptions that are now debated (e.g., effective population size has been constant; nucleotide substitutions in fossil specimens are real and not amplification artifacts; mutations are neutral in non-coding regions; divergence dates are bottleneck dates; there is no back migration; balancing is insignificant; etc.). Indeed, as pointed out by Wall (2000) and Relethford (2001a, 2001b), molecular studies cannot, at the moment unambiguously support a single model for the origins of modern humans.

Despite these important problems, four conclusions seem to emerge from these studies: i) Most haplotype trees, for all regions examined, tend to be rooted in Africa. This suggests that Africa has indeed played a very significant role in actual genetic diversity. ii) Most regions have recent coalescence dates, between 200 and 10 kya, suggesting that the impact of Africa on the actual gene pool is relatively recent. iii) Neandertals tend to fall outside of the diversity found among living humans and seem to have contributed little to the current genome based on mtDNA. iv) Despite this, an argument can be made that Neandertals were a subspecies of *Homo sapiens*, as the differences observed between these groups are not greater than the diversity observed between chimpanzee subspecies. However, even these conclusions are debatable. Divergence dates are based on the neutral theory of molecular evolution and are therefore not unambiguous. These dates may, in fact, correspond to older or more recent events. Indeed, it is still not totally clear what are the roles of contamination, population expansion, gene flow, back breeding, selection, and balancing in the picture. Finally, comparison of average nucleotide diversity between humans and chimpanzees may be complicated by the fact that these species have been shown to have very different effective population sizes and divergence times (Stone 2002). The role played by the effective population size would be particularly important in the discussion. Despite all these problems, it is important to incorporate these findings in the debate on modern humans as they raise issues (e.g., variation in population size; natural selection) that are clearly important in the debates on modern human origins.

Problems and contradictions in the Neandertal replacement model

In the debates about the origins of modern humans in Western Europe, three dimensions —physical replacement, genetic replacement, and cultural replacement— are usually conflated into a single event: the replacement of Neandertals by incoming anatomically modern Aurignacians. Although changes along these dimensions may be interrelated, it is necessary to explore these issues separately, as they may not covary as tightly as generally argued. In most replacement scenarios, an inferred lack of anatomical continuity between Neandertals and early modern humans has generally been explained by physical replacement. However, this is not the only plausible explanation. For instance, sampling bias in the skeletal record appears to be significant for this time period (Gambier 1989a, 1989b; Gambier *et al.* 1990) and may explain some of the purported anatomical discontinuities (some transitional fossils may exist, but may not have been found yet). Another possibility is genetic drift, as discussed by Howell (1951). This possibly is raised indirectly by Ayala (1995:1934) in his discussion of the Eve theory: "'Eve' could have belonged to a population of many thousands or tens of thousands of females, the remainder of whom left no descendants to the present day, due simply to the stochastic lineage extinction associated with reproduction."

In this context, the small population density of the Neandertals (Hayden 1993; Mellars 1996) would have made them particularly prone to this type of process. In other words, it might be true that many molecular markers and derived features of the Neandertals are no longer present in extant humans. However, this does not mean that the Neandertals were physically replaced or that an Aurignacian migration occurred. This is a simplistic interpretation of demographic and genetic processes. Besides genetic drift, other factors like changes in gene flow networks or in selective pressures can contribute to important anatomical and/or genetic changes (Relethford 2001b; Harpending and Rogers 2000; Templeton 1997). *Therefore, the lack of anatomical continuity does not necessarily imply any large-scale population movement or physical replacement, nor does a lack of continuity in molecular markers*. Even though these are suggestive of important allelic shifts, linking these to a physical replacement of the Neandertal populations is an unwarranted assumption given our knowledge of evolutionary processes. In this regard, the fact that ”hybrid” characters are found in the Pestera cu Oase specimen (Trinkaus *et al.* 2003), some of which are derived characteristics specific to the Neandertals, might as well be interpreted as support for the Multiregional model rather than evidence of hybridization.

We have seen that prior to the sixties, sudden changes in the archaeological record, for instance, between the Mousterian and the Châtelperronian or the Gravettian and the Solutrean, were generally understood in terms of large-scale migrations and physical replacement of local populations. This diffusionist paradigm, promoted by Breuil, Capitan, Keith, Verneau, Boule, Garrod, Peyrony, and Pradel is at the very root of the replacement model. But where does this assumption come from? According to F. Bordes (1972a), historical accounts depicting, for instance, the invasion into Western Europe of remote populations like the Indo-Europeans, the Moors or Asian “barbarians” were used as analogies, and unjustifiably extended to the Paleolithic, conjectured to have recorded a comparable series of far-flung incursion events. Keeping this in mind, the notion that the Aurignacian represents one of these large-scale migration and replacement events has been adopted by most since its formulation by Breuil and Boule, with surprisingly little opposition (but see Clark 1992 and Straus 1997). Genetic arguments have been used to support these propositions (e.g., Stringer and Andrews 1988). Because of a purported synchronism in anatomical and cultural changes during the Middle to Upper Paleolithic transition in Western Europe, the hypothesis of an Aurignacian migration was perceived as better supported than most other replacement events proposed by Breuil. However, there are several reasons to think that the hypothesis of a modern human Aurignacian migration event is controversial.

First, it is important to note that we still know very little about the anatomy of the Early Aurignacians of Western Europe. The few specimens known are from Isturitz, Fontéchevade, Font de Gaume, La Ferrassie, La Crouzade, Les Cottés, Acy-sur-Cure, and Les Rois, but are very fragmentary, being mostly limited to skull fragments and teeth (Leroi-Gourhan 1958; Gambier 1989a, 1989b; Gambier *et al.* 1990). We can add to this list a proximal phalanx found in the Aurignacian I of Saint-Césaire (this study). In fact, questions can legitimately be raised about the makers of this industry. Although some skeletal features, mostly from the cranium, mandible, and teeth, suggest an affiliation with modern humans, it is not possible to be absolutely positive about this attribution, as pointed out by Gambier (1989a). This taxonomic uncertainty also holds for the early Upper Paleolithic of the Levant (Bar-Yosef 2002). Thus the issue of which hominid group is associated with the Early Aurignacian should remain open, given what we have learned from the Saint-Césaire discovery.

The re-dating of several supposedly early modern humans now known to be very recent, for instance Velika Pecina and Staroselje (Marks *et al.* 1997; Smith *et al.* 1999), or more recent than previously thought, as is the case for the Cro-Magnon remains (Henry-Gambier 2002), raise further difficulties concerning this issue. In spite of these problems, proponents of the replacement model have generally assumed that modern humans produced the Early Aurignacian. Similarly, Neandertals, found in association with a Châtelperronian industry at Saint-Césaire, are assumed by most to be the authors of this industry. These assumptions are adopted here in order to conform to the replacement model as currently formulated. These statements will be re-evaluated in the discussion of the results of the study of Saint-Césaire.

Although it is not the goal of this study to analyze spatio-temporal patterning of artifacts during the Middle to Upper Paleolithic transition, it is relevant to our discussion to look at some general trends in culture change. Despite almost a century of work since Breuil's proposition of an oriental origin for the Aurignacian, every attempt to find the source of this technocomplex has met with failure (Breuil and Lantier 1951; Garrod 1938; Bordes 1972a; Otte 1990; Valoch 1990; Bar-Yosef 2002). Indeed, there is only superficial resemblance between the Western Aurignacian and the Early Upper Paleolithic of the Balkans, including the Bacho Kirian technocomplex (Rigaud 2001; Tsanova and Bordes 2003; Teyssandier 2003; Zilhão and D'Errico 1999), which is the most commonly cited evidence for the earliest Aurignacian (Stringer and Gamble 1993; Kozlowski 2000).

In the Levant, the Aurignacian would be younger than the Aurignacian of Western Europe (Belfer-Cohen and Bar-Yosef 1981; Bar-Yosef 2000, 2002). In fact, while most scholars think that modern humans migrated out of the Levant, the Aurignacian, or more appropriately, some of its stylistic characteristics, have been argued to have diffused from Europe *to* the Near East (Straus 1997; Bar-Yosef 2000). In addition, recent work (Bon 2002; Bon and Bodu 2002; Bordes 2002; Teyssandier 2003) detected more variation within this technocomplex than hitherto believed. Therefore, the Aurignacian does not appear to be the homogeneous phenomenon usually depicted (e.g., Stringer and Gamble 1993:209), and simple cultural mechanisms, diffusion of ideas for instance, may more parsimoniously account for the emergence, spread, and adoption of *some* of its features (e.g., split-based points) than replacement.

A recent detailed techno-typological analysis of the lithic assemblages from Roc de Combe and Le Piage confirms the notion that the Aurignacian I is not the oldest Aurignacian in the Périgord. More importantly, a study of the assemblage underlying the Aurignacian I at Le Piage brings into question the supposed gap existing between the Châtelperronian and the Aurignacian (Bordes 2002). This gap is also questioned at Arcy-sur-Cure based on a new analysis of the Châtelperronian (Connet 2002). These findings might be interpreted as as a case of possible *in situ* evolution of the Aurignacian in France. Some of these incongruities prompted Bar-Yosef (2002:372) to reject the possibility that the Aurignacian was the "first culture of the Cro-Magnons." We can only agree with this conclusion. The problem then is that if the Aurignacian is not the "first culture of the Cro-Magnons," which one was?

In these discussions, little attention has been paid to the archaeology of Australasia. One reason is that the archaeological sequences of this vast region are still very sketchy for the Middle and the Upper Paleolithic. Nonetheless, continuity seems to be documented in the archaeological sequences of Asia during the late Pleistocene (Brantingham *et al.* 2001), in apparent contradiction with the replacement model, which assumes that the Upper Paleolithic was essentially a modern human phenomenon corresponding to the demise of Neandertals and Australasian archaic *sapiens* (Stringer and Andrews 1988; Mellars 1996). An additional complication comes from Australia. The LM3 individual from Lake Mungo, an anatomically modern human whose DNA has been discussed in our review of the genetic evidence, is approximately 60 ky old, thereby giving a minimum date for the colonization of Australia (Thorne *et al.* 1999; Grün *et al.* 2000). This is confounding because Neandertals are present at Kebara at Amud at approximately the same time. Then, how can we explain that modern humans were successful in replacing archaic populations who occupied Asia and Australia but did not outcompete Neandertals in the Levant, an obligate corridor during the dispersal out of Africa? Obviously, the replacement model runs into many problems in Australasia.

Several publications have contrasted cognitive abilities and adaptation between Neandertals and modern humans (e.g., White 1982; Binford 1982; Trinkaus 1986; Mellars 1989a, 1989b, 1996; Stringer and Gamble 1993; Soffer 1994; Lieberman and Shea 1994; Shea 1998; Gamble 1999). In these models, biological and cultural features are often put forward to explain the purported Neandertal extinction. For instance, it has been claimed that the Neandertals were not able to speak or had only a rudimentary language (Lieberman and Crelin 1971; Milo and Quiatt 1993; Stringer and Gamble 1993). Specialists have since shown, however, that these claims are baseless (Holloway 1985; Arensburg *et al.* 1989). Contrasting the adaptation of these two populations is, however, a difficult task. This is because many studies collapse time periods when presenting modern humans, a problem that plagues our understanding of the transition. This problem, glanced at in our discussion of Boule's Pre-sapiens hypothesis, extends behaviors typical of more recent periods, often the Magdalenian, to the early Aurignacians (see also Conkey 1987; Lindly and Clark 1990). In doing this, behavioral patterns that are separated in time, sometimes by tens of thousands of years, become synchronous, transforming the recent evolution of modern humans into an a-historic process. When contemporaneous or nearly contemporaneous periods are compared, that is, when recent Mousterian and Châtelperronian adaptations are contrasted with early Aurignacian adaptations, most of the inferred differences between Neandertals and modern humans disappear.

The wide shift to blade production at the onset of the Upper Paleolithic is also commonly argued to represent a significant technological improvement over flake production. However, these arguments usually ignore the fact that several Mousterian sites from Western Europe and the Near East are dominated by blade production (Bordes 1984; Meignen 1988; Marks 1990; Conard 1990; Boëda 1989, 1990, 1993; Révillion 1995; Moncel 1996). Moreover, contrary to a widely held belief, blades are not necessarily more efficient or adaptive than flakes, as demonstrated by Bar-Yosef and Kuhn (1999). In fact, other parameters like nodule shape, raw material quality and abundance, type of hafting or edge resistance may all be as important, or even more important, for investigating efficiency than blank shape (Binford 1979; Andrefsky 1994). In this perspective, to argue that modern humans outcompeted Neandertals, based on a technological advantage provided by blade production, is totally unsupported by the evidence.

We have seen that arguments based on contrasts in capacities for producing language and art between Neandertals and modern humans are also problematic.

Nonetheless, this is not to deny the existence of significant contrasts between the Middle and the Upper Paleolithic. It is clear that the emergence of elaborated bone technology, the materialization of symbolic and social concerns through portable items, the use of soft organic hammers in blank production (and not only for retouching tools), the *general* shift to blades (not blade production *per se),* the production of bladelets, and the increase of raw material transfers are true changes observed in the Early Upper Paleolithic. These changes need to be explained. However, because the Châtelperronian shows most features later found in the Early Aurignacian, the available data cannot be used to support the notion that this behavioral complexity was *only* restricted to modern humans. Rather, most of these "modern" features seemed to have been developed prior to the beginning of the Aurignacian by Châtelperronian, and possibly Uluzzian, Neandertals.

It is generally argued that early modern humans had essentially modern behavioral capacities (White 1982; Stringer and Gamble 1993; Mellars 1996). Few, however, have attempted to test this assumption. The fact that several skeletal characteristics of the early modern humans fall within the modern range does not necessarily imply that this population also possessed "modern" cognitive and cultural abilities. For instance, what is the significance of skeletal robustness in early modern humans? Is there evidence that they had a full language or a complex social organization? Were they planning ahead? Did they have a division of labor comparable to that seen in modern hunters and gatherers? Did they practice storage? Was symboling a habitual behavior prior to the Upper Paleolithic? Like for the Neandertals, these propositions must be tested and should not be extended to early modern humans simply because they cluster anatomically with living people.

In sum, most studies of the transition are based on the assumption, inherited from Boule, that the Neandertals were not as behaviorally complex as modern humans. As a result of this assumption, the presence of "modern" features in an archaeological industry is almost automatically attributed to modern humans or their direct influence. This, unfortunately, leads to circular reasoning. Indeed, because early modern humans are assumed to have been the inventors of "advanced" features like art, elaborated bone technology, and storage, the presence of these features in a site is interpreted as evidence of the presence of modern humans. This type of reasoning is clear in the definition of the Upper Paleolithic provided by Stringer and Gamble (1993:202): "The first 'true' Upper Paleolithic industry –in the sense that it was made by anatomically modern humans and has all the technological features and artistic additions normally expected of the Moderns- is widely recognized to be the Aurignacian." Therefore, according to this proposition, despite the fact that it presents most if not all the "modern" characteristics of the Early Aurignacian, the Châtelperronian cannot be considered a "true" Upper Paleolithic industry as it was made by Neandertals. Bar-Yosef (2002:374) adopted a similar assumption in his discussion of the Early Ahmarian and the transitional industries of Ksar 'Akil and Boker Tachtit: "In the Levant human fossils from this period are lacking, but it is assumed that the two early entities were the creation of modern humans, as their contexts contain decorative elements crafted from sea shells (Kuhn *et al.* 2001)." A problem with this argument, however, is that the Châtelperronian and Uluzzian Neandertals also produced decorative elements.

In this context, the complexity of transitional Neandertal industries like the Châtelperronian and the Uluzzian has been downplayed or simply ignored. Because the complexity of these technocomplexes do not fit the perception that most people have of the Neandertals, the hypothesis of *acculturation* has been proposed, which alleges that Neandertals emulated modern humans (Mellars 1989a, 1989b, 1999; Demars and Hublin 1989; Demars 1990, 1996; Valoch 1990; Allsworth-Jones 1990; Stringer and Gamble 1993; Bar-Yosef 1994, 2002; Gamble 1999; White 2002). This position represents the mainstream opinion today. However, this position is not shared by all, as several specialists on the Châtelperronian and supporters of the migration and replacement model argue that the last Neandertals developed *independently* the "modern" features that are later documented for the Early Aurignacian (Cabrera Valdés and Bernaldo de Quirós 1990; Baffier and Julien 1990; Pelegrin 1995; D'Errico *et al.* 1998; Zilhão and D'Errico 1999; Baffier 1999; Rigaud 2000, 2001). In addition, the reason that would have induced Neandertals to "emulate" modern human technology is obscure. Nevertheless, these scholars generally concede that the end of the Châtelperronian was precipitated by the arrival of anatomically modern Aurignacians.

The acculturation model presupposes the coexistence of Neandertals and modern humans in Western Europe. Interstratifications of Châtelperronian and Aurignacian occupations were usually interpreted as strong evidence of this coexistence (Bordes and Labrot 1967; Laville 1971; Sonneville-Bordes 1972; Laville *et al.* 1980; Demars and Hublin 1989; Demars 1990, 1996; Harrold 1981; Mellars 1989a, 1996). However, J.-G. Bordes (2002, 2003) has recently shown through a careful study of refits and taphonomic processes that the interstratifications described at Roc de Combe and Le Piage are, in fact, spurious, as these were based on reworked material and errors in the interpretation of the stratigraphy. At El Pendo, Laville and Hoyos (1988) showed the existence of several geomorphologic perturbations that led to mixing of some of the cultural components of the site, which created the purported interstratifications.

These results support the argument made by D'Errico *et al.* (1998), Zilhão and D'Errico (1999), and Rigaud (2000, 2001) that the Châtelperronian invariably underlies the Early Aurignacian in the more than twenty stratified deposits in which both industries are recognized. This means that the Châtelperronian is unambiguously older than the Aurignacian, as far as stratigraphy is concerned, and that there is no stratigraphic support for the coexistence of Neandertals and modern humans in Western Europe. On the other hand, overlapping C-14 dates have been used to support this notion. This argument is, however, very controversial (D'Errico *et al.* 1998; Mellars 1999; Zilhão and D'Errico 1999), and overstates the precision and accuracy of C-14 dating methods for this time period (Jöris and Weninger 1999; Jöris *et al.* 2003). These recent stratigraphic findings highlight the fact that scientific inquiry does not always follow the shortest path. In this case, it has come full circle back to Breuil and his proposition of a linear succession of industries in the Early Upper Paleolithic.

Proponents of the acculturation model generally argue for “borrowings” and “imitation” to make sense of the complexity of the Châtelperronian and the Uluzzian, yet they also assert that Neandertals and modern humans used different territories, an “avoidance” strategy, in order to explain the absence of gene flow between these groups (e.g., Demars and Hublin 1989; Demars 1996; Mellars 1996, 1999). The problem then is how can exchange of fine-grained information be possible if Neandertals and modern humans were practicing an “avoidance” strategy and, therefore, had little interaction? In contradiction, when we look at the archaeological record, it is apparent that despite differences in artifact production strategies, Neandertals and modern humans appear to have shared information to a notable extent, as their assemblages show parallel shifts to bone tool production and laminar reduction sequences during the Middle to Upper Paleolithic transition.

In the Near East, there is a general consensus that no necessary relationship exists between hominid type and industry (Bordes 1972b, Bar-Yosef 2002). This conclusion, referred to here as the disconnection argument, was prompted by the discovery that Neandertals and modern humans produced very similar Levallois-based assemblages and the fact that skeletal remains of these populations are, sometimes, found in the same sites in this area. However, how can we explain the absence of obvious cultural and stylistic contrasts between these supposedly distinct populations? Indeed, this lack of patterning is in total contradiction with style theory. Learning, and overlearning ("rote" learning), the complex motor habits that materialize the system of dynamic templates underlying the Levallois concept imply some form of direct or indirect teaching. Because transmission of information about how to reproduce adequately a specific system of templates is not uniform over the landscape, but is strongly conditioned by learning networks, it is expected that groups with little interaction will show significant differences in production methods, tool manufacture, use, and discard patterns, due to random drift in template selection, as well as a result of conscious, differential, manipulation of variation (Wobst 1999). In southwestern France, patterns in the spatial and chronological distribution of Mousterian of Acheulean Tradition assemblages is indicative of the existence of a regionally circumscribed learning network close to the end of the Mousterian (Bordes 1984; Mellars 1996). Interestingly, this Mousterian facies appears to be quite different from the contemporaneous Mousterian assemblages documented immediately east in the Rhône Basin (Combier 1990). These Mousterian facies, both produced by Neandertals, signal the persistence, and, to some extent, the evolution of two distinct learning networks just before the beginning of the Upper Paleolithic. The contradiction is obvious here: how can we explain the existence of distinct learning networks in southern France where a single biological population is recognized but not in the area of the Levant where two species or subspecies are presumed to have coexisted? This suggests that the disconnection argument is theoretically flawed, if not untenable.

Interestingly, the disconnection argument disappears with the Early Upper Paleolithic. Indeed, the Châtelperronian and the Aurignacian are attributed by most to, respectively, Neandertals and modern humans. In a similar way, the Early Upper Paleolithic of the Levant is almost universally believed to be the product of modern humans. Does this mean that biology and material culture only became interconnected with the appearance of the Upper Paleolithic? This is doubtful given the arguments raised above about the nature of the Mousterian in France. In fact, the disconnection hypothesis is a post-hoc accommodation. This argument, tentatively put forward to eliminate contradictions in the replacement model, does not resolve anything. In light of the evidence for stylistic boundaries in Western Europe at the end of the Mousterian, evolutionary explanations are clearly needed to account for the apparent lack of cultural boundaries in the Levant where two genetically, and, presumably, socially isolated populations are believed to have coexisted.

In response to skepticism raised about the plausibility of a large-scale Aurignacian migration, some have used the "Neolithic revolution" as an analogy (e.g., Bar-Yosef 2000, 2002). This analogy is based on the argument that in both episodes (the Aurignacian and the Neolithic), a social entity, said to be large, viable, and successful, would have spread relatively fast into Western Europe out of a "core area" as colonizers and distributors of new techniques (Bar-Yosef 2002:381). There are problems with this proposition, however. First and foremost, the spread of Neolithic groups was apparently accompanied by significant gene flow (Semino *et al.* 2000), which makes one wonder what would have prevented this phenomenon from occurring between Neandertals and modern humans before or during the Middle to Upper Paleolithic transition.

Another problem with the Neolithic analogy relates to the type of adaptation that is discussed in the case of the Middle to Upper Paleolithic transition. *Foraging is an inherently local adaptation based on an extensive knowledge of the landscape, weather, animal forages, paths usually taken by prey, patch locations, scheduling of resources, and so on* (e.g., Steward 1938; Lee 1976). Although there appear to be general "rules" of animal behavior that can be built upon, critical information, for instance about patch locations and resource scheduling, is not fully transferable and is heavily context-dependent. Because of this unpredictability, hunter-gatherers require a tremendous amount of information about local conditions in order to survive and, therefore, are tightly tethered to a particular ecological setting. A real-life example drawn from the Nunamiut illustrates well this point:

> John Morry had married Simon's daughter against the wishes of Simon. After the marriage John and his wife had lived on the Killik River; they only recently joined the Tulugakmiut. Although Simon and his relatives tolerated John there was little cooperation at this time and John was at a disadvantage since he was unfamiliar with the

> country. Rumor has it that John was very unsuccessful with hunting during his early residence with Elyjah's band and life was very hard (Binford 1978:205).

A second example confirms the fragility of the foraging adaptation once groups are delocalized:

> Informants sadly recall the lack of hunting success in the mountains, although expeditions were set out regularly. Such attempts at local hunting by the migrants provided another source of some bitterness, since they wanted to hunt very badly and the good hunters of the Tulugakmiut were not going very often since their stores of dried meat were judged adequate for their demands. This meant that the men of the Killikmiut were greatly disadvantaged, since they did not know the local terrain and the behavior of the animals in that terrain during the summer (Binford 1978:326).

These examples draw attention to a very important problem faced by foragers: migrants are at a disadvantage compared to local groups. It should be stressed that these examples are particularly relevant, being derived from foragers living in an environment not too dissimilar from the one that characterized the late Pleistocene in many areas of Western Europe.

This has very important implications concerning human evolution. It means that large-scale migrations by foragers are unlikely to have been common in the past, given their heavy reliance on local information. Early modern human hunter-gatherers may have been well adapted to the ecology of the Levant. It does not follow, however, that this adaptation was equally productive and efficient when transferred to Western Europe. Therefore, it can be hypothesized that modern humans would have faced serious subsistence problems in their purported migration out of Africa. Importantly, this point is also valid about biological adaptation. Although this is very controversial, the biological "package" evolved by modern humans in Africa and the Levant might have favored them over Neandertals in these areas. Again, however, it does not follow that this biological package was equally fit and efficient in the quite different climate of Western Europe where other evolutionary formulas were possibly better adapted. In this area, Neandertals developed body proportions and specific features adapted to the cold climates of late Pleistocene Europe (Trinkaus 1986; Trinkaus *et al.* 1998). On the other hand, modern humans, characterized by their tropical body proportions, do not seem to share these characteristics (Vandermeersch 1981; Trinkaus 1986). Thus, it can be hypothesized that modern humans were biologically disadvantaged, compared to Neandertals, for coping with the relatively colder climates of Western Europe.

According to Lieberman and Shea (1994) and Shea (1998), modern humans would have coexisted and/or alternately occupied the Levant with Neandertals during the Mousterian. Dates for the earliest remains of modern humans and for the latest remains of Levantine "Neandertals" suggests that the latter would have competed successfully with the former population over a minimum of 40,000 years, sometimes even encroaching on their territory. If this is true, how can we explain that Neandertals were suddenly replaced in a few millennia? Some have suggested that a "mutation," allowing the emergence of language for instance, would have conferred a decisive advantage to modern humans (e.g., Milo and Quiatt 1993). We have already seen the problems with this assumption. Recently, Mellars (1998) and suggested that climatic changes would have triggered the modern human migration. Although this is possible, the timing does not explain why these changes would have favored modern humans and not Neandertals, nor does it explain why it happened at that moment and not during prior or later oscillations (see discussion of this issue in D'Errico and Sánchez Goñi 2003).

These problems cast strong doubts on the hypothesis of a replacement of Neandertals by incoming modern humans at the beginning of the Upper Paleolithic. With the accumulation of archaeological, paleoanthropological, and genetic data, the situation has become much more complex. This is because the replacement model is flawed by several untested, deeply rooted, *a priori* assumptions. Although various attempts have been made to accommodate this growing noise, the "Neandertal acculturation" model being one of the most recent examples, the proposed explanations are very unsatisfactory. The review of these problems makes it clear that we need to review our theories about the Middle to Upper Paleolithic transition and test the assumptions underlying these models.

Before going into the details of the theoretical foundations of the archaeological predictions, a brief overview of the Middle to Upper Paleolithic transition is first outlined for the research area. This review emphasizes fauna, as subsistence strategies are central to the test implication used in this study.

A brief review of the Middle to Upper Paleolithic transition in France and Cantabria

In southwestern France, the Middle to Upper Paleolithic transition is closely associated with two technocomplexes, the Châtelperronian and the Early Aurignacian.

These technocomplexes are found associated in several stratified deposits, including the Saint-Césaire site used here to test the replacement model.

The Châtelperronian phenomenon

The Châtelperronian has been identified in the central and southwestern portions of France and in northeastern Spain, and is especially well represented in Poitou-Charente and Périgord, the Pyrenées piedmont, and Cantabria (Figure 2). The Châtelperron "point," a backed blade retouched into a crescent shape, is diagnostic of this time period (Breuil 1912). In general, Châtelperronian assemblages show a variety of chipped stone artifacts typical of the Upper Paleolithic, for instance, blades, bladelets, burins, endscrapers, and truncated pieces. On the other hand, sidescrapers, denticulates, and notches, more common in the Mousterian, are also frequently found (Bordes 1984; Harrold 1981; Pelegrin 1990, 1995; Lévêque *et al.* 1993; Guilbaud 1993).

Bordes (1961, 1984) considered that the origin of the Châtelperronian was to be found in the Mousterian of Acheulean Tradition (MAT) and stressed the typological continuities between the backed knives of this industry and the Châtelperron knives. This interpretation has been supported by most specialists (e.g., Laville *et al.* 1980; Pelegrin 1990, 1995; Mellars 1996). However, at Saint-Césaire two MAT assemblages *underlie* three Denticulate Mousterian levels (Lévêque *et al.* 1993). This might imply that the MAT is not the most recent Mousterian facies in southwestern France.

Conversely, the Châtelperronian is believed by most to differ considerably from the Aurignacian in terms of geographic distribution, bone tool production, toolkit composition, and technology (Bordes 1961; Leroi-Gourhan 1965; Laplace 1966; Mellars 1996; White 2002), although this notion has recently been seriously questioned as discussed above (Bordes 2002; Connet 2002).

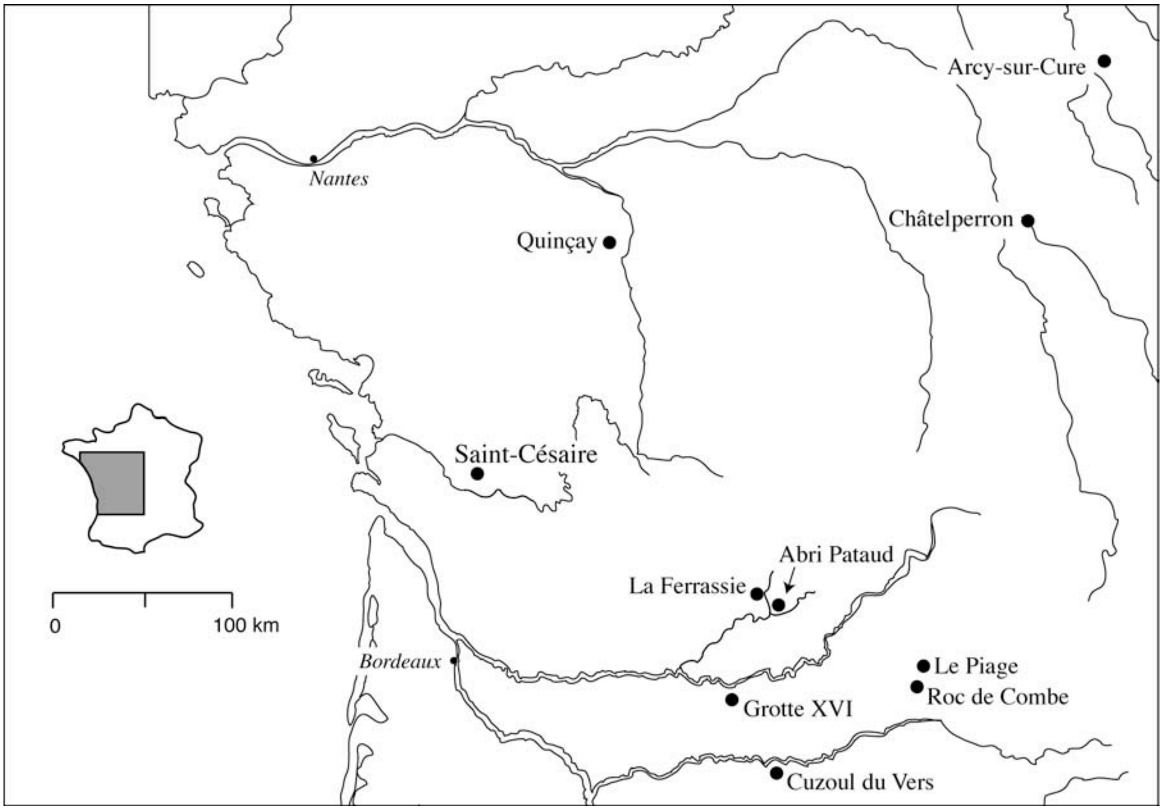

Figure 2. Location of Saint-Césaire and some other important sites cited in the text.

Pelegrin (1990, 1995) has conducted a detailed technological study of the Châtelperronian assemblages from Roc de Combe and La Côte in southwestern France. His analysis suggests that the production of Châtelperron knives and, to a lesser extent, endscrapers and bladelets, was the main focus of the reduction sequence. At Roc de Combe and La Côte, the strategy was to use the thickness of a flat flake as a core volume in order to produce blades. Similarities have been noted with this production method at Arcy-sur-Cure (Connet 2002; Gouedo 1990; Bodu 1990).

Bone tools as well as items indicative of symbolic behavior are documented in several Châtelperronian sites (Leroi-Gourhan and Leroi-Gourhan 1964; Poplin 1988; Baffier and Julien 1990; Taborin 1990; D'Errico *et al.* 1998; Baffier 1999). These include grooved and pierced teeth, pendants, "curios," awls, "digging tools," *baguettes*, and *lissoirs*. Moreover, ocher is very abundant in some sites (Harrold 1981; Couraud 1991; D'Errico *et al.* 1998). However, these items are rare in most Châtelperronian sites with the exception of Arcy-sur-Cure and Quinçay (Julien *et al.* 2002; Granger and Lévêque 1997). In terms of spatial organization, it is of significance to note that several superimposed hut structures have been discovered in layers X and IX of the Grotte du Renne at Arcy-sur-Cure (Farizy 1990).

There is unfortunately little information available on subsistence patterns during the Châtelperronian. Early studies were often restricted to species lists and were usually based on very small, heavily sorted, samples. Except when stated otherwise, the discussion will focus here exclusively on published faunal assemblages that have been completely collected.

Several Châtelperronian assemblages from the site of Quinçay were studied by Lavaud-Girard (1987). This site is exceptional given that eight Châtelperronian layers, combined in four units, are stratified at this location (Lévêque and Miskovsky 1983). Unfortunately, the faunal samples are small (Lavaud 1980; Lavaud-Girard 1987). NISP counts for the most recent Châtelperronian level (level Ej) suggest that reindeer horse, and bison are the best-represented taxa in the occupation. Carnivores are relatively well represented, especially foxes. Other carnivores are rare. The underlying Em assemblage is similar in both species composition and sample size, although fewer bison specimens appear to have been recovered. Very small numbers of faunal remains are available for the earlier levels En and Eg.

At Grotte XVI, a faunal assemblage has been recovered in layer B attributed to the Châtelperronian (Grayson *et al.* 2001; Grayson and Delpech 2003). Based on NISP, the most common ungulates are, in decreasing order, reindeer, red deer, and roe deer. Bovine and horse elements are relatively rare. The most abundant reindeer body parts are metapodials, skull, tibias, and ribs. Shaft fragments outnumber epiphysis fragments in the assemblage. However, bear remains are very abundant (n=426) in this occupation. Nonetheless, the abundance of cutmarks on ungulate taxa in the assemblage indicates that most remains other than carnivores were accumulated by humans (Grayson and Delpech 2003). Moreover, these authors note that within the Upper Paleolithic sequence of Grotte XVI, the Châtelperronian appears as the taxonomically most even sample in a succession through time of assemblages of decreasing evenness and increasing emphasis on reindeer. This pattern would suggest, in agreement with paleotemperature reconstructions, a relatively temperate climate for the Châtelperronian followed by occupations of increasingly depressed summer temperatures (Grayson *et al.* 2001).

A small faunal assemblage has been found in the Châtelperronian levels L3a and L3b of La Ferrassie. The stratigraphy of this site, however, is known to be complex (Delporte 1984). Delpech and her colleagues (2000) have recently published some results concerning this faunal assemblage. Importantly, some zones shown to be stratigraphically unreliable were excluded from the original sample studied by Delpech (1983). Although very small (NISP=70), this new sample is dominated by reindeer and bovine elements (probably bison). Similarly, the faunal assemblage of Roc de Combe, for which a new interpretation of the site formation processes has been offered (Bordes 2002, 2003), shows the co-dominance of reindeer and bovines (Delpech *et al.* 2000). The sample is also, unfortunately, relatively small. Potentially more problematic is the fact that the faunal material was not systematically collected during the excavations, a decision that might have biased species and skeletal representation. Similar problems plague the analysis of the small Châtelperronian assemblage from Le Piage studied by Beckouche (1981).

Faunal assemblages associated with the Châtelperronian and Aurignacian were also exhaustively collected from Grotte du Renne at Arcy-sur-Cure (David and Poulain 1990, 2002; David *et al.* 2001; David 2002). These faunal assemblages are discussed in detail in the comparison with Saint-Césaire (Chapter 8).

The Early Aurignacian

In France, the Early Aurignacian (Aurignacian I or "Classical" Aurignacian) is characterized by an abundance of blades with the typical "Aurignacian" retouch, strangulated blades, carinated "endscrapers," thin endscrapers made on blades, *pièces esquillées*, and Dufour bladelets (Sonneville-Bordes 1960). A high proportion of endscrapers is generally noted, while burins are less common (Demars and Laurent 1992; Laville *et al.* 1980). The split-based sagaie, generally made of antler, is the most diagnostic artifact of this episode (Liolios 1999). Several variants have been described for this industry based on tool type frequencies, the Castanet and the Ferrassie facies being the best known examples (Sonneville-Bordes 1960; Demars and Laurent 1992). In contrast, the Proto-Aurignacian (or Aurignacian 0), anterior to the Aurignacian I, is still poorly known (Bon 2002; Bordes 2002). The EJO sup (described in Chapter 4) assemblage at Saint-Césaire (Lévêque *et al.* 1993), and layer VII from Arcy-sur-Cure may belong to this period (Bon and Bodu 2002), as well as a small number of assemblages in southwestern and Mediterranean France (Bazile 1976; Bazile and Sicard 1999; Bon 2002; Bordes 2002, 2003).

Recently, Bon (2002), Bon and Bodu (2002), Bordes (2003), and Lucas (1997) have provided us with a discussion of the reduction sequences for the Early Aurignacian. Two types of reduction sequences, clearly dissociated in terms of production methods and blank metrics, have been described. A laminar reduction sequence seems to have been designed to produce large and heavy blades through a frontal and unidirectional exploitation of cores. In most cases, these cores show little preparation prior to blade production and have intensely facetted striking platforms. A second, and distinct, reduction sequence appears to have focused on the production of straight and slightly curved, but non-twisted, bladelets, using “carinated endscrapers,” themselves made out of thick flakes, as cores. These products were then retouched into Dufour bladelets.

There is slightly more information about subsistence strategies for the Proto-Aurignacian and the Early Aurignacian than is available for the Châtelperronian. Furthermore, this information is new and based on controlled samples from well-excavated sites. Because some of these are described in Chapter 8, only a short summary is given here. These assemblages include those studied by David and Poulain (1990, 2002; David 2002) for the Grotte du Renne, Grayson and Delpech (1998) for Le Flageolet I, Delpech *et al.* (2000) for La Ferrassie, and Bouchud (1975), Spiess (1979), and Sekhr (1998) for the Abri Pataud. Similar trends are observed at these sites: reindeer is the dominant species, often followed by horse. Bovines are usually rare. The presence of the arctic fox (*Alopex*) in many assemblages suggests that the climate was cold (Delpech 1983; Beckouche 1981; Lavaud 1980), an observation corroborated by microfaunal studies (Marquet 1993). In general, skeletal part representation is dominated by heads and long bones. The axial skeleton tends to be poorly represented. In some assemblages, procurement of reindeer seems to be restricted to the snow-covered season (Spiess 1979). The large faunal assemblages available for the Early Aurignacian of the Abri Pataud (Bouchud 1975; Sekhr 1998) are discussed in fuller detail in the comparison with Saint-Césaire (Chapter 8).

Chronology of the Middle to Upper Paleolithic transition in southwestern France

In the past five years, the chronological position of the Châtelperronian and the Aurignacian has been a source of considerable disagreement (e.g., Mellars 1999; Zilhão and D'Errico 1999). Absolute dates have been used to demonstrate either the precedence of the Châtelperronian over the Aurignacian (D'Errico *et al.* 1998; Zilhão and D'Errico 1999) or the coexistence of these two phenomena (Harrold 1981, 1989; Allsworth-Jones 1990; Demars and Hublin 1989; Mellars 1989, 1996, 1999; Boquet-Appel and Demars 2000). To further complicate the picture, claims have been made for the existence of a very Early Aurignacian at El Castillo dated around 40,000 BP (Bischoff *et al.* 1989; Bernaldo de Quirós and Cabrera Valdés 1993). This last proposition remains controversial, however, as the typo-technological composition of this assemblage includes several Mousterian tools (Cabrera Valdés *et al.* 2001). Currently, there is a growing consensus that the Châtelperronian is chronologically older than the Early Aurignacian, based on stratigraphic arguments (D'Errico *et al.* 1998; Rigaud 2000, 2001; Bordes 2002, 2003). These new developments are compared in Figure 3 with previous interpretations of the Middle to Upper Paleolithic transition.

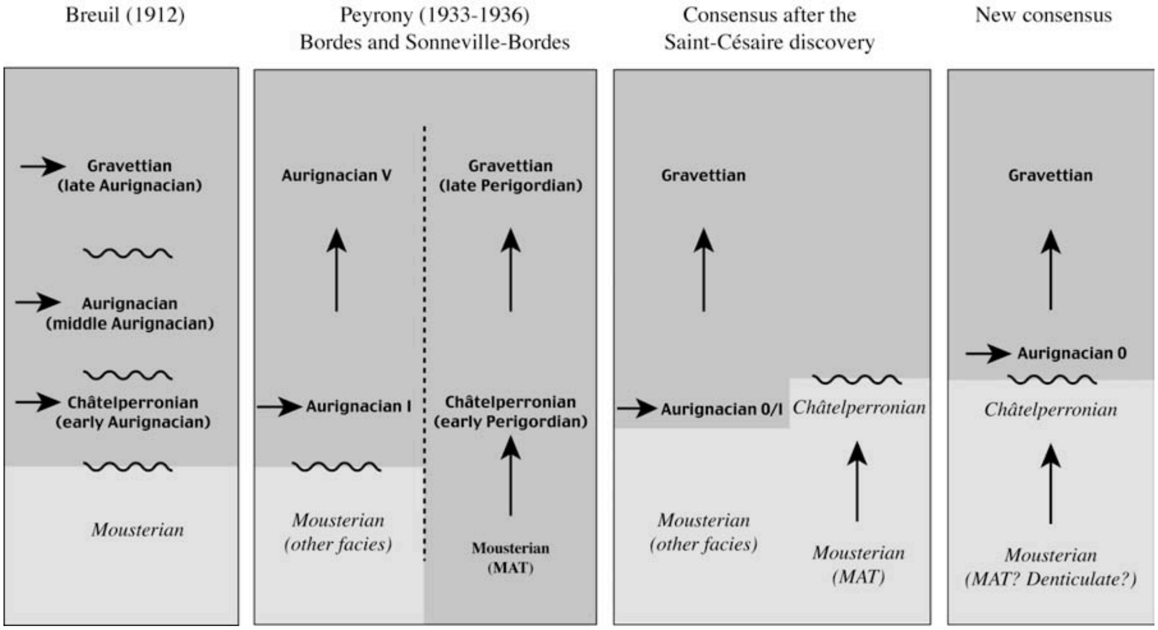

Figure 3. Simplified representation of the evolution of the interpretation of the Middle to Upper Paleolithic transition in southwestern France during the twentieth century. Horizontal arrows indicate migration. Vertical arrows denote filiation. Waves represent replacement events.

Several methods, for instance conventional C-14, AMS C-14, and thermoluminescence have been used to date Châtelperronian sites. However, because these methods are based on different assumptions and materials, and have different degrees of precision, dates are usually not fully comparable. The most commonly used technique, C-14 dating, is unfortunately unreliable in this time period because there is little C^{14} left in organic materials (Jöris and Weninger 1999). The AMS technique seems to be more precise for dating Châtelperronian and Early Aurignacian occupations than conventional C-14, as organic material beyond 30-35 kya are more easily plagued by contamination from flux of soluble organic matter (Bischoff *et al.* 1989), but, more importantly, because this method is less likely to provide underestimates (Evin 1990). An additional problem is that results will differ depending on whether they are based on bone or charcoal (Jöris *et al.* 2003).

Taking these problems into account, Châtelperronian and Aurignacian dates can best be compared using AMS dates. The sample, however, is small (Table 1). Fifteen dates for the Châtelperronian and seventeen dates for the Early Aurignacian (Aurignacian 0 and I) have been published. Using two standard deviations, most AMS dates fall between 38,500 and 34,500 BP for the Châtelperronian and between 37,500 and 33,500 BP for the Aurignacian. Clearly, there is a considerable overlap between these date intervals. This is likely to be an artifact of the dating method (Jöris and Weninger 1999), and here stratigraphic arguments should prevail. Based on these dates, the Châtelperronian is estimated to span roughly between 39,000 BP and 36,000 and the Early Aurignacian between 36,000 and 34,000 BP, in general agreement with other propositions (Zilhão and D'Errico 1999; Rigaud 2000). As a result of the problems underlined above, these are approximations.

Period	*Site*	*Layer*	*Lab Number*	*Dates*	*Reference*
Châtelperronian	Grotte du Renne	IX	OxA-3465	45,100 ± 2,800	Hedges *et al.* 1994
	(Arcy-sur-Cure)	Xa	OxA-8450/Ly-893	25,280 ± 280	David *et al.* 2001
		Xb	OxA-3464	33,820 ± 720	Hedges *et al.* 1994
		Xb1	OxA-9122/Ly-1055	33,400 ± 600	David *et al.* 2001
		Xb1	OxA-8451/Ly-894	38,300 ± 1,300	David *et al.* 2001
		Xb2	OxA-8452/Ly-895	34,450 ± 750	David *et al.* 2001
		Xc	OxA-8533/Ly-896	31,300 ± 600	David *et al.* 2001
	Combe-Saunière	X	OxA-6503 (tripep.)	38,100 ± 1,000	Mellars 1999
		X	OxA-6504	33,000 ± 900	Mellars 1999
	Grotte XVI	B	AA-2674	>39,800	Grayson&Delpech 2003
		B	AA-2997	38,100 ± 1,670	Rigaud 2001
		B	GifA-95581	35,000 ± 1,200	Rigaud 2001
	Roc de Combe	8	GifA-101264	39,540 ± 970	Bordes 2002
		8	GifA-101265	45,100 ± 2,100	Bordes 2002
		8	GifA-101266	40,000 ± 1,300	Bordes 2002
Early Aurignac.	Caminade	G	GifA-97185	37,200 ± 1,500	Bordes 2002
		F	GifA-97186	35,400 ± 1,100	Bordes 2002
		D21	GifA-97187	34,140 ± 990	Bordes 2002
	Castanet	Inf	GifA-97313	35,200 ± 1,100	Pelegrin[1]&White 1999
	Combe-Saunière	VIII	OxA-6507	34,000 ± 850	Mellars 1999
	Le Flageolet I	XI	GifA-95559	34,300 ± 1,100	Rigaud 2001
		XI	OxA-598	33,800 ± 1,800	Rigaud 2001
		XI	GifA-95538	32,040 ± 850	Rigaud 2001
	Roc de Combe	7b	OxA-1262	34,800 ± 1,200	Bordes 2002
		7c	OxA-1263	33,400 ± 1,100	Bordes 2002
	Isturitz	U27 4d	GifA-98232	36,510 ± 610	Turq[2] *et al.* 1999
		U27 4d	GifA-98233	34,630 ± 560	Turq *et al.* 1999
	L'Arbreda (Spain)	CE103	OxA-3729	37,340 ± 1,000	Hedges *et al.* 1994
		BE111	AA3779	37,700 ± 1,000	Bischoff *et al.* 1989
		BE111	AA3780	37,700 ± 1,000	Bischoff *et al.* 1989
		BE111	AA3781	39,900 ± 1,300	Bischoff *et al.* 1989
		BE111	AA3782	38,700 ± 1,200	Bischoff *et al.* 1989
		BE111	OxA-3730	35,480 ± 820	Hedges *et al.* 1994

[1] J. Pelegrin, pers. com. 2004

[2] C. Normand, pers. com. 2004

Table 1. Published AMS dates for the Châtelperronian and Early Aurignacian in France and Cantabria. Following Bordes (2002), the dates published by Mellars (1999) for Roc de Combe are not included due to problems related to layer misidentification.

CHAPTER 3

FORMULATION OF A TEST APPLICABLE TO ARCHAEOLOGICAL REMAINS

Despite their diversity, most of the models reviewed in the preceding chapter share the assumption that modern human migrants replaced the Neandertal populations. However, many problems were highlighted concerning the core assumptions of the replacement model. The most serious of these problems are related to the the assumption that modern humans had a selective advantage over Neandertals and expanded into Western Europe. In order to address some of these problems, demographic and ecological implications were derived from the replacement model based on findings concerning the minimal number of people necessary for allowing the biological survival of a population. These implications are then used to make archaeological predictions. These predictions are laid out in the next section and will be used to test the replacement model.

Theoretical foundations of the archaeological test

The size of human groups is not subject to unlimited variation. Several ecological and social factors constrain forager demography. Causes are numerous, but certain features are likely to be universal, being related to biological reproduction and ecology. These limitations have important implications for the replacement model and are discussed here according to two possible scenarios of dispersal. However, several assumptions and bridging arguments underlie the archaeological implications derived from these scenarios, and it is important to examine them first.

Assumptions underlying the test of the replacement model

Following the replacement model, it is assumed here that the end of the Mousterian corresponds to T=0, that is, it reflects the Neandertal adaptive system immediately prior to the purported modern human incursion. In other words, late Mousterian assemblages would testify to the "normal" subsistence conditions in Western Europe before the arrival of modern humans.

As emphasized earlier, it is generally argued that the Châtelperronian is associated with the Neandertals, whereas modern humans would have produced the Aurignacian (e.g., Mellars 1989a, 1996; Demars 1990; D'Errico *et al.* 1998; Gamble 1999; Bar-Yosef 2002). These technocomplexes are also generally presented as direct evidence of the modern human expansion (e.g., Bordes 1984; Mellars 1989a; Demars and Hublin 1989; Demars 1990; D'Errico *et al.* 1998; Zilhão and D'Errico 1999; White 2002). In sites where Châtelperronian and Early Aurignacian (0 and/or I) occupations are stratified, these are taken to indicate various stages of the inferred replacement. The Evolved Aurignacian might postdate the replacement event. Despite the various challenges to some of these assumptions, for the purposes of this study, it will be assumed that they are correct. This will allow for the evaluation of the replacement model under the conditions for which it was designed.

Another critical assumption is that Neandertal population densities were close to the carrying capacity of the environment prior to the arrival of modern humans. Two lines of argument support this assertion. Evidence of marrow-cracking of parts with marginal amounts of marrow, like mandibles and phalanges, signal that Neandertals were periodically under stress in the Mousterian, including the end of this episode (Guadelli 1987:440; Stiner 1994; Rendu 2002; this study). Importantly, marrow exploitation of these parts is not considered worth the effort by some modern foragers, but was performed by the same people in conditions of food scarcity in the past (Binford 1978). This assumption might also be supported by the high frequency of developmental stress indicators noted on Neandertal remains, some of which, like dental enamel hypoplasias, have been associated with food stress (Goodman *et al.* 1984, 1987; Goodman and Armelagos 1985; Trinkaus 1995; Ogilvie *et al.* 1989; Goodman 1991). Trinkaus (1995:138) emphasized that Neandertal mortality data: "imply a population under severe demographic stress, primarily through the exceptionally high prime-age adult mortality rates and a consequent dearth of older individuals." A second study reached similar conclusions:

> These data therefore suggest that there were relatively high levels of stress with increasing age among the Neandertals. This probably reflects a significant role for dietary fluctuations, and possibly trauma, in Neandertals DEH [dental enamel hypoplasias]. The overall implication is that the European and Near-Eastern Neandertals experienced

> frequent nutritional deprivation, perhaps on an annual basis given the multiple episodes evident in many of the more complete dentitions (Ogilvie *et al.* 1989:32).

However, the etiology of dental enamel hypoplasias, on which these studies are based, is complex (Goodman and Armelagos 1985), and its implications concerning nutrition have been challenged (Neiburger 1990, 1991). Therefore, these results should be considered provisional.

These observations suggest that the last Neandertals were relatively close to the carrying capacity of their environment given their mode of subsistence. Similarly, it is assumed that no significant or extended food storage techniques were used by Neandertals to resolve scheduling conflicts or for increasing predictability in food acquisition. Moreover, a last assumption is that the Neandertal extinction is linked to the migration of modern humans, and that it cannot be explained *solely* by climatic changes or competition with other animals.

Lastly, one can argue that the above implications are not exhaustive, as plants are not considered as an adaptive solution. However, ecological studies of climates relatively similar to those inferred for France during the Middle to Upper Paleolithic transition (e.g., the Canadian Subarctic) show that plants would have been a marginal food resource in this kind of environment (Binford 1978, 1980; Smith 1991). This is especially the case during the snow-covered season, the period of the year with the least predictability in terms of abundance of resources. Importantly, these assertions about Neandertal diet are supported by isotopic studies (Ball *et al.* 1987; Bocherens *et al.* 1991; Fizet *et al.* 1995; Richards *et al.* 2000; Balter *et al.* 2001; Bocherens and Drucker 2003). Palynological analyses of pollen sequences recording the shift from the Middle to the Upper Paleolithic in France also support the notion that plant foods were relatively unimportant in the Neandertal diet (Guyot 1990; Guyot *et al.* 1993).

These assumptions underlie the archaeological implications derived from the replacement model. Two scenarios of replacement are considered most plausible. The first scenario, implicit in many replacement hypotheses, is that a limited number of group of modern human migrants replaced the archaic *sapiens*. The second scenario is that the replacement of archaic *sapiens* was made possible through a demic expansion of modern humans (e.g., Eswaran 2002). Although the second model seems a more viable hypothesis, test implications are derived from both scenarios.

Scenario 1: Migration of a limited number of modern human groups

Wobst (1974, 1976) published provocative ideas about Paleolithic social system size based on a Monte Carlo simulation. Wobst (1974:154) was especially interested in finding the *minimal equilibrium size* (MES) of Pleistocene populations: “defined as the number of people which will consistently guarantee the presence of a suitable mate for a group member upon reaching maturity.” The advantage of such an approach is that “since all animals have mating networks, the concept is more general and more flexible than maximum band, dialectical tribe, or connubium” (Wobst 1976:50). To accomplish this, he designed a computer simulation to find the minimum number of people necessary to insure the biological perpetuation of a population. The mating network of the simulation was composed of two-tiers of hexagons (each corresponding to a minimum “band”), a geometric abstraction commonly used to render human spatial organization. According to

Wobst, 7 to 19 interacting *minimum bands*, each composed on average of 25 individuals, were necessary to allow the perpetuation, over the long term, of the breeding unit. This would give a range of 175 to 475 individuals to the mating network, figures that are remarkably close to those found in the ethnographic literature (Birdsell 1953, 1958, 1968; Yengoyan 1968; but see problems with Birdsell's estimates in Kelly 1995). Because most of the values generated by his simulations fell in the upper part of this range, Wobst (1976:50) argued that given that since "these are minimal size estimates, 475 people may be considered a practicable lower limit."

The postulate underlying Wobst's minimal mating network is that the breeding unit can perpetuate itself in isolation of other mating networks (sets of hexagons). This is an important point for our discussion, as it can be used to assess the lower group size limit needed to ensure the biological persistence of a migrating population over time. It may also be productive to investigate the spatial extent of the mating network of the migrant population. Wobst used population density estimates of pre-contact hunter-gatherer groups in Canada, Alaska, and Siberia to infer mating network areas. The lowest estimates range from 0.05 to 0.005 persons/km^2 for an area of 9,500 to 95,000 km^2. These population density estimates are useful, as they are associated with an environment broadly similar to the one reconstructed for Western Europe during the Middle/Upper Paleolithic transition (e.g., Delpech 1983; Gamble 1999). In the literature, it is generally argued that archaic *sapiens* and early modern humans had low population densities (Wobst 1976:50; Mellars 1996:345). In this perspective, even in using population densities that are five times lower than the lowest of these ethnographic estimates (Table 2), the distance between the migrants (once in France) and the mother population is still too large (some 3,500 km) to be simply occupied by a portion of a mating network connected with the Levant. Using population density estimates that are lower might be unrealistic as mates would not be likely to find each other. This means that an *independent* breeding unit would have been necessary for maintaining the migrant population. In other words, a modern human group migrating into a new, in this case *already* occupied, environment would have needed at least one (no more is theoretically necessary) breeding unit of 475 people in order to allow its biological perpetuation. Wobst's results show that a substantially smaller population would have most probably led the migrants to extinction.

Population Density (persons/km^2)	*Number of People in the Mating Network*	*Diameter (km) of the Mating Network*	*Area (km^2) of the Mating Network*
0.05	475	120	9,500
0.005	475	382	95,000
0.001	475	500	475,000

Table 2. Areas of mating network for some given population densities. The first two population density estimates (0.05 and 0.005) are based on ethnographic reports (data from Wobst 1976:51, Table 1). The other one (0.001) is a deliberately low estimate.

It is important to remember in this discussion that a slight difference in mortality (2%) is enough to lead a human population to extinction in no more than a millennium (Zubrow 1989). However, the probability for the extinction of modern humans might in fact have been higher than for the local populations (Neandertals and other archaic populations), as extinction is very common in small colonizing groups (<500 individuals). This is due to the effects of stochastic processes affecting reproduction, in particular with respect to the maintenance of a 50:50 sex-ratio (McArthur *et al.* 1976; Lande 1988). In reality, a large body of work in conservation biology shows that small populations often go extinct (e.g., Boyett *et al.* 2000). In addition, inbreeding enhances the fixation of deleterious alleles, which also decreases fitness (Abrams 2002). However, demography appears to be a more important factor in this discussion than allelic changes (Lande 1988). A large population (>500 individuals) of modern human migrants would have reduced the chance of extinction, but would have increased pressure on resources (see below). Therefore, contrary to a widely held notion, modern human groups would have been as exposed to extinction, and perhaps even more so, once in Eurasia. In sum, from a demographic perspective, a migration out of Africa is not likely to have met with success, especially in an already populated area.

Although the probabilities are not high, let us assume that modern humans succeeded in maintaining a viable population over time in Eurasia. In that context, the addition of a modern human breeding unit to an archaic *sapiens* one would have increased population densities very significantly. Because archaic *sapiens* population densities were apparently close to the carrying capacity of the environment, it seems reasonable to expect population pressure to occur as a result of the superimposition of these independent breeding units. In fact, no matter how slow or rapid the migration might have been, population pressure would have followed either as a direct consequence of the presence of the migrants, or indirectly as the result of displaced archaic *sapiens* groups moving into marginal niches. Thus, the logical consequence of a modern human migration is straightforward: archaic *sapiens* and modern humans should have experienced serious subsistence stress as a result of overpopulation. With respect to modern humans, a lack of information on local resource distribution and availability in the new environment, which decreases foraging efficiency considerably, might have amplified this problem.

Scenario 2: A modern human expansion out of Africa

Eswaran (2002) has recently discussed mechanisms that would have been involved in a modern human demic expansion out of Africa during the late Pleistocene. In this model, modern human groups would have budded off regularly from an expanding parent population and colonized Eurasia and Australia. Importantly, the modern human expansion is argued to have resulted in the continuous formation of a population bottleneck at its *edge* under conditions: "involving a low rate of interdeme admixture ("interbreeding") and strong selection" (Eswaran 2002:749). A low rate of interdeme admixture implies little gene flow between the groups that bud off and the parent population. Ultimately, this demic expansion would have culminated in the progressive replacement of archaic *sapiens*. The characteristics of this scenario, presented as support to the hybridization model, led Harpending (2002) to refer to Eswaran's mechanism as a "rolling bottleneck." However, these interesting ideas were criticized because the coadapted combination of novel genes said to have favored modern humans over archaic *sapiens*, a gene complex presumed to have promoted changes in pelvis shape and have reduced childbirth mortality, does not find support in the skeletal data (Rosenberg 2002; Trinkaus 2002). Furthermore, as stressed earlier, a biological feature that is selectively advantageous in one type of habitat might not have been as comparably advantageous in another. Lastly, an additional difficulty with the rolling bottleneck model is that it does not provide an explanation for the lack of interdeme admixture.

Because they rely on explicit mechanisms, replacement hypotheses based on a demic expansion of modern humans, as the one envisioned by Eswaran (2002), appear more viable than propositions relying on vaguely defined "migrations." Problems specific to Eswaran's model were discussed in the previous chapter. However, what would be the ecological implications of a modern human expansion out of Africa?

In contrast to the migration scenario, the replacement of archaic populations is assumed in demic expansion models to have occurred through the cumulative effects of the budding off of small modern human groups (e.g., less than 50 individuals) at the edge of the expanding parent population. The colonization of niches already occupied by archaic *sapiens* is likely to have increased pressure on local resources. This would follow from the fact that segments of the habitats in which modern human migrants moved in would have became unavailable to archaic *sapiens* groups, assuming, as seems likely, that interaction between both populations was tense and often conflictual. The presence of modern human migrants would have had for effects of limiting access to some food patches. In a context in which food stress was apparently already a source of concerns, these additional constraints on patch exploitation are likely to have promoted resource depression. This situation would have been repeated over and over as the "diffusion wave," to use an expression common in replacement hypotheses, proceeded.

In this scenario, the physical presence of modern humans limits access to food patches. However, constraints might have been indirect. For instance, the purported diffusion wave probably fueled conflicts and promoted the emergence of buffer zones between the modern human colonizing groups and their archaic neighbors. Buffer zones commonly appear between competing neighboring groups. For instance, in southern Québec, the St.Lawrence River, which was previously used by the Hurons as a hunting ground, became a buffer zone between this group and the Iroquois during the fur trade period (Trigger 1991). Buffer zones would also have had the effects of limiting access to food patches.

Because food stress appears to have been relatively common in some, perhaps most, of the archaic populations prior to their inferred replacement, it is reasonable to assume that both migration and demic expansion scenarios resulted in more limited access to food patches, competition for resources, and, declines in foraging efficiency. Resource depression is expected to have followed from these constraints. In these conditions, archaic *sapiens* and modern human populations would have reacted to resource depression, as would any predator species, by adapting. Specifically, they are expected to have redefined their ecological niche. In other words, it is argued here that these populations did not simply and passively “decline in numbers,” but reacted in trying to solve the problem of decreased foraging efficiency.

These propositions are interesting because they lead to test implications that can be falsified with archaeological material. Moreover, this hypothesis also tests the hybridization model, which assumes, like the replacement position, a modern human migration, although some limited interbreeding is allowed in the former model.

Displaced archaic *sapiens*?

It might be argued that archaic *sapiens* responded to modern human expansion by migrating to new and poorer environments, which may already have been occupied by other archaic populations. Resource depression would ensue inevitably. A similar conclusion was reached concerning the Neandertals by Stringer and Gamble (1993:193-194), two strong supporters of the replacement model: "With only finite resources, the Neanderthals would have suffered from economic competition unless they withdrew to more marginal areas (such as, in this context, the southern Iberian and northern British peninsulae)." Therefore, a decrease in foraging efficiency seems an inescapable conclusion. With respect to archaic *sapiens*, it would either be caused by i) direct competition with modern humans, ii) direct competition with displaced archaic *sapiens* populations, or iii) displacement into unoccupied but more maginal habitats. With respect to modern humans, a decline in foraging efficiency might result from i) direct competition with archaic *sapiens*, *and* ii) due to lack of information relative to resource availability and distribution.

Operationalizing the resource depression hypothesis

A major implication of the replacement model is that overpopulation would have resulted in resource intensification during the Middle to Upper Paleolithic transition. By resource intensification, is meant that the total amount of calories extracted per area would have been increased in response to an overall decrease in foraging efficiency

(Broughton 1994a). This concept leads to the formulation of several lines of evidence, which are used to determine whether resource intensification is documented during the Middle to Upper Paleolithic transition.

According to Binford (1978:44): "Under conditions of game scarcity when search and pursuit time would necessarily be high, we would expect maximizing to take the form of maximum utilization of available food regardless of labor costs in transport and processing." This maximizing behavior can be investigated across *individuals* and across *sets* of individuals (species). In the first case, a likely solution is to widen the breadth of body parts that are consumed by including in the diet low-ranked elements that are usually not exploited (Grayson 1989). Therefore, it might be predicted that Neandertals and modern humans optimized food exploitation by increasing transfers of body parts from kill locations to campsites in periods of chronic food stress. Parts in which fat is mobilized late, for instance the mandible and feet (Speth 1983; Blumenschine and Madrigal 1993), might have been transported more often during the Châtelperronian and Early Aurignacian. This might also include parts with high field-processing costs like the vertebral column (O'Connell *et al.* 1990; Oliver 1993) and bulky parts like the male head in the case of caribou (Binford 1978). Utility models, which gained wide influence in archaeology, (e.g., Binford 1978; Metcalfe and Jones 1988; Emerson 1993) will be used to investigate decision-making relative to skeletal part transport. However, because animal body condition varies throughout the year in many ungulate species (e.g., Kelsall 1968; Berger and Cunningham 1994), some parts might have been discarded due to low fat content depending on the season of the kill. For instance, necks and forelegs (including the metacarpal) of caribou are often selected against in spring by the

Nunamiut, these parts being too lean (Binford 1978:40). Consequently, this dimension needs to be included in the analysis of utility models.

Another solution to resource depression is pointed out by Binford (1978: 31, 36, and 43) who was told by Nunamiut informants that in times of food shortage people adapted by exploiting the marginal amount of marrow present in the scapula, pelvis, phalanges, and mandible (Binford 1978:31, 36 and 43). A small amount of marrow can also be extracted from the talus (astragalus) and calcaneum. If the replacement model is correct, we might observe an increase of parts exploited for marrow in the Châtelperronian and Early Aurignacian.

In addition to these strategies, Neandertals and modern humans might have initiated scavenging or increased the monitoring of dead carcasses. It is important to stress that scavenging is not uncommon among modern foragers (O'Connell *et al.* 1988; Bunn *et al.* 1988). In this context, an increase in carnivore-damaged bones might be expected in Châtelperronian and Early Aurignacian assemblages. This, however, requires careful taphonomic control, for instance by looking at the incidence of cutmarks on carnivore-damaged bones, as well as through the examination of the species and types of elements modified by carnivores and/or humans. This will help to address problems of equifinality relative to the distinction of these two agents of bone accumulation.

Grease rendering might also have been used as an adaptive solution, as fat is highly valued by foragers and herders (Ingstad 1992; Binford 1978; Levine 1998). One reason for this might be that fat plays a very important nutritional role, especially in periods of growth and stress (Speth and Spielman 1983). Because epiphyses are rich in fat (Brink 1997), we might expect these parts to have been processed extensively for grease or transformed into bone cakes in Châtelperronian and Early Aurignacian assemblages. However, despite recent efforts (Outram 2001; Church and Lyman 2003), the detection of these activities in archaeological assemblages remains intricate, due to the difficulty of determining bones fractured behaviorally from those fragmented postdepositionally. Nonetheless, it is possible to offer some interpretations for the assemblages studied here based on indirect evidence.

Optimal foraging theory is increasingly used as a conceptual framework for studying subsistence (Winterhalder *et al.* 1988; Smith 1991; Hawkes *et al.* 1991; Broughton and Grayson 1993; Broughton 1994b, 1997; Cannon 2000; Jones 2003). This body of theory predicts that items are selected starting with the highest ranked resource. When foraging efficiency declines, lower-ranked items are added sequentially to the diet in order of decreasing rank (Stephens and Krebs 1986; Smith 1991; Winterhalder and Lu 1997). With respect to fauna, ranking of items is usually based on prey body size, argued to be a reliable proxy for determining net energetic returns (Broughton and Grayson 1993; Broughton 1994b, 1997; Cannon 2000a; but see exceptions in Madsen and Schmitt 1998 and Jones 2003). It is important to note that resource rank is independent of encounter rate (Broughton 1994a).

The prey choice model predicts that, when encountered, high-ranked items are always taken. Conversely, low-ranked resources are selected only when there has been a significant decrease in the encounter rates of higher-ranked taxa (Broughton 1994a). Based on their size, mammoth, Irish elk, bison, horse, red deer, and reindeer would have represented high-ranked taxa in the area and time span under study. In fact, the last four are the best candidates, as handling (pursuit and processing) costs for the first three were probably relatively high. Lagomorphs, birds, carnivores, and fishes appear to have been low-ranked taxa in Western Europe during the late Pleistocene. Small carnivores are included in this list because it has been observed that they are "only used as human food in extreme emergencies" by some high-latitude foragers (Binford 1978:99).

It is important to stress that finding differences in the relative abundance of low-ranked taxa during the Middle to Upper Paleolithic transition does not necessarily imply a shift in foraging efficiency. At least four variables: season of occupation, site function, technology, and climate can induce substantial changes in the taxonomic composition of an assemblage unrelated to resource depression (Grayson and Delpech 1998; Grayson and Cannon 1999). As an example, the use of drives and nets in hunting may increase the foraging returns significantly for a given species and raise its relative rank (Broughton 1994a). This is because the "patch" of individuals, a school of fish for instance, rather than the individual alone, becomes the unit of observation (Madsen and Schmitt 1998). Similarly, climatic changes can increase or decrease the breadth of resources potentially exploitable (Grayson and Delpech 1998). These factors, therefore, need to be taken into account.

When one looks at the list of species commonly identified in archaeological and natural assemblages from the late Pleistocene, a natural break in body-size between high-ranked and low-ranked taxa is found, with few intermediates (Figure 4). Badgers, lagomorphs, birds, and fishes are much smaller than the smallest ungulate available. This is even more true if we exclude the roe deer, an ungulate characteristic of wooded environments poorly represented in most late Pleistocene assemblages (Delpech 1983).

In the French Paleolithic, taxa smaller than the roe deer were rarely acquired by humans before the Magdalenian (Bouchud 1966; Delpech 1983; Laroulandie 2000, 2003). Assuming that hunting techniques did not change significantly during most of the Late Pleistocene, this might be taken to suggest that caloric returns from these taxa were not considered high enough to warrant their inclusion in the diet. However, some assemblages older than the Magdalenian have been interpreted as being exceptions to this rule (Cochard 2004).

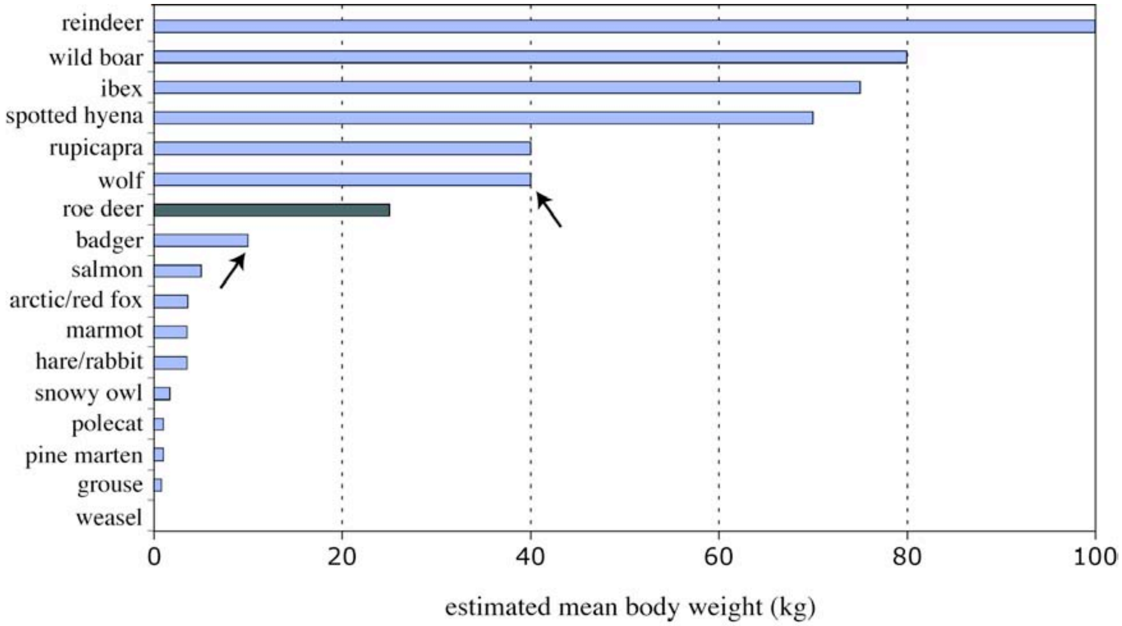

Figure 4. Estimated mean body weight (males and females) for various resources commonly found in the late Pleistocene of southwestern France. The arrows show the gap in body weight occupied only by the roe deer. Data from MacDonald and Barrett (2001). Body weights for species with no living counterparts are based on estimates based on their closest analogues.

All else being equal, if Neandertals came to be into direct competition with modern humans for resources, we might expect shifts in the proportion of low-ranked resources, particularly lagomorphs, small carnivores, and birds, during the Middle to

Upper Paleolithic transition (see further discussion in Chapter 7). Cutmarks and percussion notches will be used to determine whether these taxa were accumulated by humans rather than by carnivores or other natural agents.

In summary, the resource depression hypothesis is examined using six lines of evidence:

i) increase in transport of skeletal parts with low utility, high processing costs or that are bulky (e.g., vertebral column, heads, phalanges)
ii) marrow exploitation of low utility parts (mandible, scapula, pelvis, calcaneum, talus, phalanges)
iii) increase in scavenging
iv) development of the grease rendering of long bone epiphyses and other fatty parts
v) exploitation of low-ranked taxa

An additional line of evidence, cutmark frequencies, may also be used to document resource depression, as it may signal change in intensity of part processing (Grayson and Delpech 2003). However, *observed* cutmark frequencies are not unambiguously related to intensity of processing, as other factors, for instance differential preservation, may contribute to decrease the abundance of cutmarks (Lupo and O'Connell 2002). However, bone surface preservation varies, as we will see (Chapter 5), within and between the Saint-Césaire assemblages. Because variation in bone surface preservation probably affects the interpretation of cutmark frequencies in the assemblages, this line of evidence is not pursued further here.

These lines of evidence are here used to test the Neandertal replacement model. For a variety of reasons, including choices that are culturally motivated, some of these predictions may fail individually. However, if *all* these lines of evidence fail to show evidence of resource depression, one must seriously consider the alternate explanation of significant gene flow between Neandertals and modern humans. A second possibility might be that the proposed modern human migration never occurred.

Materials for the test

An archaeological sequence has been selected for testing the Neandertal replacement model. Three criteria were considered in the site selection. First, the site should be characterized by well-dated occupations relevant to the period in which the Neandertal replacement is presumed to have occurred. Second, the samples should be large and well preserved. Third, detailed information about the archaeological context in which the assemblages were found should be available in order to assess precisely the origin and taphonomy of the faunal samples.

Sites located in southwestern France are especially well suited for testing the archaeological model presented in this study, given that this region has always played, as we have seen, an important role in the replacement model. Indeed, several "classic" Neandertal skeletons, for instance those from La Ferrassie, La Chapelle-aux-Saints, La Quina, and Le Moustier, were excavated in this region (Boule 1923). Because many Châtelperronian sites were discovered and exploited a long time ago, there are, unfortunately, few carefully excavated sites (Sonneville-Bordes 1960). Saint-Césaire is a notable exception. This site presents a long sequence of occupation, including late Mousterian, Châtelperronian, and Early Aurignacian occupations (Lévêque 1993; Lévêque and Miskovsky 1983). Faunal samples are relatively large and well preserved. Importantly, recovery of the specimens has been maximal; that is, all the sediment was dry-sieved with a fine mesh (see Chapter 4 and 5). All detectable bones and flakes have been collected, recorded, and bagged, therefore obviating the thorny issue, common in numerous old excavations, of bone sorting (Turner 1989; Marean and Kim 1998; Bartram and Marean 1999). As a result of this exceptional archaeological sequence, Saint-Césaire may be appropriately used for making propositions about variation in subsistence stress during the Middle to Upper Paleolithic transition.

CHAPTER 4

FAUNAL REMAINS AT SAINT-CESAIRE

Many of the implications derived from the replacement model are based on taxonomic composition and skeletal element representation. As a result, it is necessary to provide an accurate picture of these dimensions in the assemblages. Taxonomic composition and body part representation are detailed in this chapter for each of the major assemblages from Saint-Césaire. This follows a presentation of previous research on the site and a summary of its stratigraphy.

Presentation of the Saint-Césaire site

The Saint-Césaire site, locally known as La Roche-à-Pierrot, takes its name from a village located 10 km northeast of the city of Saintes in Charente-Maritimes, France. The site consists of a collapsed rockshelter at the base of a 5 to 6 m Upper Turonian limestone cliff exploited in the past as a quarry. The quarry galleries have been used to grow mushrooms and it is during the construction of an access road to one of these mushroom farms that the site was discovered and partially destroyed (Lévêque 1993a). This means that the site was probably somewhat larger than the excavated surface. Excavation of the site was carried out during twelve consecutive seasons ending in 1987 under the direction of F. Lévêque, former chief curator of the *Service Régional d'Archéologie* for the Poitou-Charente area (Lévêque 1993a). In addition, some test pits were subsequently dug in 1993 in the slope deposits (Backer 1994). Before its collapse, the rockshelter would have faced north-northwest in the direction of the valley of the Coran, a stream feeding the Charente River.

Saint-Césaire has a remarkable sequence of late Mousterian, Châtelperronian, and Aurignacian occupations. The excavation methods that prevailed at Saint-Césaire have been presented by Lévêque (2002). The site has been dug using a metric grid system composed of 1 m square units. Except for a few test pits, squares were all divided into four quadrants (sub-squares). As usual on Paleolithic sites, excavation proceeded through *décapages*, the site minimal stratigraphic unit, defined as a 50 x 50 cm horizontal slice usually 5 to 10 cm thick[2] (Lévêque 2002). In stratigraphy, a layer consists usually of several superimposed décapages. Knives were used as excavation tools. Artifacts that were considered particularly informative, stone tools and taxonomically identifiable faunal remains for instance, were piece-plotted *in situ*, while the rest of the material was collected by décapage. It is very important to note that all sediments were dry sieved using a 5 mm and 2 mm mesh screen (Lévêque 2002). Most of the bones that were preserved were collected and made available for study, thus countering the problem of biases against mid-shafts frequently observed in old excavations (Turner 1989; Marean and Kim 1998; Bartram and Marean 1999). Moreover, a life-size cast of a portion of the excavated surface, with the archaeological vestiges still *in situ,* was made by J. Airvaux

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[2] Lévêque uses the term *demi-taille* for the 5 cm unit and *taille* for the 10 cm unit.

(*Service Régional d'Archéologie*, Poitou-Charente) for both the Denticulate Mousterian (EGPF) and Châtelperronian (EJOP sup) occupations (Lévêque 2002).

The site stratigraphy

The Saint-Césaire stratigraphy has been described in several studies (Lévêque and Miskovsky 1983; Miskovsky and Lévêque 1993; Lévêque *et al.* 1993; Lévêque 1987, 1989, 1997) and is summarized in Table 3. Only the assemblages relevant to this study, that is, the eight uppermost faunal assemblages in the sequence, from the terminal Denticulate Mousterian to the Evolved Aurignacian (levels EGPF to EJJ), are detailed below. The other Mousterian levels have not been studied yet. The following description of the sedimentologic sequence, based on an east-west (frontal) cut in line 3/4, is a summary of a description provided by Miskovsky and Lévêque (1993).

The Saint-Césaire site shows a superposition of two major stratigraphic groups (gray and yellow) sitting on a red group (*ensemble rouge*) found on top of the limestone bedrock. These major groups are: i) an Upper Yellow Group (*ensemble jaune*), which includes the Châtelperronian and Aurignacian assemblages, overlying ii) a Lower Gray Group (*ensemble gris*) constituted of Mousterian of Acheulean Tradition and Denticulate Mousterian occupations.

The lower gray group is 1.20 m thick on average and contains all the Mousterian occupations. In the lower part of the gray group are found two occupations attributed to the Mousterian of Acheulean Tradition and three low-density layers. Three Denticulate Mousterian occupations cap the Mousterian sequence (Lévêque 1987). Bison, horse, and reindeer are the most common remains in the very rich Denticulate Mousterian EGPF occupation (Ferrié 2001).

The upper yellow group, corresponding to the Upper Paleolithic sequence, is approximately 1.60 m thick on average and sits on top of the EGPF level. At the bottom of the yellow group is found a small occupation moderately rich in bones called EJOP inf. Although this occupation has been attributed to the Châtelperronian, this cultural attribution is not as strongly supported as for EJOP sup and its status is currently unclear (F. Lévêque, pers. com. 2003). As a result, this assemblage will be referred to as the "Châtelperronian?" assemblage throughout the test. It is in the overlying Châtelperronian (EJOP sup) level that the Neandertal skeleton discussed in Chapter 2 was discovered, as well as elements of a human hand (Lévêque and Vandermeersch 1980; Vandermeersch 1984; Crèvecoeur 2002). This level also shows evidence of hearth construction and maintenance, and rare traces of wood charcoal (Lévêque 1987; Backer 1993, 1994). As we will see, bison, reindeer, and horse are, in that order, the most abundant species in this occupation.

The level above the Châtelperronian is the low density EJO inf layer. This low-density layer is found below the EJO sup occupation associated with a Proto- or Aurignacian I assemblage, in which evidence of bone tool making is documented. The cultural affiliation of this level being unclear, the EJO sup occupation is designated in the text as the Aurignacian 0? assemblage.

Reindeer remains are extremely abundant in the EJO sup level and in the overlying Aurignacian occupations. Several boulders are found in the above Aurignacian I (EJF) level, an occupation characterized by the presence of numerous hearths (Backer 1994). Split-base bone points, carinated endscrapers, Dufour bladelets, and strangulated blades, elements characteristic of the Aurignacian I (Sonneville-Bordes 1960), were also recovered in this level. The uppermost levels of the site, EJM and EJJ, are attributed to the Evolved Aurignacian.

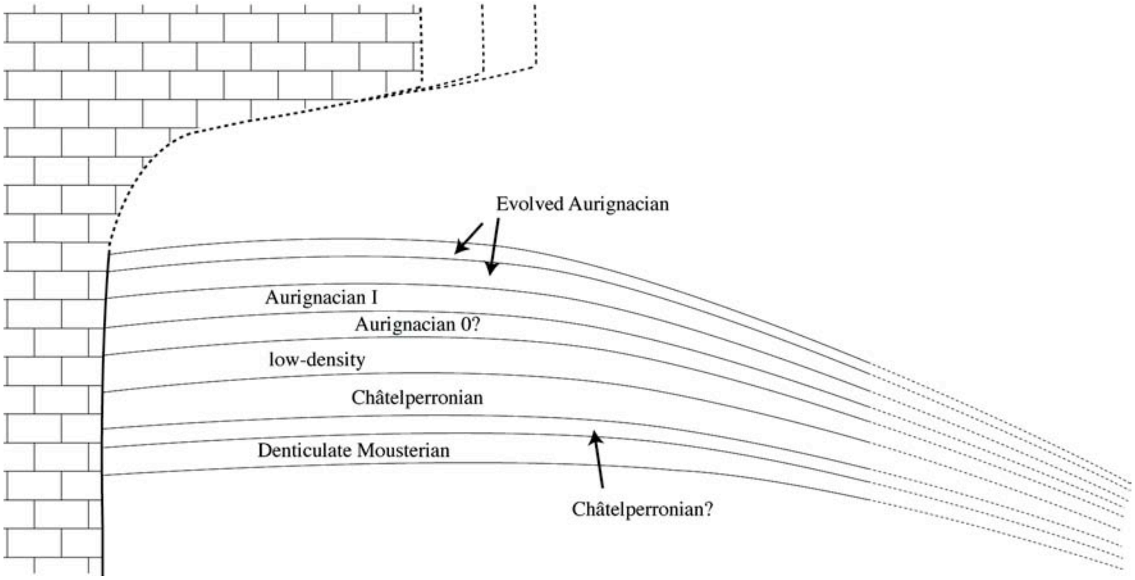

Figure 5. Reconstruction of the Saint-Césaire sagittal stratigraphy based on a three-dimensional analysis of piece-plotted artifacts. The dashed section indicates the area of the deposit in which layers tend to merge.

A north-northeast dip has been observed in the Saint-Césaire deposits. The excavation grid is therefore slightly off of the natural slope of the site. In general, the archaeological levels get thinner the farther we move from the cliff (Figure 5). Starting on rows 6 and 7, but most obvious in rows 8 and 9 where the slope is steeper, cultural levels tend to merge into a single layer (Lévêque 1997). The Mousterian levels, at the bottom of the sequence, are sub-horizontal over a distance of 10 m, after which the slope becomes steeper away from the cliff. In the upper part of the sequence, the Aurignacian layers are relatively slanted and tend to be thicker near the cliff. The slope of the underlying Châtelperronian occupation is not as marked.

Unit	*Level*	*Cultural Attribution*	*TL Dates*	*Level Characteristics*
	Humus (1)	Post-Paleolithic		humus
	Eboulis (2)	?		characterized by large limestone slabs
Upper group (yellow)	EJJ (3)	Evolved Aurignacian		yellow clayey-sandy sediment with small limestone elements. Small reindeer-dominated sample
	EJM (4)	Evolved Aurignacian		yellow-brown clayey sediment with limestone elements that are generally bigger than in EJJ. Moderate size assemblage dominated by reindeer
	EJF (5)	Aurignacian I		yellow clayey sediment containing several medium to large clasts. Characterized by several hearths and dark soil color. Rich Aurignacian I assemblage dominated by reindeer
	EJO sup (6)	Aurignacian 0?	30.8 ± 3.3 34.0 ± 3.9	yellow-orange sediment with small limestone rubbles. Small assemblage dominated by reindeer. Aurignacian 0?
	EJO inf (7)	Low-density		yellow-orange sediment of fine texture. Almost devoid of blocks and artifacts.
	EJOP sup (8)	Châtelperronian	36.6 ± 5.0 38.2 ± 5.3 33.7 ± 5.4 36.6 ± 4.9 37.4 ± 5.2 35.6 ± 4.6	pale yellow-orange clayey-sandy sediment with numerous angular limestone blocks. Relatively rich Châtelperronian assemblage dominated, respectively, by bison, reindeer, and horse remains.
	EJOP inf (9)	Châtelperronian?		pale yellow-orange clayey-sandy layer with only rare limestone fragments. Fauna dominated by bison, reindeer, and horse. Châtelperronian?
Lower group (gray)	EGPF (10)	Denticulate Mousterian	41.4 ± 4.2 (average of 9 dates)	pale gray level with hearths. Extremely rich assemblage. Faunal sample dominated by bison, horse, and reindeer remains
	EGP (11)	Denticulate Mousterian	39.7 ± 3.9 36.8 ± 3.7	pale gray sediment, sometimes indurated, with limestone fragments. Small assemblage
	EGF (12)	Denticulate Mousterian	42.4 ± 4.3	gray sediment with evidence of burning. Small assemblage
	EGC sup (13)	Few artifacts		light gray sediment. Small assemblage
	EGC (14)	Mousterian of Acheulean Tradition		light gray sediment characterized by several patches of burning. Small assemblage
	EGC inf (15)	Few artifacts		light gray sediment. Very small assemblage. Probably Mousterian
	EGB sup (16)	Mousterian of Acheulean Tradition		gray-tan sandy sediment. Small assemblage
	EGB inf (17)	Few artifacts		gray-tan to reddish sandy sediment. Very small assemblage. Probably Mousterian
Basal group (red)	ER	Sterile		Interface with the bedrock. Red sandy-clayey matrix with flint nodules and limestone elements

Table 3. Summary of the Saint-Césaire stratigraphy. TL dates are in ky and are drawn from Mercier *et al.* 1993.

Although the site is not protected today by an overhang of the cliff, a sagittal view of the piece-plotted artifacts suggests that Saint-Césaire had been a rockshelter or a small cave in prehistoric times, as the portion of the levels immediately adjacent to the cliff is inclined toward it, a feature often seen in this type of setting. This is inferred to reflect the preferential accumulation of sediments near the prehistoric dripline.

Chronology of the occupations

The chronology of Saint-Césaire is well documented, as several occupations have been dated. According to Mercier *et al.* (1993), thermoluminescence is the only method that gives reliable results at the site, as bones tend to contain too little collagen for C–14 dating. The three uppermost Mousterian occupations were dated successfully using the thermoluminescence method. All occupations seem to cluster around 40,000 B.P. (Table 3). If this apparent synchronicity is not an artifact of the method, these dates would testify of a rapid sedimentation rate. The Châtelperronian EJOP sup level would be slightly younger and is dated at *ca.* 36,300 B.P. (Mercier *et al.* 1991). In addition, dates of 30,800 ± 3,300 and 34,000 B.P. ± 3,900 were obtained for the Aurignacian 0? occupation. These last dates appear too young, however, compared with assemblages with similar artifactual composition. Importantly, with the improvement of C-14 dating, it may be possible to obtain reliable C-14 dates for the site in the future.

The archaeological context of the assemblages

Artifactual composition

Little information is available for the uppermost Denticulate Mousterian (EGPF) assemblage from Saint-Césaire. The assemblage is dominated by denticulate and notches (approximately 60%), and sidescrapers (approximately 20%). Endscrapers, truncations, points, foliates, burins, beaks, and other tools are also present (Backer 1994).

The Châtelperronian level (EJOP sup) in which the Neandertal skeleton was found is a moderately rich assemblage. Its attribution to the Châtelperronian is based on the recovery of 33 Châtelperron point fragments, reduced to 30 specimens after refitting, in addition to the occurrence of several tools commonly found in Châtelperronian contexts, for instance thin circular endscrapers, prismatic cores, and blades (Lévêque *et al.* 1993; Guilbaud 1993). The lithic assemblage from the EJOP sup level has been presented by Lévêque (1993b) and Guilbaud (1993). Both studies have highlighted the "archaic" and "Mousterian" character of the assemblage. Lévêque (1993b) has published stone tool counts, based on a sample of 305 specimens (Table 4). Sidescrapers, usually laterally retouched, are the most common tools in the assemblage followed, in decreasing order, by denticulates, backed knives, endscrapers, burins, backed blades, and beaks. Points, foliates, and tools with scalar and abrupt retouch are rare. Some of these tools were removed from the core with a soft organic hammer (Backer 1994; Soressi, pers. com. 2003).

Tool Type	*n*	*%*
sidescrapers	122	40.0
denticulates	59	19.3
Châtelperron knives	26	8.5
endscrapers	18	5.9
burins	14	4.6
backed blades	14	4.6
beaks	13	4.3
tools with scalar retouch	13	4.3
tools with abrupt retouch	13	4.3
points	8	2.6
foliates	5	1.6
total	305	100.0

Table 4. Stone tool counts for the Châtelperronian (EJOP sup) occupation (data from Lévêque 1993b:26 and 27).

Guilbaud *et al.* (1994) estimate that about half of the cores from the assemblage are clearly Mousterian-like, while 25% would be characteristic of the Upper Paleolithic. A little more than 27% of the cores show blending of Middle and Upper Paleolithic characteristics. Interestingly, some of these cores are similar to those found in the Denticulate Mousterian EGPF level (Guilbaud *et al.* 1994:188). This duality has been discussed with respect to concerns about the homogeneity of the Châtelperronian occupation (Bordes 1981; Sonneville-Bordes 1989; Backer 1994; Guilbaud *et al.* 1994). This important issue is discussed in the Chapter 5.

Guilbaud (1993) has identified three types of reduction sequence in the EJOP sup assemblage. The first type led to the production of large flakes with tapered edges and flat retouched scrapers obtained from flat and centripetally exploited cores. The second type of reduction sequence used centripetally exploited and undifferentiated cores in order to make small short flakes retouched into scrapers, denticulates, beaks, steeply retouched tools, and endscrapers. Finally, backed blades and Châtelperron knives were manufactured from elongated and cylindrical cores. It seems that a significant proportion of the raw materials was procured from deposits located near the site (Guilbaud 1993). About 5% of the lithic assemblage, however, has an exogenous origin (Backer 1994).

Some data are provided by Backer (1994) for the large Aurignacian I (EJF) assemblage. According to her, endscrapers, often on strangulated blades, are the most common tools in the assemblage. Carinated endscrapers would be very well represented in the tool sample. Lastly, bone tools and split-based sagaies were also recovered in this occupation (Lévêque *et al.* 1993).

Unfortunately, stone tool counts are not yet available for the other levels, although some information on assemblage composition can be found in Lévêque *et al.* (1993), Guilbaud (1993), and Backer (1994).

Fauna

The faunal material from Saint-Césaire has been studied in a paleontological perspective by Lavaud-Girard (1987, 1993). According to her, three taxa, reindeer, horse (probably *E. caballus germanicus*), and bovines dominate all levels. Using the material identified by Lavaud-Girard, Patou-Mathis (1993) conducted a preliminary archaeozoological study of the Châtelperronian (EJOP sup) level and concluded that the role of carnivores had been negligible in assemblage formation and that body part representation favored teeth and metapodia. Based on the presence of shed antlers and the absence of unshed antlers, she argued that the site was occupied in winter and spring (Patou-Mathis 1993:91-92). Recently, Ferrié (2001) presented his results on the

Denticulate Mousterian (EGPF) assemblage. His work, which includes some additional material from the earlier and smaller Mousterian assemblages, shows that *Bison priscus, Equus caballus germanicus,* and *Rangifer tarandus* are the most common species in the assemblage. As in the Châtelperronian, carnivores are rare in the Mousterian occupations. Cutmarks and percussion notches were recorded on many long bones. More complete results on the faunal remains of Saint-Césaire, including many unstudied levels, are presented in the next section.

Paleoecological setting

A study of pollen samples from Saint-Césaire suggest that the climate at the beginning of the Châtelperronian was relatively temperate and humid, associated by Leroi-Gourhan (1984) with the "Cottés interstadial," while the end of the Châtelperronian and the Aurignacian I would be marked by a colder and dryer climate (Leroi-Gourhan 1984; Leroyer 1988; Leroyer and Leroi-Gourhan 1993). Thermophylous species, corresponding to the "Arcy interstadial," are said to be more common in the later Aurignacian occupations. These interstadials have, however, been strongly disputed, as they rely on sequences that have not been studied from a taphonomic point of view (Sãnchez Goñi 1994). At approximately the same time that these criticisms were raised, evidence for a temperate interstadial at Saint-Césaire (Leroi-Gourhan 1984) was reconsidered after Leroyer and Leroi-Gourhan (1993) obtained dissimilar pollen spectra from new samples taken between the fingers of the isolated human hand found in the

Châtelperronian occupation. These conclusions underline the difficulty of interpreting pollen sequences in complex environments like caves and rockshelters.

Other results on the paleoecology of Saint-Césaire have also been published. Marquet (1988, 1993) conducted an analysis of the Saint-Césaire microfauna. He found that the common vole (*Microtus arvalis)* is prevalent in the lower part of the cultural sequence, whereas the narrow-skulled vole *(Microtus gregalis*) is more abundant in the Aurignacian levels. These results suggest to him that the Aurignacian was relatively cold. Within the Aurignacian sequence, the Aurignacian I (EJF) is interpreted to have been somewhat dryer, and the Evolved Aurignacian (levels EJM and EJJ), more humid. In contrast, the Mousterian and the Châtelperronian would have been more temperate. In a subsequent paper, Marquet (1988) focused on the EJOP layer (his data was collected before the adoption of the revised stratigraphic framework) and proposed that the landscape was open and associated with a cold and dry climate during that episode. We will see that the study of the macrofauna appears to confirm these results.

Human remains

In July 1979, the remains of a Neandertal skeleton were found in the Châtelperronian layer. These remains were consolidated in place, removed in block, and excavated in lab conditions by D. Gambier under the supervision of B. Vandermeersch. Most of the human bones (save for some isolated human hand bones) were distributed over a surface 70 cm in diameter and compressed within a few centimeters (Vandermeersch 1984). The skeleton is incomplete. The feet and the left half of the cranium, as well as some teeth, among others, were lacking. Several aspects of these remains have since been studied by Vandermeersch (1984, 1993; Lévêque and Vandermeersch 1980; Vandermeersch and Mann 2001; Del Prête and Vandermeersch 2001), Lalueza *et al.* (1996), Trinkaus *et al.* (1998), and Zollikofer *et al.* (2002). It has been suggested that the skeleton might have been buried intentionally (Vandermeersch 1993). The fact that many parts of the human skeleton were still in connection, in striking contrast with the fauna with respect to which few specimens were found articulated (Morin *et al.* 2004), seems to support this hypothesis. However, the human skeleton would not be the only individual represented in the Châtelperronian of Saint-Césaire, as teeth from two additional individuals are reported (Vandermeersch and Mann 2001).

Trinkaus *et al.* (1998) have highlighted the hyperarctic body proportions of the Neandertal skeleton. The femur indicates locomotor patterns comparable to those known for modern humans. Crèvecoeur (2002) has studied the human hand bones uncovered in the Châtelperronian. In addition, the skeleton was also studied for its stable isotope composition in order to infer Neandertal diet. Results suggest strong reliance on meat sources (Drucker *et al.* 1999; Balter *et al.* 2001; Bocherens and Drucker 2003).

An additional human remain, a proximal phalanx, was identified during this analysis. This specimen belongs to the Aurignacian I occupation and was found within the "charnier" ("charnel" or bone midden), a zone characterized by a high concentration of animal bones.

Methodological procedure followed in the study of the macrofauna

Eight occupations from Saint-Césaire were included in this analysis. However, some modifications of the samples were necessary before proceeding to the study of the faunal remains. One reason for this is that the interpretation of the stratigraphy has been refined during the site excavation. For instance, some units were dug using a slightly different stratigraphic framework depending on the year they were excavated. The EJOP layer was dug as a unit at the beginning of the excavation. In 1980, however, it was decided to divide this level into an upper (EJOP sup) and a lower (EJOP inf) unit after new stratigraphic observations. During the same season, the EJO level was similarly split into two stratigraphic units (EJO sup and EJO inf). Therefore, the décapages dug in these layers *before* 1980 are not fully comparable with those excavated *after* this date.

In this study, when EJOP décapages were found to stratigraphically overlay EJOP sup décapages, the former were attributed to EJOP sup, given that no reversal of stratigraphy is known for the site. This simply reflects the fact that the excavation of the EJOP sup décapages was initiated before 1980 but ended after the adoption of the revised stratigraphy. This situation applies to 15% of the EJOP décapages. This could not be done for EJOP décapages capping EJOP inf décapages, given that it is not possible to know whether the former décapages belong to EJOP inf, EJOP sup or both layers. For these units, the initial attribution was kept unmodified. However, some décapages were reattributed to more specific units with the help of François Lévêque, the excavator of the site, using field notes and stratigraphic descriptions. Changes were made only in situations where the stratigraphic description was absolutely clear and unambiguous.

Approximately 5 % of the EJOP décapages have been reattributed to more precise stratigraphic units based on this method. The remaining units (80% of the décapages) were studied according to their initial attribution.

For the EJO level, only 1% of the assemblage has been reattributed to either EJO inf or EJO sup following a similar procedure. Regarding the other levels of the site, few modifications were made. Square G4 was deleted from the Aurignacian I (EJF) and the Evolved Aurignacian EJM samples because of stratigraphic problems. In addition, forty-two décapages (approximately 2.5% of the total) were removed from the samples due to a lack of data concerning provenience or discordant stratigraphic information. Lastly, décapages that include materials from more than one layer were ignored in this study.

Certain stratigraphic units have not been detected in some squares, principally in lines 6 through 9 where the layers are thin. In addition, heavy machinery truncated lines B and C, particularly in the most recent levels. Squares concerned by these problems are not included in the density maps and have been deleted from most counts. However, taxonomically identified bones recovered in these squares were included in this study. The very rich EGPF level, the most recent Mousterian occupation of the site, has not been entirely studied yet and only a sample could be included in this study. This sample, limited to the uppermost décapages, represents approximately 15% of the faunal material of the EGPF level.

Estimating abundance in the faunal samples

Two different study grids were used in the analysis of the faunal material according to whether the bone has been identified to a specific taxon or not. By convention, NISP (Number of Identified SPecimens) refers to specific animal body part identified taxonomically, generally at least to the genus level (Grayson 1984). Foxes, lagomorphs, birds, and fishes are exceptions to this rule, however, as it was not always possible to identify them as precisely as the other taxa. NISP also includes some less precisely defined body segments like “metapodials” if the specimens could be identified taxonomically. Scientific and common names for the species identified at Saint-Césaire are provided in Table 5. All non-refitted fragments that could be identified taxonomically were counted as a single item in NISP calculations. However, mammoth teeth and antlers were sometimes severely fragmented. To avoid overestimating the abundance of these elements, fragments smaller than 2 cm were excluded from NISP counts.

Although reindeer bones are relatively easy to isolate in the samples from Saint-Césaire Saint-Césaire samples, fragmentary specimens from horse, bison, red deer, and Irish elk were in some cases hard to set apart from each other, as homologous bones tend to overlap in shape and characteristics. Following Costamagno (1999), these were generally combined in the *ungulate 3-4* size class (abbreviated as UNG3-4). Some of the other size classes (Table 6) were defined empirically, based on mean animal body size and average bone thickness, rather than body size alone. Red deer and Irish elk being poorly represented at Saint-Césaire, most UNG3-4 specimens are likely to belong to horse or bison.

Latin Name	Common Name
Artiodactyla	
Rangifer tarandus	reindeer, caribou
Bos primigenius	aurochs
Bison priscus	steppe bison
Cervus elaphus	red deer
Megaloceros giganteus	megaceros
Capreolus capreolus	roe deer
Sus scrofa	wild boar
Perissodactyla	
Equus caballus	horse
Coelodonta antiquitatis	wooly rhino
Equus hydruntinus	wild ass
Proboscidea	
Mammuthus primigenius	mammoth
Carnivora	
Crocuta crocuta	spotted hyena
Canis lupus	wolf
Alopex lagopus	arctic fox
Vulpes vulpes	red fox
Felis lynx	lynx
Mustela sp.	polecat
Mustela nivalis	weasel
Martes martes	pine marten
Meles meles	badger
Panthera (Leo) spelaea	cave lion
Ursus spelaeus	cave bear
Lagomorpha	
Lepus timidus	hare
Oryctolagus cuniculus	rabbit
Insectivora	
Talpa europaea	common mole
Pisces	
Salmo trutta	trout
Leuciscus sp.	cyprinid
Aves	
Anser sp.	goose
Anas acuta	pintail
Anas crecca	teal
Aquila chrysaetos	golden eagle
Lagopus sp.	grouse
Alle alle	little auk
Pluvialis sp.	plover
Corvus corax	raven
Rodentia	
Microtus gregalis	narrow-skulled vole
Microtus arvalis	common vole
Citellus superciliosus	ground squirrel
Chionomys nivalis	snow vole
Arvicola terrestris	water vole
Pitymys subterraneus	pine vole
Microtus agrestis	field vole
Eliomys quercinus	garden dormouse
Microtus oeconomus	root vole
Microtus malei	Male vole
Dicrostonyx torquatus	collared lemming
Rattus sp.	rat

Table 5. Scientific and vernacular names of the species identified at Saint-Césaire.

Although reindeer bones are relatively easy to isolate in the samples from Saint-Césaire Saint-Césaire samples, fragmentary specimens from horse, bison, red deer, and Irish elk were in some cases hard to set apart from each other, as homologous bones tend to overlap in shape and characteristics. Following Costamagno (1999), these were generally combined in the *ungulate 3-4* size class (abbreviated as UNG3-4). Some of the other size classes (Table 6) were defined empirically, based on mean animal body size and average bone thickness, rather than body size alone. Red deer and Irish elk being poorly represented at Saint-Césaire, most UNG3-4 specimens are likely to belong to horse or bison.

Size Class	
size 1:	size 3:
roe deer	horse
wolf	cave lion
fox	red deer
badger	cave bear
	size 4:
size 2:	aurochs/bison
reindeer	woolly rhinoceros
wild ass	Irish elk
hyena	
wild boar	size 5:
	mammoth

Table 6. Size classes adopted in this study. Birds, lagomorphs, mustelids, fishes, and rodents are excluded from this table.

To further address issues of species identification and classification, the category *"Number of Specimens of Uncertain Taxonomic Status"* (NSUTS) is introduced here. This category includes fragments for which identification is limited to skeletal part and, sometimes, body size class, without precise information regarding taxonomic status (e.g., UNG3-4 humerus, mammal tibia). Less precise skeletal identification, for instance "long bone shafts," are not included in this category, and are simply referred to as *indeterminate* specimens. Indeterminate specimens also include the *debris* category, which denotes specimens for which no precise anatomical and taxonomic information is available (e.g., spongy fragment).

In addition to NISP counts, MNI (Minimum Number of Individuals) counts were also calculated by species and occupation. This method allows one to determine the minimum number of different individuals that are represented in a sample.

Although most archaeologists are knowledgeable about NISP and MNI, few non-specialists are familiar with the MNE. The MNE is the minimum number of elements necessary to account for the specimens observed. For example, 13 left and 14 right complete distal tibiae give a MNE of 27 for this part. Because foragers often butcher carcasses, especially the larger ones, according to body units, MNE can be useful for investigating subsistence decisions (Binford 1978).

The analytical unit used to describe skeletal part frequencies in the Saint-Césaire assemblages is the %MAU, an analytical unit derived from MNE counts (Lyman 1994). MAU values are calculated by dividing the MNE for an element by the number of times this element is represented in a living individual. These values are then standardized (%MAU) by dividing them by the greatest MAU value in the assemblage. This procedure is carried out for each taxon represented in an occupation.

In addition to these counting methods, MNE values are sometimes summed in the tables by species and presented as *TMNE* (Total Minimum Number of Elements). TMNE provides a minimum value to account for the sum of all elements present in a site for a given taxon. This calculation method, designed to explore taxonomic composition, has the advantage of providing higher values than the MNI and can be used to estimate the number of food "packages" represented in an assemblage. From the perspective of taxonomic composition, this might be more productive than trying to determine the number of individuals that contributed to the sample (Binford 1978).

In the present study, data gathered using all four counting methods (NISP, MNI, TMNE, %MAU) are provided.

Derivation of MNE values

MNE counts are provided in this analysis for both proximal and distal ends, as well as midshafts, and were calculated using the most common landmark (Todd and Rapson 1988) or zone (Morlan 1994a) for each skeletal element or portion. The procedure is comparable to the one followed by Bunn and Kroll (1986), except that here age, sex, and size were not taken into account. This is justified by the fact that such a procedure contributes to inflate the representation of diagnostic parts like teeth and epiphyses over less diagnostic ones like ribs and long bone shafts. For reindeer, landmarks used by Enloe (1991) were adopted with minor modifications, whereas the terminology supplied by Barone (1999) has been followed for bovines and horses. Because antlers tend to be highly fragmented and might have been procured for reasons other than subsistence, these are excluded from most counts (additional problems concerning antlers are discussed in Chapter 5).

A different method was adopted for some specific bones for which MNE derivation is more difficult (see also Chapter 5). Castel (1999a) developed a simple tool to cope with the uniformity of the reindeer metatarsal shaft. He measured the length of the anterior groove on all the metatarsal fragments identified in a sample and divided the sum of the measurements by the total groove length of a known complete specimen. The result is a minimum number of complete metatarsal shafts, based on length measurement.

Castel (1999a:25-27) extended this principle to three other bones: the metacarpal, rib, and mandible. As he did with the metatarsal, Castel used the length of the anterior groove of the metacarpal for estimating MNE. For ribs, the total rib length was calculated on complete skeletons and compared with values generated from archaeological assemblages. MNE estimates were also produced based on the length of the marrow-bearing part of the mandible.

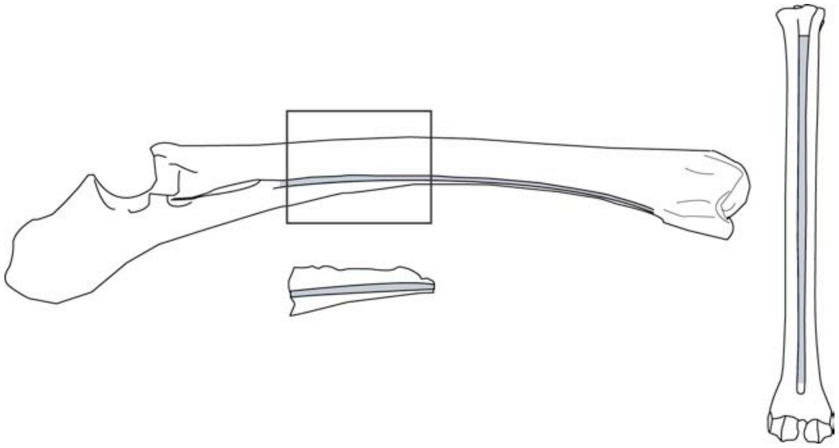

Figure 6. Features that are measured on the reindeer radio-ulna and metatarsal for calculating the MNE in this study. An hypothetical radio-ulna fragment is shown below the complete radio-ulna. The shaded area represents the section of the groove that is actually measured.

Except for this last method, these techniques were used in the study of Saint-Césaire. In addition to the methods presented by Castel, the length of the lateral groove on the reindeer radio-ulna was also measured in this study (Figure 6). Some "standard" bones are necessary to calculate the MNE in this manner. The mean length of the anterior groove on two relatively complete metacarpals from Saint-Césaire is 120 mm. For the metatarsal, the anterior groove on a complete specimen is estimated, based on a modern individual, to be 180 mm long. It is believed that this specimen is comparable in size to those found in the archaeological assemblages. The total length of the radio-ulnar groove on a nearly complete specimen from Saint-Césaire is 180 mm. These values were used as standard values for computing MNE in the assemblages.

Refitting

In order to address the concerns raised about the homogeneity of the Saint-Césaire occupations, an extensive refitting program was implemented in the study of the material (Morin *et al.* 2004). Because it may affect the interpretation of the faunal remains, it is important to detail how this refitting program has been carried out.

Due to the large quantity of material included in this analysis, it was logistically impossible to refit all bone fragments. It was therefore decided to limit refitting to certain classes of bones. Spongy fragments were not included in this program because they are difficulty to refit. As a result, the first step of the procedure was limited to the *intra-décapage* refitting of indeterminate long bones and ribs for large ungulates (UNG3-4; see below for a definition), and of ribs only for smaller taxa (Morin *et al.* 2004). Refitting focused on large ungulates because these appeared to have suffered greater postdepositional damage than smaller taxa.

The second step of the refitting program consisted in refitting most categories of bones for which taxonomic identification was available (Table 7). In contrast to the first part of the program, refitting was performed systematically across *all décapages and levels* in this case. Most taxonomically identified long bones were included in this part of the refitting program. However, because reindeer metatarsal and rib fragments were very abundant, only intra-décapage refitting was carried out for these elements.

Skeletal Element	*Reindeer*	*Bison and Horse*	*Other Taxa*
long bones	refitting across all levels[1]	refitting across all levels	refitting across all levels
short bones	intra-layer refitting only	intra-layer refitting only	refitting across all levels
teeth	intra-layer refitting only	intra-layer refitting only	refitting across all levels
antlers/horns	intra-décapage refitting only	intra-layer refitting only	refitting across all levels
ribs	intra-décapage refitting only	refitting across all levels	refitting across all levels

[1] except for the metatarsal limited to intra-décapage refitting

Table 7. Protocol adopted in refitting the faunal remains from Saint-Césaire. Short bones are carpals, tarsals, sesamoids, patellas, phalanges, and vertebrae.

Specimen coding: marks, burning, and preservation

Analysis of the indeterminate portion of the material was limited to counts, study of fragment length, burning, and spatial and vertical distribution. Maximum length and width were measured on most specimens identified to taxon in order to document fragmentation. In order to assess biases in identification and fragmentation, an attempt was made to assign all unidentified long bones to specific size class categories. Shaft fragments were coded according to shaft circumference (<1/2; >1/2; complete; Bunn and Kroll 1986), side, and length (<1/4, 1/4-1/2, 1/2-3/4; >3/4; Villa and Mahieu 1991). Long bones were also analyzed according to five regions: proximal epiphysis, proximal shaft, midshaft, distal shaft, and distal epiphysis. In most tables, however, counts are provided for complete long bones or according to three portions, that is, the shaft versus each of the epiphyses.

Burning was determined based on changes in color, the latter being a relatively reliable indicator of burning (Shipman *et al.* 1984; Stiner *et al.* 1995; Shahack-Gross *et al.* 1997). Traces of calcareous concretions, striations, longitudinal cracks, sheeting, exfoliation, and marks of human and carnivore activities were examined on each specimen. *Sheeting* refers to bones that have broken down into one or more sheets according to fracture planes that tend to be parallel to the cortical surface, usually on midshafts of large ungulates (Figure 7). This type of fracture seems to be strongly associated with postdepositional breakage.

Exfoliation (Figure 8) is the desquamation of the first mms of cortical bone on a specimen and is typically observed on fetuses or very young individuals. It should be pointed out that the coding system advocated by Behrensmeyer (1978) in which bone surfaces are classified with respect to degree of weathering was not used here because this type of damage differs from the one encountered at Saint-Césaire. This can, perhaps, be explained by the fact that karstic environments are protected from the sun and tend to be damp, conditions that probably slow down the process of bone weathering considerably. The observation made by Tappen (1994) that weathering is also infrequent on bones from wet tropical environments, contexts in which bones are also often protected from the sun, indirectly supports this interpretation.

Figure 7. Bison metatarsal from Saint-Césaire showing evidence of sheeting.

Figure 8. An exfoliated long bone from Saint-Césaire.

In order to get an overall idea of specimen preservation at the site, bone surfaces were classified into four categories. An *intact* surface is one for which virtually no surface damage is recorded. Skeletal features, muscle attachments for instance, are undamaged. Cutmarks are also perfectly clear. A bone with a *slightly damaged* surface shows only superficial damage. The bone surface is locally eroded or damaged and morphological features are still visible, as are marks when they are present. Sometimes, only a portion of the bone surface shows damage, while the rest of the bone is intact. *Damaged* bones have significantly altered surfaces. Muscle attachments and other skeletal features are faint. Marks, when present, are difficult to detect but are still visible.

Shallow marks may be completely eroded. Specimens with an *extensively damaged* surface are basically useless for studying any type of marks; the bone cortical surface is considerably damaged.

Several methods for classifying bone fractures have been proposed in the last two decades (reviewed in Lyman 1994:315-324). All these show discrepancies because they are either too complicated and/or too subjective. This chaos results probably from the complexity of the bone fracture process, the diversity of bone shapes, and the wide spectrum of taphonomic situations. Two systems were adopted in the analysis of Saint-Césaire. Fracture morphologies were described following Villa and Mahieu (1991), a system whose advantage is to allow comparison with several published faunal assemblages. A second system, which only takes into account unambiguous dry-bone and green-bone fractures, was also employed.

In this study, dry-bone fractures are more or less transverse fractures with an irregular section. These fractures are *sometimes* darker or lighter in color than the rest of the bone. Green-bone fractures, often characterized by a spiral shape, smooth cross-section, and a uniform color (Haynes 1983), were also recorded on refitted fragments (Morin *et al.* 2004). Because it is not always possible to distinguish these two types of fractures, their identification being no more than probabilistic statements, only the unambiguous specimens were coded. Fracture edges were also studied for the information they may provide on site formation processes. Edges were described as *fresh* when angles are sharp. *Slightly abraded* edges have angles that show slight smoothing as a result of abrasion or other processes. When smoothing is pronounced, edges are considered *abraded*. Finally, *very abraded* edges are almost perfectly rounded or damaged. These frequently present a shiny aspect.

Marks related to carnivore activity have been the focus of important work in the last two decades (e.g. Brain 1981; Binford 1981, 1984; Haynes 1983; Blumenschine 1986; Binford *et al.* 1988; Marean and Spencer 1991; Capaldo and Blumenschine 1994; Selvaggio 1998). At Saint-Césaire, gnawing marks were studied using the typology proposed by Binford (1981). Extent of carnivore marks on the bone cortical surface was also recorded because it was hypothesized that bones covered with gnawing marks should be more common in carnivore dens than in anthropic assemblages ravaged by carnivores. *Marginal gnawing* indicates that carnivore marks are few on the specimen. Zones of gnawing that are *limited to one section* refer to specimens with marks restricted to one part of the bone, covering less than half of the bone surface. When carnivore marks are widespread on the specimen, the bone is said to be *covered* with gnawing marks.

Frequencies and types of percussion marks were computed to assess the incidence of marrow-cracking in the assemblages following the terminology presented by Capaldo and Blumenschine (1994). A conservative approach was adopted in recording cutmarks. Dubious cutmarks were not counted. All identified bones were studied using a 10X magnifying hand lens.

In this study, differences in means between samples are generally assessed using the arcsine transformation (denoted here as t_s, Sokal and Rohlf 1995:419-422). Changes in skeletal representation are explored using Spearman's rho (see Chapter 7). Tests are considered significant when $p \leq 0.05$.

Retouchers

Several bone retouchers have been identified at Saint-Césaire. Characteristically, these consist of large ungulate midshaft fragments. Because the status of these "tools" has been debated (e.g. Binford 1981), it is necessary to discuss them at fuller length.

Almost a century ago, Henri-Martin (1907) noted a series of peculiar marks on certain skeletal elements, predominantly phalanges, humerus, and various long bone fragments, from the Mousterian site of La Quina (southwestern France). These marks were interpreted as resulting from the use of these elements as tools in flintknapping activities. These bone tools, called *compresseurs*, were said to be similar to other finds reported at the end of the nineteenth century at the Grotte des Fées and Pair-non-Pair, two sites also located in southwestern France (Patou-Mathis and Schwab 2002).

The marks described by Henri-Martin consist of small zones of linear depressions aligned more or less perpendicular to the long axis of the specimen, presumably inflicted by an object driven through, not across, the bone surface. Typically, these concentrations of marks are restricted to the cortical face, most often near the end of a long bone fragment (Figure 9). Unambiguous carnivore marks are generally absent from the surface of these objects. At present, this type of marks, sometimes discussed in the Anglo-Saxon literature (Binford 1981; Chase 1990, 1999; Villa and d'Errico 2001), is referred to in French publications as "retouchoirs" (retouchers). These objects have been identified in a growing number of sites, from Spain to Russia (Chase 1990, 1999; Armand and Delagnes 1998; Armand 1998; Castel 1999a; Malerba and Giacobini 2002; Auguste 2002; Schwab 2002; Valensi 2002a, 2002b; Julien *et al.* 2002; Costamagno 1999; Sekhr 1998). It is currently unknown whether this type of mark exists in Africa and Asia, as the presence of retouchers has yet to be investigated in these areas. Retouchers are common in the European Middle and Upper Paleolithic, but are especially well documented in the former.

The number of mark concentrations by specimen has been recorded on all the retouchers identified at Saint-Césaire. These retouchers are included in the study of the faunal assemblages, as these are probably *ad hoc* tools made out of long bone splinters discarded during subsistence activities carried out at the site. The taphonomy of these tools is examined in Chapter 5.

Figure 9. Retouchers from Saint-Césaire. The uppermost specimen is a red deer metacarpal, while the lowermost specimen is from an unidentified long bone from a large ungulate. Scrape marks are also present on this last specimen.

The Saint-Césaire fauna: Presentation of the data

The archaeological model presented in Chapter 3 aims at unraveling processes of population interaction during the Middle to Upper Paleolithic transition. As a result, only those assemblages that are directly relevant to the research problem are discussed here. Eight levels, from the uppermost Denticulate Mousterian to the Evolved Aurignacian (levels EGPF to EJJ), are used to test the replacement model. The Mousterian levels EGB through EGP will be the focus of a future study.

Layer	*Cultural Attribution*	*Surface Studied (m^2)*	*Volume Studied (m^3)*
EJJ (3)	Evolved Aurignacian	21.50	5.1
EJM (4)	Evolved Aurignacian	17.25	3.1
EJF (5)	Aurignacian I	31.00	9.3
EJO sup (6)	Aurignacian 0?	17.50	2.9
EJO inf (7)	low-density	17.50	2.2
EJO (6-7)	Early Aurignacian?	16.50	3.0
EJOP sup (8)	Châtelperronian	28.75	7.1
EJOP inf (9)	Châtelperronian?	29.50	5.7
EJOP (8-9)	Châtelperronian?	16.50	3.5
EGPF sample (10)	Denticulate Mousterian	16.75	2.2
Total		212.75	44.1

Table 8. Saint-Césaire. Surface and volume studied by level. Lines B and C are excluded from these counts.

The surface studied for each occupation ranges between 17 and 40 m^2, resulting in large faunal samples for most occupations and relatively high faunal density (Table 8 Table 9, Figure 10). The total sample studied consists approximately of 1,650 décapages and slightly more than 132,500 bones. All bones were counted and studied, and many were refitted.

Layer	*Total Bone Counts*	*Pre-Refit NISP Counts*	*Volume (m^3)*	*Density Total Bones/m^3*	*Pre-Refit NISP/m^3*
Evol Auri (3)	4231	473	5.1	830	93
Evol Auri (4)	8033	1210	3.1	2591	390
Auri I (5)	40075	4533	9.3	4309	487
Auri 0? (6)	5610	522	2.9	1934	180
low dens (7)	801 *(147)*	103 *(18)*	2.2	364 *(67)*	47 *(8)*
EJO (6-7)	4505	335	3.0	1502	112
Châtel (8)	28872	1154	7.1	4066	163
Châtel? (9)	9510	422	5.7	1668	74
EJOP (8-9)	9791	569	3.5	2797	163
Moust (10)	21084	970	2.2	9584	441
Total/average	132512	10291	44.1	3005	233

Table 9. Saint-Césaire. Density of total faunal remains and taxonomically identified specimens per level, excluding birds and microfaunal remains. NISP counts are based on pre-refit counts. Italic numbers are counts after excluding the three unusually "rich" squares I4, I5, and J5. These squares are showed separately because they inflate abundance appreciably in this otherwise low-density level. Density is probably exaggerated for the Denticulate Mousterian, as the sample included in this study favor rich décapages. Legend in this table and the following ones: Evol Auri: Evolved Aurignacian; Auri: Aurignacian; low dens: low-density; Châtel: Châtelperronian; Moust: Denticulate Mousterian.

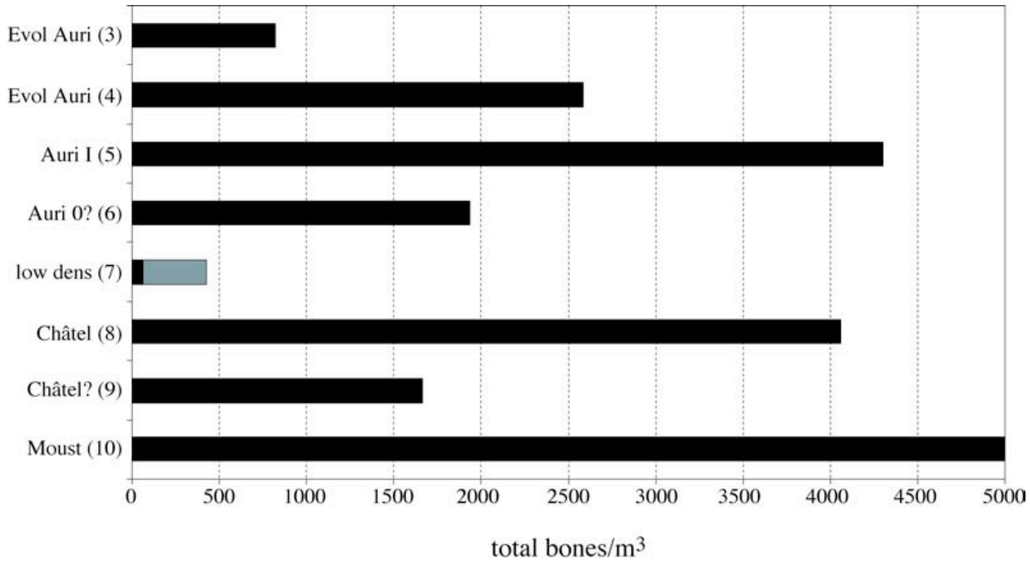

Figure 10. Density of bones (NISP/m^3) by level at Saint-Césaire. Data from Table 9. The gray bar includes squares I4, I5, and J5 that are unusually rich. Density of bones in the Denticulate Mousterian occupation is estimated, as the study of this level is not completed yet.

Layer	*Pre-Refit NISP*	*Post-Refit NISP*
	n	n
Evolved Aurignacian (3)	473	426
Evolved Aurignacian (4)	1210	1083
Aurignacian I (5)	4533	4102
Aurignacian 0? (6)	522	480
low-density (7)	103	83
EJO (6-7)	335	292
Châtelperronian (8)	1154	966
Châtelperronian? (9)	422	331
EJOP (8-9)	569	484
Denticulate Mousterian (10)	970	867
Total	10291	9114

Table 10. Pre-refit and post-refit NISP counts for the levels of Saint-Césaire. Birds and microfauna excluded. Pre-refit counts correspond to the sum of fragments that have been refitted.

With one exception, all of the occupations from Saint-Césaire have pre-refit NISP counts greater than 420 specimens (excluding the mixed EJOP and EJO samples). Refitting reduced the NISP sample by 11.4% for a post-refit total of 9,114 specimens (Table 10). Pre-refit and post-refit NISP counts are highest, in that order, for the Aurignacian I, Evolved Aurignacian EJM, Châtelperronian, and Denticulate Mousterian occupations. In comparison, the low-density, Châtelperronian?, and Aurignacian 0? occupations have smaller assemblages. One should note that in the following pages, post-refit NISP counts are used exclusively, as they minimize the problem of differential fragmentation, and, therefore, portray more accurately species and body part representation. As indicated above, data for the EJOP sample, including materials from both EJOP inf and EJOP sup, are sometimes provided in the tables as complementary information. This is true of the EJO sample as well. One should note that MNI and MNE counts have a limited analytical value in these mixed samples, as they are strongly influenced by the way the samples were aggregated (Grayson 1984). Microfaunal (small rodents, insectivores, and batracians), and bird remains, most probably unrelated to the human occupations (see below and Chapter 5), are presented in a separate table.

Taxonomic composition of the assemblages

Many authors have shown that NISP and MNI, two of the most commonly used analytical units for estimating specimen and skeletal element abundance, suffer from various shortcomings (Klein and Cruz-Uribe 1984; Grayson 1984; Marshall and Pilgram 1993; Brugal *et al.* 1994). Problems with NISP are related to specimen interdependence, variation in the number of bones between taxa, the overrepresentation of easily identified elements and taxa, and its sensitivity to fragmentation (Todd and Rapson 1988; Marshall and Pilgram 1993; Bartram 1993). The difficulties are somewhat different concerning MNI. Foremost among these are the nonlinear increase of MNI with increasing sample size and with sample aggregation, and variation in how analysts calculate it (Klein and Cruz-Uribe 1984; Grayson 1984). Many of the problems associated with MNI plague the use of MNE (minimum number of elements) as well (Lyman 1994).

In addition to the above problems, the value of these analytical units might also be structured by site function and the position of an assemblage in a behavioral sequence. As stressed by Thomas (1971) and Binford (1978), skeletal elements initially derived from a single carcass are likely to be dissociated and dispersed as a result of culling at intermediate stages in the move from kill back to basecamp, caching, sharing, exchange, and other activities. The function of the site, as well as its relation to other types of sites on the landscape, is another variable that may contribute to the dispersing of skeletal elements. Therefore, it seems that skeletal parts originally associated will be disassociated from each other as a function of the complexity of the settlement and subsistence patterns and of the overall foraging system.

Estimating the abundance of skeletal parts and their interdependence in a site is a separate, although interrelated, issue. MNI and MNE are probably reliable estimators of abundance when investigating kill sites, the odds being relatively high, compared to non-kill sites, that two randomly selected specimens belong to the same carcass. In other words, the probability that specimens are interdependent is greater at death sites than at other settlement types. In contrast, the reliability of NISP for estimating abundance is expected to increase the farther we are sequentially from the death site.

To use a concept borrowed from paleontology (Shotwell 1955, 1958), in a behavioral sequence of increasing carcass reduction, the faunal samples from Saint-Césaire would be best described as distal assemblages, whereas kill sites like Pincevent and Verberie would be proximal assemblages. This makes intuitive sense, as kills of medium- and large-sized ungulates are unlikely to have been common in rockshelters and caves like Saint-Césaire. Rather, it seems more logical to expect parts to be transported in these types of locations from open-air sites. As argued, the problem of specimen interdependence may be of lesser importance in probable distal assemblages like Saint-Césaire. The relatively low percentage of green-bone refits in the faunal samples from this location (Morin *et al*. 2004) seems to support the argument that specimen interdependence is minor in distal assemblages. Therefore, NISP is probably a reliable method for estimating taxonomic abundance at Saint-Césaire and comparable sites. For reasons discussed later, MNE might be more reliable, however, when exploring skeletal representation.

Ungulates and carnivores

Ungulates are extremely abundant in all of the Saint-Césaire assemblages, representing between 92 and 99% of the NISP samples (Table 11). Among these, three taxa predominate: reindeer, bovines (bison or aurochs), and horse (Table 12). In contrast, carnivores and other ungulates, like red deer, mammoth, and rhinoceros, essentially represented by teeth, ribs, and some long bones, are poorly represented (Table 13 and Table 14).

Layer	*Ungulates*	*Carnivores*	*Other*	*Total NISP*
	%	%	%	n
Evol Auri (3)	98.7	1.2	0.0	329 (426)
Evol Auri (4)	99.3	0.7	0.0	833 (1083)
Auri I (5)	98.6	1.2	0.1	3459 (4102)
Auri 0? (6)	96.7	3.0	0.2	417 (480)
low dens (7)	91.6	6.7	1.7	60 (83)
EJO (6-7)	97.5	2.4	0.0	244 (292)
Châtel (8)	96.1	3.2	0.4	824 (966)
Châtel? (9)	98.8	1.0	0.0	286 (331)
EJOP (8-9)	97.7	1.6	0.8	391 (484)
Moust (10)	99.4	0.4	0.0	867 (867)
Total	98.3	1.5	0.2	7710 (9114)

Table 11. Proportions of ungulates, carnivores, and other taxa in the assemblages from Saint-Césaire. Counts based on total NISP excluding antlers (total NISP including antlers are shown in parentheses). Birds and microfauna are excluded.

Fox is the most common carnivore at Saint-Césaire. Because bones of arctic fox (*Alopex lagopus*) overlap in shape and dimensions with those of the red fox (*Vulpes*

vulpes), a precise distinction of these taxa is not always possible. Using observations made by Poplin (1976), Cédric Beauval (Université de Bordeaux I) helped the author to study the fox sample, which led to the identification of arctic fox in the material. Red fox might be present as well, although no specimen could be positively attributed to this taxon. Other carnivores like hyena, bear, and wolf, well-known bone accumulators during the European Pleistocene (Stiner 1994; Tournepiche *et al.* 1996; Fosse 1997), are rare at Saint-Césaire.

Layer	*Reindeer*	*Bovines*	*Horse*	*Other Ungulates*	*Carnivores*	*Other*	*Total*
	%	%	%	%	%	%	%
Evol Auri (3)	68.7	11.8	17.3	0.9	1.2	0.0	99.9
Evol Auri (4)	72.0	9.4	13.6	4.3	0.7	0.0	100.0
Auri I (5)	81.6	4.7	11.1	1.2	1.2	0.1	99.9
Auri 0? (6)	83.7	4.6	5.3	3.1	3.0	0.2	99.9
low dens (7)	33.3	23.3	21.7	13.3	6.7	1.7	100.0
EJO (6-7)	66.4	15.2	13.1	2.8	2.4	0.0	99.9
Châtel (8)	19.7	47.4	17.0	12.0	3.2	0.4	99.7
Châtel? (9)	32.9	35.7	26.2	4.0	1.0	0.0	99.8
EJOP (8-9)	33.0	35.0	20.2	9.5	1.6	0.8	100.1
Moust (10)	24.7	37.9	34.0	2.8	0.4	0.0	99.8
Total	62.0	17.0	15.7	3.6	1.5	0.2	100.0

Table 12. Relative abundance (in NISP) of reindeer, bison, horse, and of some major taxonomic groups in the occupations from Saint-Césaire. Birds and microfauna are excluded.

Looking at broad patterns in taxonomic composition, two faunal "sets" can be recognized in the Saint-Césaire sequence (Figure 11). The lowermost set, starting with the Denticulate Mousterian up to the Châtelperronian, consists of assemblages with similar proportions of bison, reindeer, and horse. In general, the former two taxa tend to be slightly more abundant in these levels than horse remains. In the Denticulate Mousterian (EGPF), however, reindeer specimens are not as numerous as those from horse and bison. The relative abundance of horse remains decreases almost steadily during the time span of this part of the sequence. In contrast, ungulates other than reindeer, bison, and horse are more abundant in these occupations than in the more recent levels described below.

	Moust (10)		*Ejop (8-9)*		*Châtel? (9)*		*Châtel (8)*		*EJO (6-7)*		*low dens (7)*	
Artiodactyla	n	%	n	%	n	%	n	%	n	%	n	%
reindeer	214	24.7	129	33.0	94	32.9	162	19.7	162	66.4	20	33.3
bison	329	37.9	137	35.0	102	35.7	391	47.4	37	15.2	14	23.3
red deer	9	1.0	11	2.8	7	2.4	41	5.0	2	0.8	1	1.7
megaceros	7	0.8	2	0.5	1	0.3	.	.	1	0.4	.	.
roe deer	.	.	.	.	.	.	4	0.5	.	.	.	.
wild boar	.	.	2	0.5	1	0.3	4	0.5	1	0.4	.	.
Perissodactyla												
horse	295	34.0	79	20.2	75	26.2	140	17.0	32	13.1	13	21.7
wooly rhino	2	0.2	7	1.8	1	0.3	28	3.4	3	1.2	6	10.0
wild ass	.	.	1	0.3	.	.	2	0.2	.	.	.	.
Proboscidea												
mammoth	7	0.8	14	3.6	2	0.7	21	2.5	.	.	1	1.7
Carnivora												
spotted hyena	2	0.2	1	0.3	.	.	3	0.4	1	0.4	1	1.7
wolf	1	0.1	.	.	2	0.7	2	0.2	2	0.8	.	.
arctic fox	.	.	.	.	.	.	2	0.2	.	.	1	1.7
unspecif. fox	1	0.1	4	1.0	1	0.3	17	2.1	3	1.2	2	3.3
bear			1	0.3					.	.	.	.
polecat	.	.	.	.	.	.	1	0.1	.	.	.	.
pine marten	.	.	.	.	.	.	.	.	.	.	.	.
lynx	.	.	.	.	.	.	.	.	.	.	.	.
badger	.	.	.	.	.	.	.	.	.	.	.	.
cave lion	.	.	.	.	.	.	2	0.2	.	.	.	.
Lagomorpha												
hare	.	.	.	.	.	.	.	.	.	.	.	.
unspec. lagom	.	.	3	0.8	.	.	1	0.1	.	.	1	1.7
Pisces												
cyprinid	.	.	.	.	.	.	1	0.1	.	.	.	.
brown trout	.	.	.	.	.	.	2	0.2	.	.	.	.
Total NISP	867	99.8	391	100.1	286	99.8	824	99.8	244	99.9	60	100.1
Total with antlers	867	-	484	-	331	-	966	-	292	-	83	-

Table 13. Saint-Césaire. NISP counts by species and level for mammal and fish remains. Antlers counted separately.

	Auri 0? (6)		*Auri I (5)*		*Evol Auri (4)*		*Evol Auri (3)*		*Total 10-3*	
Artiodactyla	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
reindeer	349	83.7	2823	81.6	600	72.0	226	68.7	4779	62.0
bison	19	4.6	164	4.7	78	9.4	39	11.8	1310	17.0
red deer	2	0.5	10	0.3	2	0.2	2	0.6	87	1.1
megaceros	.	.	7	0.2	.	.	.	.	18	0.2
roe deer	.	.	.	.	.	.	.	.	4	0.0
wild boar	.	.	1	0.0	.	.	.	.	9	0.1
Perissodactyla										
horse	22	5.3	385	11.1	113	13.6	57	17.3	1211	15.7
wooly rhino	3	0.7	8	0.2	1	0.1	.	.	59	0.8
wild ass	.	.	.	.	.	.	.	.	3	0.0
Proboscidea										
mammoth	8	1.9	16	0.5	33	4.0	1	0.3	103	1.3
Carnivora										
spotted hyena	.	.	1	0.0	.	.	1	0.3	10	0.1
wolf	3	0.7	9	0.3	1	0.1	1	0.3	21	0.3
arctic fox	1	0.2	3	0.1	.	.	.	.	7	0.1
unspecif. fox	6	1.4	23	0.7	4	0.5	2	0.6	63	0.8
bear	.	.	.	.	.	.	.	.	1	0.0
polecat	1	0.2	1	0.0	.	.	.	.	3	0.0
pine marten	2	0.5	.	.	.	.	.	.	2	0.0
lynx	.	.	1	0.0	.	.	.	.	1	0.0
badger	.	.	1	0.0	1	0.1	.	.	2	0.0
cave lion	.	.	2	0.1	.	.	.	.	4	0.0
Lagomorpha										
hare	1	0.2	.	.	.	.	.	.	1	0.0
unspec. lagom.	.	.	4	0.1	.	.	.	.	9	0.1
Pisces										
cyprinid	.	.	.	.	.	.	.	.	1	0.0
brown trout	.	.	.	.	.	.	.	.	2	0.0
Total NISP	417	99.9	3459	99.9	833	100.0	329	99.9	7710	99.6
Total (with antlers)	480	.	4102	.	1083	.	426	.	9114	.

Table 14. Saint-Césaire. NISP counts by species and level for mammal and fish remains (continued). Antlers counted separately.

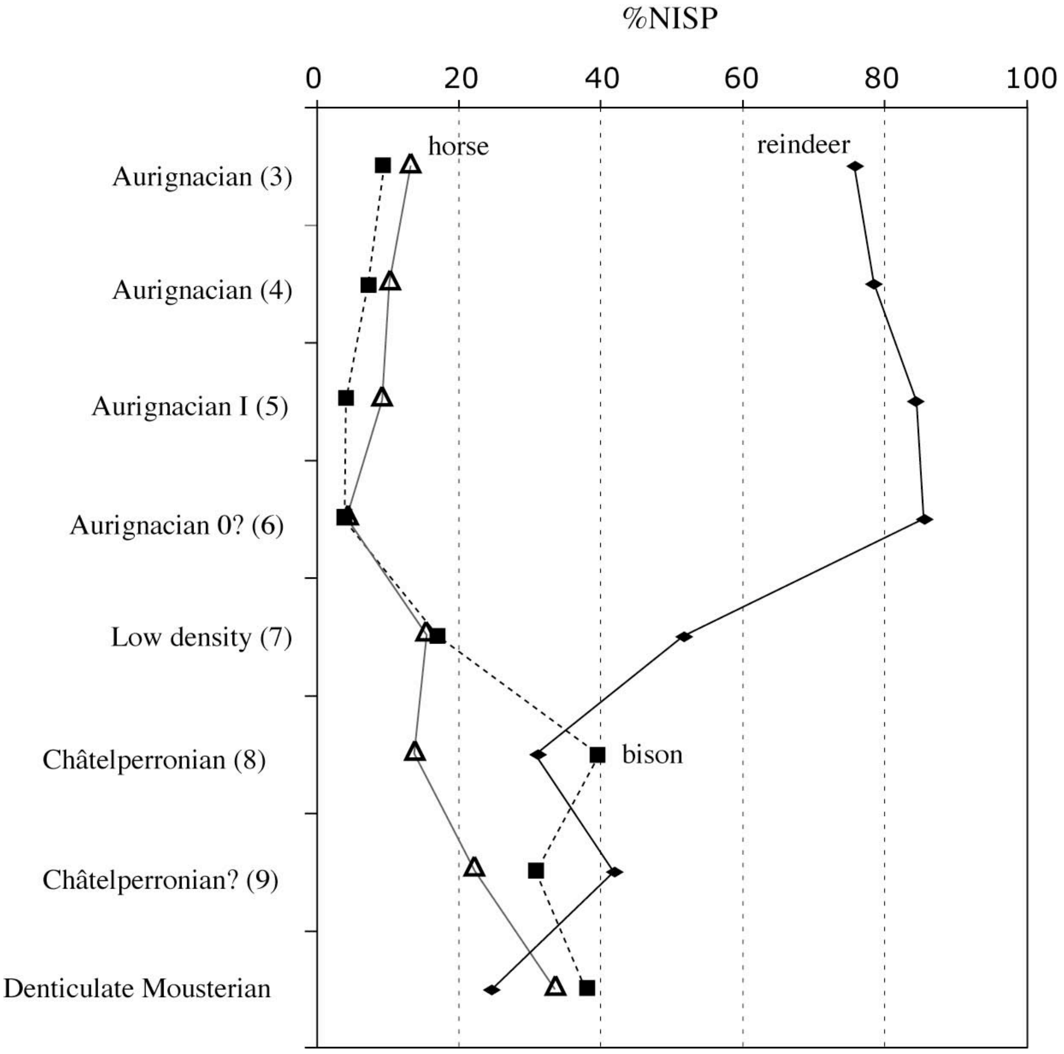

Figure 11. Proportions of reindeer, horse, and bison remains by level at Saint-Césaire. Data from Table 13 and Table 14

In marked contrast, the upper faunal set, which includes all of the Aurignacian levels, indicates a heavy focus on reindeer, a taxon that appears to decrease slightly after a peak in the Aurignacian 0? occupation. Compared to the older levels from Saint-Césaire, the Aurignacian occupations are depleted in bison.

The EJO inf assemblage, stratigraphically located between the two faunal “sets,” is intermediate in composition. However, the very small faunal sample available from this level limits considerably its interpretation.

	Moust (10)		*Ejop (8-9)*		*Châtel? (9)*		*Châtel (8)*		*EJO (6-7)*		*low dens (7)*	
Artiodactyla	TMNE	%	TMNE	%	TMNE	%	TMNE	%	TMNE	%	TMNE	%
reindeer	56	31.6	48	37.8	29	31.9	60	24.5	39	52.0	9	29.0
bison	60	33.9	44	34.6	35	38.5	97	39.6	15	20.0	8	25.8
red deer	5	2.8	6	4.7	3	3.3	15	6.1	2	2.7	1	3.2
megaceros	3	1.7	1	0.8	1	1.1	.	.	1	1.3	.	.
roe deer	.	.	.	.	.	.	4	1.6	.	.	.	.
wild boar	.	.	1	0.8	1	1.1	3	1.2	1	1.3	.	.
Perissodactyla												
horse	46	26.0	13	10.2	17	18.7	30	12.2	10	13.3	5	16.1
wooly rhino	2	1.1	5	3.9	1	1.1	8	3.3	2	2.7	2	6.4
wild ass	.	.	1	0.8	.	.	2	0.8	.	.	.	.
Proboscidea												
mammoth	1	0.6	1	0.8	1	1.1	1	0.4	.	.	1	3.2
Carnivora												
spotted hyena	2	1.1	1	0.8	.	.	3	1.2	1	1.3	1	3.2
wolf	1	0.6	.	.	2	2.2	2	0.8	2	2.7	.	.
arctic fox	.	.	.	.	.	.	2	0.8	.	.	1	3.2
unspecif. fox	1	0.6	4	3.1	1	1.1	12	4.9	2	2.7	2	6.4
bear	.	.	1	0.8	.	.	.	.	.	.	.	.
polecat	.	.	.	.	.	.	1	0.4	.	.	.	.
pine marten	.	.	.	.	.	.	.	.	.	.	.	.
lynx	.	.	.	.	.	.	.	.	.	.	.	.
badger	.	.	.	.	.	.	.	.	.	.	.	.
cave lion	.	.	.	.	.	.	2	0.8	.	.	.	.
Lagomorpha												
hare	.	.	.	.	.	.	.	.	.	.	.	.
unspec. lagom	.	.	1	0.8	.	.	1	0.4	.	.	1	3.2
Pisces												
cyprinid	.	.	.	.	.	.	1	0.4	.	.	.	.
brown trout	.	.	.	.	.	.	1	0.4	.	.	.	.
Total MNE	177	100.0	127	99.9	91	100.1	245	99.8	75	100.0	31	99.7
Total (+antlers)	177		141		93		257		80		35	

Table 15. Saint-Césaire. Total MNE counts by species and level for mammal and fish remains. Antlers counted separately.

	Auri 0? (6)		*Auri I (5)*		*Evol Auri (4)*		*Evol Auri (3)*		*Total 10-3*	
Artiodactyla	TMNE	%	TMNE	%	TMNE	%	TMNE	%	TMNE	%
reindeer	95	74.2	594	76.0	157	68.9	70	66.0	1157	58.1
bison	9	7.0	47	6.0	24	10.5	15	14.1	354	17.8
red deer	1	0.8	8	1.0	1	0.4	1	0.9	43	2.2
megaceros	.	.	1	0.1	.	.	.	.	7	0.3
roe deer	.	.	.	.	.	.	.	.	4	0.2
wild boar	.	.	1	0.1	.	.	.	.	7	0.3
Perissodactyla										
horse	7	5.5	89	11.4	40	17.5	15	14.1	272	13.7
wooly rhino	2	1.6	3	0.4	1	0.4	.	.	26	1.3
wild ass	.	.	.	.	.	.	.	.	3	0.1
Proboscidea										
mammoth	1	0.8	1	0.1	1	0.4	1	0.9	9	0.4
Carnivora										
spotted hyena	.	.	1	0.1	.	.	1	0.9	10	0.5
wolf	2	1.6	7	0.9	1	0.4	1	0.9	18	0.9
arctic fox	1	0.8	2	0.3	.	.	.	.	6	0.3
unspecif. fox	6	4.7	19	2.4	2	0.9	2	1.9	51	2.6
bear	.	.	.	.	.	.	.	.	1	0.0
polecat	1	0.8	1	0.1	.	.	.	.	3	0.1
pine marten	2	1.6	.	.	.	.	.	.	2	0.1
lynx	.	.	1	0.1	.	.	.	.	1	0.0
badger	.	.	1	0.1	1	0.4	.	.	2	0.1
cave lion	.	.	2	0.3	.	.	.	.	4	0.2
Lagomorpha										
hare	1	0.8	.	.	.	.	.	.	1	0.0
unspec. lagom.	.	.	4	0.5	.	.	.	.	7	0.3
Pisces										
cyprinid	.	.	.	.	.	.	.	.	1	0.0
brown trout	.	.	.	.	.	.	.	.	1	0.0
Total MNE	128	100.2	782	99.9	228	99.8	106	99.7	1990	99.5
MNE (+antlers	132		829		238		108		2090	

Table 16. Saint-Césaire. Total MNE counts by species and level for mammal and fish remains (continued). Antlers counted separately.

The picture is very similar to the one observed with NISP when taxonomic composition is investigated based on the total minimum number of elements (TMNE), which corresponds to the sum of the MNE for all elements by species (Table 15 and Table 16). As documented with NISP, TMNE indicates that reindeer is very abundant, representing between 66 and 76% of the skeletal elements, in the Aurignacian occupations. In contrast, the Denticulate Mousterian and Châtelperronian occupations have a more mixed composition. Taxonomic composition is also presented using MNI in Appendix 1. These changes in faunal composition and their statistical significance are explored at fuller length in Chapter 8.

Bison or aurochs?

More needs to be said in this presentation about large ungulates. In European Paleolithic assemblages, the distinction of bison (*Bison priscus*) from aurochs (*Bos primigenius*) is a difficult task because these two species overlap significantly in skeletal characteristics. Horns and cranial features are considered generally the most reliable criteria for discriminating these species (Brugal 1983; Slott-Moller 1988). Unfortunately, at Saint-Césaire these body parts are, as in most Paleolithic sites, poorly represented and highly fragmented. The situation is not hopeless, however, as several dental and postcranial features have been explored in the last decades in an effort to differentiate these two taxa based on skeletal material (Olsen 1960; Prat 1980; Brugal 1983; Delpech 1984; Guadelli 1987, 1999; Slott-Moller 1988, 1990). Unfortunately, these criteria are rarely perfectly dichotomous and are better used for characterizing populations rather than individuals (Brugal 1983).

Focusing on the skull, most of the bovine remains from Saint-Césaire seem to fall in the bison range. In the Châtelperronian (EJOP sup), a level in which bovines are abundant, teeth were used in an attempt to determine the respective proportions of bison and aurochs in the sample. According to Slott-Moller (1990:46 and p. 44, Fig. 43), the longitudinal depression separating the two lobes of the M_1 and M_2 in lingual view is U-shaped in bison and more V-shaped in aurochs. In the assemblage, 12 out of 13 M_1/M_2 are clearly U-shaped, therefore more in line with bison. One specimen is intermediate in shape. In the EJOP sample, which comprises materials from both EJOP sup and EJOP inf, all three molars studied are U-shaped. Slott-Moller (1990:46 and p. 45, Fig. 44) also emphasized that the width of the ectostylid (measured at mid-length) tend to be greater in bison than in aurochs with a cutoff point around 4 mm. In the Châtelperronian of Saint-Césaire, the ectostylids of the M_1/M_2 measure between 3.2 and 5.0 mm. Although most specimens have width greater than 4 mm, some of the molars fall in the upper range of the aurochs distribution.

Upper teeth were also included in the analysis of the bovine teeth from the Châtelperronian occupation. In aurochs, upper molars would be frequently characterized by a small "islet" of enamel visible on the occlusal surface between the two lobes of the tooth (Slott-Moller 1990:38 and p. 40, Fig. 31), a feature said to be rare in bison. In the Châtelperronian sample, only 1 out of 22 M^1/M^2 showed the presence of an enamel islet. In addition to the above observations, the very low incidence of enamel islet in the Châtelperronian suggests that bison was by far the dominant, if not the only, bovine species represented in this occupation. However, Lavaud-Girard (1980, 1993) noted that some M_3 from this level have a pinched, elongated, and vestibularly offset third lobe, features that are argued to be more characteristic of aurochs (but see Slott-Moller 1990). If Lavaud-Girard's interpretation is correct, this might suggest the presence of a small number of aurochs specimens in the assemblage.

Ferrié (2001) has recently studied a sample of bovine remains, mostly teeth, from the Denticulate Mousterian level. Using the criteria presented above and several others, a detailed analysis of the material led him to attribute the majority of the bovine specimens to bison.

According to Guadelli (1987, 1999), the petrous bone can be used for discriminating aurochs from bison. This author has accepted to study the bovine petrous bones from Saint-Césaire (including those recovered from the Mousterian levels). Guadelli's results appear to support the above conclusions, as all the analyzable specimens (n=14) studied by him were attributed to bison. Thus, cranial and postcranial data converge to relate the majority of the bovine remains from Saint-Césaire to the bison. As a result, we will use the latter term in the text to refer to bovines. Obviously, this does not rule out the possibility raised by Lavaud-Girard (1980, 1993) that some aurochs contributed to the assemblages.

Other taxa

At a much smaller scale, birds have also sporadically contributed to the accumulations. Véronique Laroulandie, who recently completed an archaeozoological analysis of three late Upper Paleolithic bird assemblages (Laroulandie 2000, 2003), was kind enough to study the Saint-Césaire avifauna in detail, and provided some conclusions on taxonomic composition and the taphonomy of these remains (Appendix 2). Her work led to the identification of several species of the anseriform family and a small number of raptors (Table 17). We will see in the next chapters that these birds probably accumulated naturally at the site.

	Dentic Moust (10)	*EJOP (8-9)*	*Châtel? (9)*	*Châtel (8)*	*EJO (6-7)*	*Auri 0? (6)*	*Auri I (5)*	*Evol Auri (4)*	*Total*
Anseriforma									
Anser sp.	.	1	.	.	.	.	.	.	1
cf. Anser	.	.	.	.	.	.	1	.	1
Anas acuta	.	.	.	.	.	6	.	.	6
Anas cf. acuta	.	.	.	1	.	.	.	.	1
Anas crecca	.	.	.	.	.	.	1	.	1
Anas sp.	.	.	.	.	.	1	.	.	1
Aythya sp.	.	.	.	.	.	2	.	.	2
unspecified	.	.	.	1	1	3	2 (1*)	.	7
Accipitriforma									.
Aquila chrysaetos	1	.	.	.	.	.	.	.	1
unsp. vulture	.	.	1	.	.	.	3	1	5
unspecified	.	.	.	.	1	.	.	.	1
Galliforma									
Lagopus sp.	.	.	.	.	1	.	1	.	2
Charadriiforma									
Alle alle	.	.	.	.	.	3	.	.	3
Pluvialis sp.	.	.	.	.	.	1	4 (1*)	.	5
unspec. charadriidae	.	.	.	1	.	.	.	2*	3
unspec. charadriiform	.	.	2	.	.	.	1	2 (1*)	5
Strigiforma									
unspecified	.	.	.	.	.	1	1	.	2
Passeriforma									
Corvus corax	.	.	.	.	.	.	1*	.	1
unspecified	.	1	.	.	.	.	1	.	2
Total birds	1	2	3	3	3	17	16	5	50

Table 17. Saint-Césaire. NISP counts for the bird remains by species and level. Star denotes juveniles.

A few remains of lagomorphs, one of which is from a hare, were also identified in the assemblages. Rabbits have not been identified. Among the insectivores, moles are uncommon, but might be more abundant in the Châtelperronian (MNI:6). Most of the mole remains were collected when screening soil samples for rodents. Few batracian bones (n=9) were also identified in the Châtelperronian and the Aurignacian 0? by Lavaud-Girard (1993) and Marquet (pers. com. 2003). The scarcity of these remains and the lack of information on sampling procedures explain why these were not included in this study. For all these taxa, the possibility of contamination needs to be seriously evaluated, given that animal burrows have been recorded in the field (Backer 1993). As a result, these bones might be indicative of natural death, perhaps during the cold season. However, as emphasized by Morlan (1994b), the presence of these small taxa may also result from carnivore/raptor predation. This hypothesis is particularly interesting given that foxes, the most common carnivore in Saint-Césaire, are known to prey actively on small rodents (MacDonald and Barrett 2001).

Three fish specimens, possibly corresponding to as many individuals, were identified in the Châtelperronian and examined by Olivier Le Gall (CNRS, Université de Bordeaux I). Because they have the exact same three-dimensional coordinates, these may correspond to a single depositional event. No other fish remains were found at Saint-Césaire.

Compared to larger taxa, small insectivores and rodents are not common in the assemblages, possibly as a result of a recovery or collecting bias, as these remains were relatively abundant in the soil samples screened with a mesh smaller than the 2 mm mesh used in the excavations (Marquet, pers. com. 2003; and pers. observ. of soil samples).

Looking at taxonomic composition, the upper sequence of Saint-Césaire, corresponding to the Aurignacian occupations, is clearly dominated by the narrow-skulled vole, whereas the common vole is well represented in the lower sequence (Table 18). Today, the narrow-skulled vole is found in more northerly latitudes. In contrast, the common vole is more widely distributed and is found in most of Europe (Marquet 1993; MacDonald and Barrett 2001).

	Moust (10)		*Châtel? (9)*		*Châtel (8)*		*low dens (7)*		*Auri 0? (6)*		*Auri I (5)*		*Evol Auri (4)*		*Evol Auri (3)*	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
narrow-skulled vole	5	55.5	1	50.0	29	76.3	38	100	80	95.2	59	84.3	93	93.0	97	89.0
common vole	2	22.2	.	.	4	10.5	.	.	1	1.2	1	1.4	.	.	7	6.4
ground squirrel	.	.	.	.	.	.	.	.	.	.	1	1.4	1	1.0	1	0.9
snow vole	1	1.11	.	.	.	.	.	.	.	.	.	.	.	.	.	.
water vole	1	1.11	1	50.0	5	13.2	.	.	3	3.6	8	11.4	4	4.0	1	0.9
pine vole	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	0.9
field vole	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
garden dormouse	.	.	.	.	.	.	.	.	.	.	.	.	1	1.0	.	.
root/Male vole	.	.	.	.	.	.	.	.	.	.	.	.	1	1.0	1	0.9
collared lemming	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	0.9
Rattus sp.	.	.	.	.	.	.	.	.	.	.	1	1.4	.	.	.	.
total	9	99.9	2	100	38	100	38	100	84	100	70	99.9	100	100	109	99.9

Table 18. Saint-Césaire. MNI counts for microfaunal remains by species and level (data from Marquet 1993 and unpublished results).

This description of the taxonomic composition at Saint-Césaire is followed in the next section by an overview of skeletal representation in reindeer, bison, and horse, the most common taxa in the Saint-Césaire assemblages. Data on cutmark distribution are presented as well, along with information concerning burning. These data will be discussed further in Chapter 7 with respect to the test implications derived from the replacement model.

Skeletal part representation at Saint-Césaire

Except for the low-density occupation, not included here because of small sample size, general trends in reindeer, bison, and horse body part representation are laid out by assemblage. MNE values, from which the %MAU values are derived, are provided in Appendix 3 for each of these taxa and by level. Concerning the Châtelperronian, the skeletal patterns presented in this study differ to some extent from those published by Patou-Mathis (1993). This is because both studies rely on different samples. In general, most of the differences with Patou-Mathis' published data are due to the inclusion of shaft fragments in the analysis presented here.

A last but very important point needs to be stressed concerning the interpretation of body part representation at Saint-Césaire. Burning is not random in the assemblages and affects particularly the carpals, tarsals, innominates, vertebrae, and long bone epiphyses. This probably reduced the abundance of these parts in the assemblages. This issue is developed in detail in Chapters 5 and 7.

Denticulate Mousterian (EGPF)

We have seen that bison and horse are the most abundant taxa in this occupation, followed by reindeer. Based on %MAU, the head and tibia are best represented in bison (Figure 12). In horse, the most abundant parts are the head, humerus, tibia, and metacarpal (Figure 13). In both taxa, the axial skeleton is poorly represented, possibly

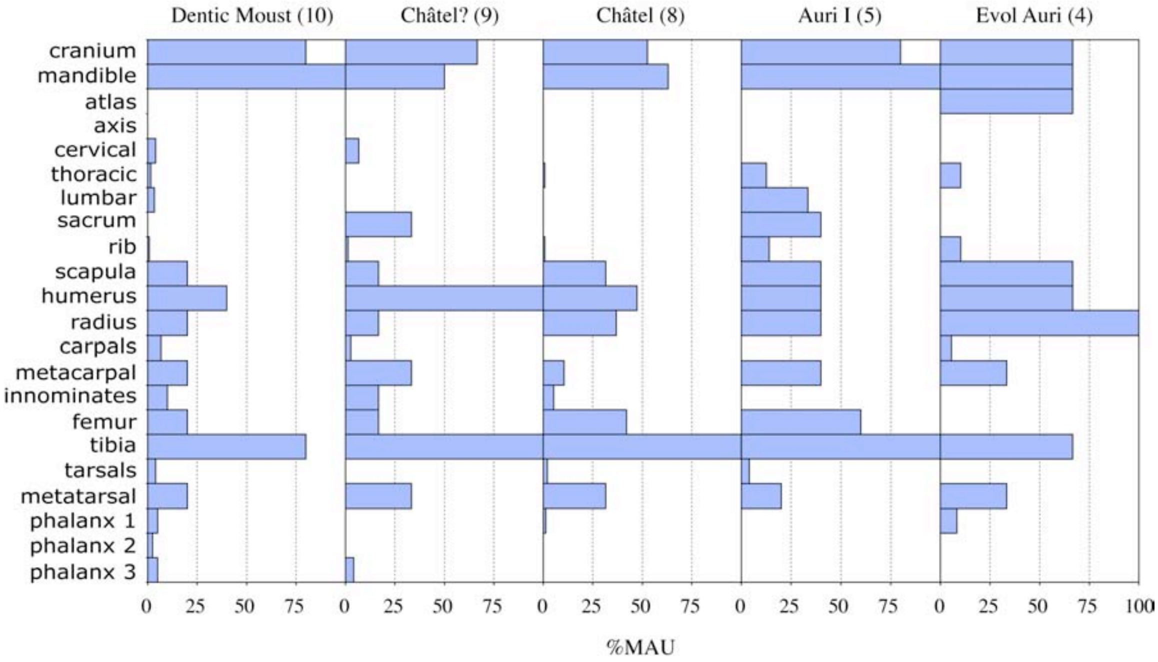

Figure 12. Bison bodypart representation in five assemblages from Saint-Césaire.

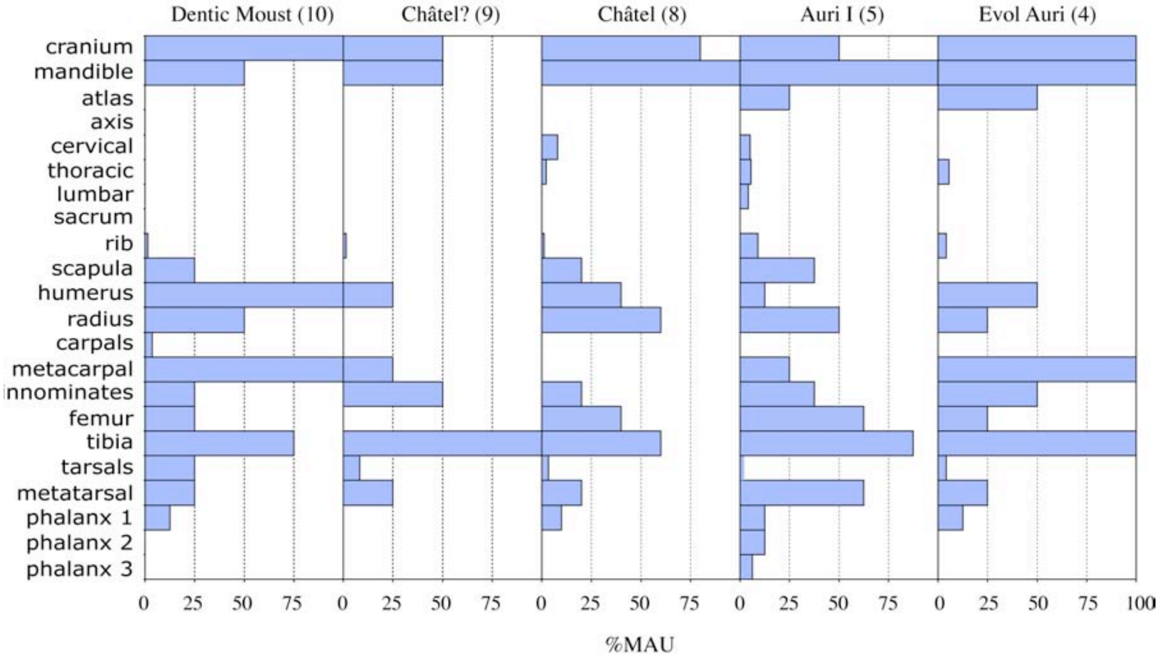

Figure 13. Horse bodypart representation in five assemblages from Saint-Césaire.

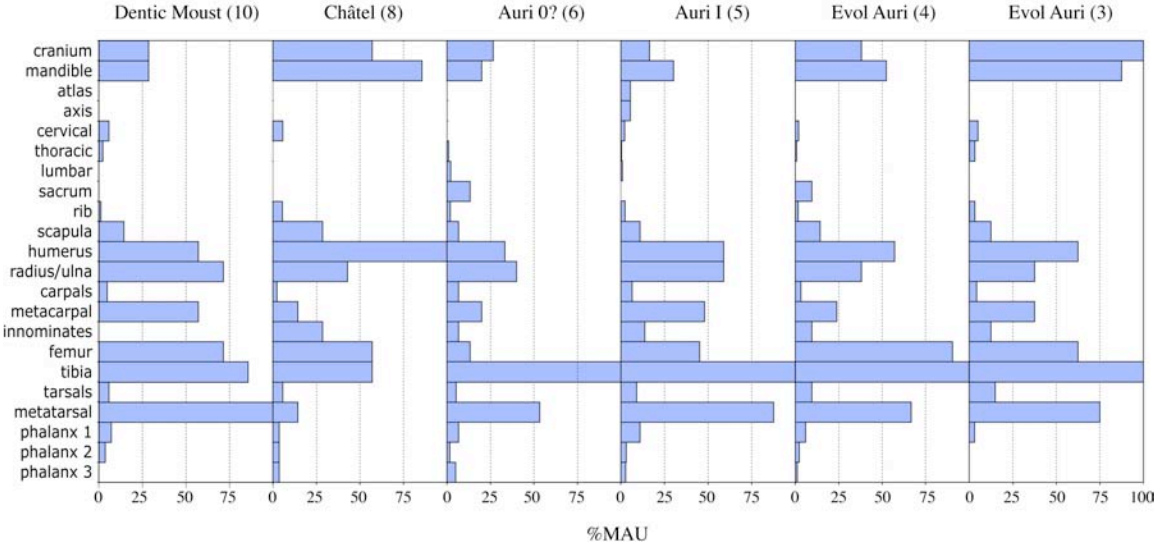

Figure 14. Reindeer bodypart representation in six assemblages from Saint-Césaire.

due to burning. As measured by MNE, epiphyses are rare compared to shafts (Figure 15 to Figure 17). This pattern seems to be consistent across long bone elements and species.

Long bones, especially those of the hind leg, are the most common elements in the reindeer sample (Figure 14). With respect to the forelimb, the radius is better represented than the humerus and metacarpal. In the hindlimb, element abundance increases distally, that is, away from the pelvis. As in horse and bison, the axial skeleton is under-represented relative to other parts and the atlas and axis are absent. Phalanges, ribs, innominates, carpals, and tarsals are also rare.

Evidence of burning was found on several elements in the occupation, few of which are identified (Table 19). The skull shows a moderately high incidence of exposure to fire. In contrast, the proportion of burned teeth is low. Burning was rarely identified on other bones, including long bones.

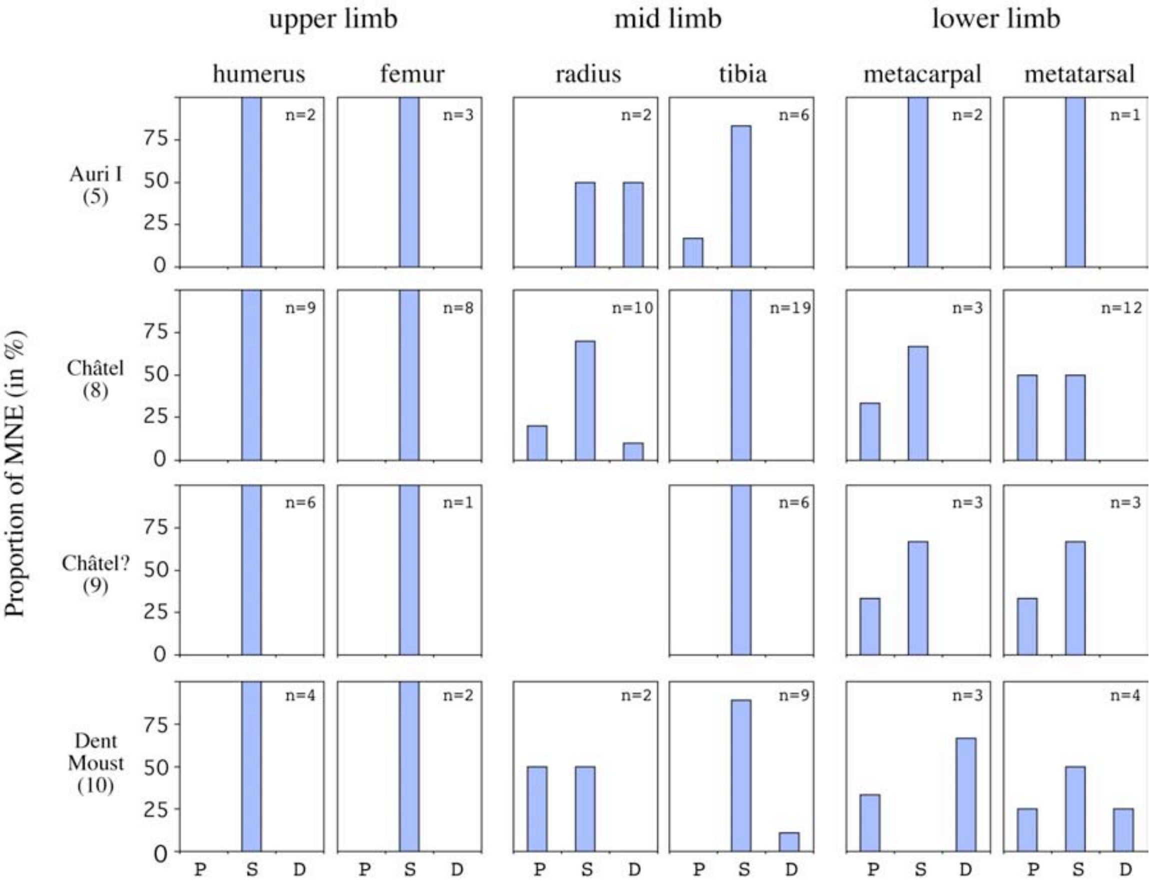

Figure 15. Relative abundance of bison proximal, shaft, and distal portions of long bones in four assemblages from Saint-Césaire. Data from Appendix 3. Proportions are calculated by dividing the MNE for each anatomical region (proximal, shaft, and distal portions) of an element by the sum of the MNE values for all three anatomical regions combined. The empty box indicates lack of data. Legend: P = proximal, S = shaft, D = distal.

Carcass butchery and processing in the Denticulate Mousterian occupation can be studied by looking at cutmarks (Table 20 to Table 22). However, the relative abundance of cutmarks should be interpreted with caution, as the degree of surface preservation and fragmentation are not identical between and within the assemblages (see discussion in Chapter 5).

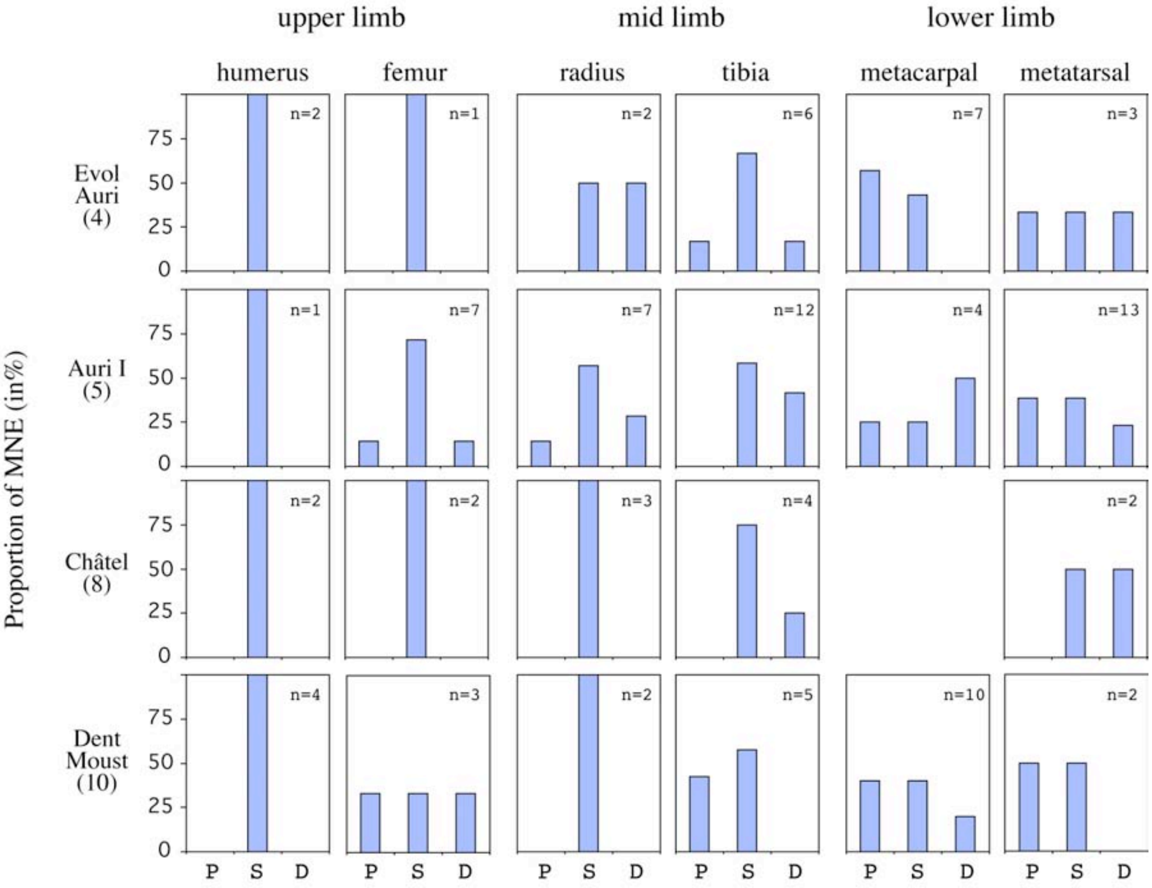

Figure 16. Relative abundance of horse proximal, shaft, and distal portions of long bones in some assemblages from Saint-Césaire. Data from Appendix 3. Proportions are calculated by dividing the MNE for each anatomical region (proximal, shaft, and distal portions) of an element by the sum of the MNE values for all three anatomical regions combined. The empty box indicates lack of data. Legend: P = proximal, S = shaft, D = distal.

A relatively high proportion of reindeer (30%) and horse (25%) long bones are cutmarked in the Denticulate Mousterian sample. This proportion is much lower in bison (8%). These differences are significant when bison is included (bison and horse: $t_s = 2.32$, $p < 0.05$; bison and reindeer: $t_s = 4.30$, $p < 0.0001$), but are not when this taxon is excluded (reindeer and horse: $t_s = 0.62$, $p < 0.54$). In general, long bones, including the metapodials, show higher percentages of cutmarks than the axial skeleton.

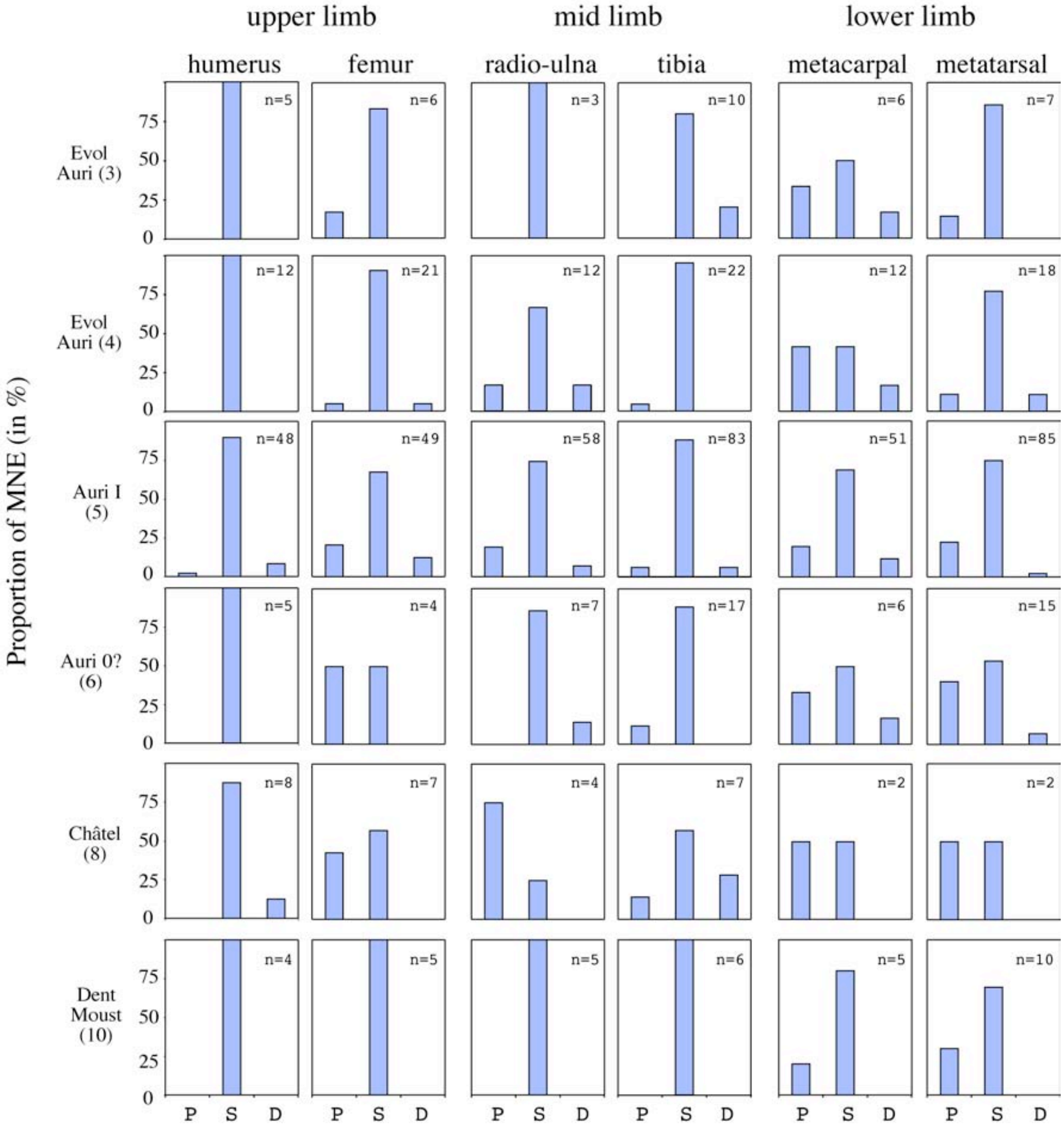

Figure 17. Relative abundance of reindeer proximal, shaft, and distal portions of long bones by level in some assemblages from Saint-Césaire. Proportions are calculated by dividing the MNE for each anatomical region (proximal, shaft, and distal portions) of an element by the sum of the MNE values for all three anatomical regions combined. The empty box indicates lack of data. Legend: P = proximal, S = shaft, D = distal.

NISP+NSUTS			
EJO (6-7)	burned	n	%burned
radio-ulna	1	13	7.7
innominates	1	1	100.0
calcaneum	1	1	100.0
metatarsal	1	58	1.7
Auri 0? (6)			
petrous bone	1	3	33.3
vertebrae	6	25	24.0
radio-ulna	2	24	8.3
carpals	3	6	50.0
femur	1	11	9.1
tibia	1	49	2.0
talus	3	6	50.0
metatarsal	2	104	1.9
sesamoid	1	5	20.0
EJOP (8-9)			
ribs	1	125	0.8
talus	2	2	100.0
tooth	9	163	5.5
Châtel (8)			
mandible/maxilla	1	47	2.1
tooth	22	564	3.9
rib	4	372	1.1
Châtel?			
tibia	1	59	1.7
metatarsal	2	42	4.8
cranial	1	13	7.7
tooth	13	142	9.1
Dent Moust			
horn	1	28	3.6
cranial	22	88	25.0
mandible/maxilla	5	132	3.8
tooth	27	526	5.1
scapula	1	27	3.7
innominates	1	8	12.5
fibula	1	3	33.3
malleolus	1	4	25.0
Evol Auri (3)	burned	n	%burned
mandible/maxilla	1	23	4.3
vertebrae	2	12	16.7
ribs	2	107	1.9
radio-ulna	2	28	7.1
metacarpal	1	13	7.7
innominates	2	5	40.0
femur	1	16	6.3
tibia	1	38	2.6
tarsals	1	8	12.5
phalanges	1	8	12.5
Evolved Auri (4)			
cranial	2	20	10.0
tooth	1	140	0.7
vertebrae	8	29	27.6
ribs	4	350	1.1
humerus	1	32	3.1
radius	5	72	6.9
femur	2	28	7.1
malleolus	1	1	100.0
tarsals	7	12	58.3
metatarsal	4	166	2.4
Auri I (5)			
cranial	6	100	6.0
tooth	28	333	8.4
vertebrae	68	165	41.2
ribs	33	1688	1.9
humerus	6	124	4.8
radio-ulna	23	304	7.6
carpals	5	30	16.7
innominates	12	42	28.6
femur	11	134	8.2
patella	1	6	16.7
tibia	25	425	5.9
malleolus	4	5	80.0
tarsals	24	47	51.1
metatarsal	10	856	1.2
metapodial	1	76	1.3
phalanges	4	86	4.6
vestigial phal.	1	8	12.5

Table 19. Summary of burning in the occupations from Saint-Césaire. Only the elements showing evidence of burning are included. Samples consist of both NISP and NSUTS.

	Moust (10)	*Châtel? (9)*	*Châtel (8)*	*EJOP (8-9)*	*Auri 0? (6)*	*Auri I (5)*	*Evol Aur (4)*	*Evol Aur (3)*	*Total*	
	n	n	n	n	n	n	n	n	n	%
cranial	0/1	.	.	.	0/3	0/25	0/5	0/3	0/37	0.0
vertebrae	0/4	0/2	0/1	0/4	0/5	0/26	0/3	2/3	2/48	4.2
ribs	0/8	0/7	1/40	0/11	2/53	10/427	2/47	0/15	15/608	2.5
scapula	0/2	0/3	0/2	.	0/1	3/20	1/9	0/1	4/38	10.5
humerus	3/10	1/2	3/10	0/1	1/9	25/108	9/26	1/9	43/175	24.6
radio-ulna	6/19	0/5	1/7	1/11	0/22	34/272	3/63	0/13	45/412	10.9
carpals	0/2	.	0/1	0/3	0/6	0/30	0/4	0/2	0/48	0.0
metacarpal	7/13	2/9	0/3	2/5	1/12	34/124	2/20	3/11	51/197	25.9
innomin.	.	.	0/2	0/3	0/1	0/23	0/5	0/2	0/36	0.0
femur	3/9	3/5	0/8	0/3	1/11	22/114	4/24	2/12	35/186	18.8
tibia	16/36	4/15	0/16	5/10	8/47	102/392	12/81	8/32	155/629	24.6
tarsals	0/1	1/2	0/2	0/5	0/5	2/41	0/11	0/7	3/74	4.0
metatarsal	14/76	1/30	0/19	0/28	3/102	24/841	6/160	1/68	49/1324	3.7
phalanges	0/3	0/1	0/4	1/5	0/18	3/75	0/12	0/2	4/120	3.3
Total	49/184	12/126	5/257	9/182	16/358	259/3161	39/720	17/277	406/5265	7.7

Table 20. Saint-Césaire. Distribution of cutmarks on reindeer bones by body part and level. Number of specimens with cutmarks versus total NISP. Antler and teeth excluded. Cranial includes mandibular bone.

	Moust (10)	*Châtel? (9)*	*Châtel (8)*	*EJOP (8-9)*	*Auri 0? (6)*	*Auri I (5)*	*Evol Auri (4)*	*Evol Auri (3)*	*Total*	
	n	n	n	n	n	n	n	n	n	%
horncore	0/28	.	0/1	0/1	.	.	.	.	0/30	0.0
cranial	0/17	0/2	0/4	0/2	.	.	0/1	0/2	0/28	0.0
vertebrae	1/4	0/3	1/3	.	0/1	0/22	0/4	0/2	2/39	5.1
ribs	1/15	1/8	0/25	0/13	0/5	0/86	2/42	0/7	4/201	2.0
scapula	1/7	0/2	0/15	0/4	0/1	0/7	0/3	0/2	1/41	2.4
humerus	4/6	3/10	7/21	0/9	.	1/2	0/2	0/3	15/53	28.3
radio-ulna	0/7	0/1	1/20	0/2	0/1	1/4	0/5	.	2/40	5.0
carpals	0/4	0/1	.	0/2	.	.	0/1	.	0/8	0.0
metacarpal	0/3	1/3	0/7	0/1	.	0/3	0/1	0/1	1/19	5.3
innominates	0/2	0/1	1/1	.	.	.	.	.	1/4	25.0
femur	0/6	1/3	6/18	2/6	.	0/4	.	0/1	9/38	23.7
tibia	2/47	3/27	21/73	5/22	0/1	0/11	0/8	0/3	31/192	16.1
tarsals	0/1	.	0/3	0/2	.	0/1	.	0/1	0/8	0.0
metatarsal	1/15	0/6	4/37	0/7	0/2	0/1	0/2	2/6	7/76	9.2
phalanges	0/7	0/1	0/3	0/5	.	.	0/1	0/1	0/18	0.0
Total	10/141	9/68	41/230	7/75	0/11	2/141	2/70	2/29	73/765	9.5

Table 21. Saint-Césaire. Distribution of cutmarks on bison bones by body part and level. Number of specimens with cutmarks versus total NISP. Teeth are excluded. Cranial includes mandibular bone.

	Moust (10)	*Châtel? (9)*	*Châtel (8)*	*EJOP (8-9)*	*Auri 0? (6)*	*Auri I (5)*	*Evol Auri (4)*	*Evol Auri (3)*	*Total*	
	n	n	n	n	n	n	n	n	n	%
cranial	0/12	0/1	0/1	.	0/1	0/10	.	0/2	0/27	0.0
vertebrae	0/1	.	2/5	0/1	0/1	1/9	0/5	0/2	3/24	12.5
ribs	0/9	0/3	1/17	0/7	0/12	2/174	0/34	0/12	3/268	1.1
scapula	0/1	.	0/1	0/1	0/1	1/5	.	0/3	1/12	8.3
humerus	4/8	2/2	1/2	0/2	.	1/7	0/3	0/1	8/25	32.0
radio-ulna	2/5	.	1/5	.	.	1/13	0/3	0/2	4/28	14.3
carpals	0/1	.	.	.	.	.	.	.	0/1	0.0
metacarpal	2/8	0/1	.	.	.	1/7	0/5	0/1	3/22	13.6
innominates	0/2	0/2	1/1	0/1	0/1	1/13	0/4	1/1	3/25	12.0
femur	0/4	.	1/4	0/1		0/13	0/4	0/1	1/27	3.7
tibia	1/8	2/7	0/5	1/3	0/1	1/16	0/7	0/1	5/48	10.4
tarsals	0/3	0/2	0/1	.	.	0/1	0/1	.	0/8	0.0
metatarsal	0/3	0/2	1/2	.	.	0/12	1/4	.	2/23	8.7
phalanges	0/1	.	0/2	.	.	1/7	0/1	0/1	1/12	8.3
Total	9/66	4/20	8/46	1/16	0/17	10/287	1/71	1/27	34/550	6.2

Table 22. Saint-Césaire. Distribution of cutmarks on horse bones by body part and level. Number of specimens with cutmarks (number left to slash) versus total NISP (number right to slash). Teeth are excluded. Cranial includes mandibular bone.

Châtelperronian? (EJOP inf)

In bison, the most abundant species in this small occupation, the humerus and tibia are over-represented relative to other parts. The skull and mandible are also abundant. The vertebral column is lacking, except for cervical vertebrae and sacrum. The head and tibia are best represented in horse. No clear pattern emerges from the very small reindeer sample associated with this occupation. For all these species, MNE indicate the prevalence of shafts over epiphyses. Because the sample is small, cutmarks are more difficult to interpret for this occupation. It seems that, in general, cutmarks are somewhat more common on long bones than on the axial skeleton. Few specimens show evidence of burning. However, burned teeth, usually crown fragments, are not uncommon (9.1%).

Châtelperronian (EJOP sup)

The sample studied for this occupation is relatively large. Bison are predominant in the assemblage, followed by reindeer and horse. Long bones and heads are the most frequent parts. Abundance of elements decreases distally in the forelimb, whereas the tibia is the most abundant bone of the hindlimb. In contrast, elements of the axial skeleton, as well as carpals, tarsals, and phalanges are rare or absent. Long bone epiphyses are also rare.

In reindeer, body part representation is typical of the Saint-Césaire sequence. Heads and long bones, especially the humerus, femur, and tibia, are well represented. Again, there are few elements of the axial skeleton. Carpals, tarsals, and phalanges are under-represented. The horse sample is dominated by the head, humerus, and tibia. A small number of fragments of cervical and thoracic vertebrae document the transport of the neck and back. Likewise, carpals, tarsals, and phalanges are rare in this occupation. Few burned specimens could be identified in this assemblage. Most are tooth fragments.

Cutmark distribution is biased toward long bones in bison. Cutmarks are most common on the tibia, humerus, and femur and are scarce on metapodials. They are also rare on elements of the axial skeleton. Cutmarks are relatively less abundant in reindeer and horse.

EJOP (8-9)

It is possible to crosscheck some of the patterns observed in the Châtelperronian by looking at this assemblage. The tibia is the best represented element in the bison sample. Next in abundance are the head and humerus. No element of the spine was identified. Carpals and tarsals are poorly represented. In reindeer, the highest %MAU values are associated with the head, radio-ulna, tibia, and metatarsal. The horse sample is too small to provide reliable information on skeletal part abundance.

In bison, the highest proportion of cutmarks is on the tibia. The small size of the reindeer and horse samples precludes interpretation. Again, very few burned specimens could be identified. Most of these are teeth. Interestingly, the only two tali identified in this assemblage are burned. We will see that this bone is frequently burned in the Aurignacian sequence.

Aurignacian 0? (EJO sup)

This reindeer-dominated assemblage presents the same general characteristics observed previously. The tibia and metatarsal are well represented in the reindeer sample. Elements of the forelimb, especially the humerus and radio-ulna, are slightly less common. The cervical vertebrae, ribs, scapula, innominates, carpals, tarsals, and phalanges are rare or absent. Little data is available with respect to the other taxa.

Cutmarks are preferentially distributed in reindeer on long bones and are scarce on the skull, vertebrae, phalanges, and ribs. Many more burned specimens could be identified in this sample compared to the previous assemblages. Vertebrae are frequently burned (24%). The proportion of carpals and tarsals that were exposed to fire is also significant, although the sample is small. A small number of burned long bones could be identified. Four of the six burned specimens are epiphyses.

Information is too limited concerning bison and horse to be useful here.

Aurignacian I (EJF)

A large reindeer assemblage is available from this level. The tibia and metatarsal are the most abundant elements, followed by the humerus, radius, and femur. The metacarpal is poorly represented compared to other long bones. As usual in the reindeer samples from Saint-Césaire, elements of the axial skeleton, especially the spine, are under-represented. Frequencies of head parts are low compared to long bones. Ribs, carpals, tarsals, innominates, and phalanges are also uncommon. Several vertebrae have also been burned. Conversely, ribs, heads, and phalanges were rarely burned, if at all. It is interesting to note that the abundance of phalanges decreases distally.

The most common horse elements are the tibia, mandible, femur, and metatarsal. In contrast, the vertebral column is under-represented. This is also true of humeri, carpals, tarsals, and phalanges. The bison sample is relatively small, which limits interpretation. The tibia and mandible are the most abundant parts in this taxon. The skull and femur are also well represented. Few carpals, tarsals, and phalanges were identified. However, a nearly complete portion of a vertebral column, consisting of the last five lumbar vertebrae and the sacrum, was refitted in the lab (Figure 18). Their spatial distribution shows that the fragments were found over a relatively small area in the so-called "charnier" (see section on human remains).

Figure 18. A refitted portion of a bison vertebral column from the Aurignacian I occupation from Saint-Césaire.

A fairly large number of burned bones (n=264) has been identified in this assemblage. Most are from reindeer. As in the previous occupation, the proportions of burned vertebrae (41%), carpals (17%), and tarsals (41%), are high in this assemblage. The innominates and lateral malleolus are also frequently burned. The incidence of burning on long bones is low. However, most of the burned specimens are epiphyses (46/76 or 60.5%). Burning is rarely observed on the skull, antlers, ribs, and phalanges.

In reindeer, cutmarks are mostly concentrated on the humerus, tibia, femur, and scapula. Few cutmarks were identified on the metatarsal. Cutmarks are not infrequent, however, on the metacarpal. A small number of cutmarks were noted on the skull, vertebrae, ribs, phalanges, carpals, and tarsals. In horse, cutmarks are more prevalent on long bones than on the rest of the skeleton.

The Evolved Aurignacian EJM

Reindeer also dominates this fairly large assemblage. The distribution of skeletal parts is comparable to that described for the previous samples. Elements of the hindlimb, especially the femur and tibia, are abundant. Parts of the forelimb are also well represented, as are the skull and mandible. This is in marked contrast with vertebrae, carpals, tarsals, and phalanges that are scant in this occupation. Again, the abundance of phalanges decreases distally.

The horse sample is fairly small. The head, metacarpal, and tibia are best represented. Some elements of the axial skeleton are present. Very few carpals, tarsals, and phalanges have been identified. Little can be said about bison, due to small sample size.

Many vertebrae and tarsals are burned (28%) in the reindeer sample, in agreement with the pattern highlighted above. No burned carpals were identified, however. Five of the twelve burned long bone fragments are from epiphyses. The skull, ribs, and phalanges are rarely burned.

Cutmarks are common in reindeer and are most frequent, in decreasing order, on the humerus, femur, tibia, and metacarpal. Cutmarks are rare in the axial skeleton in general. This is true of the radio-ulna, phalanges, and metatarsal as well.

The Evolved Aurignacian EJJ

In the reindeer sample, elements of the skull and hindlimb, especially the tibia and metatarsal, are most common. Forelimb parts are slightly less abundant. Cervical and thoracic vertebrae were identified, but are rare. Lumbar and sacral vertebrae are absent. Carpals, tarsals, and phalanges are also significantly under-represented. Most cutmarks tend to be located on long bones. Percentages of burning are highest on the innominates and vertebrae. A tarsal and a phalanx are also burned. As usual, antlers, teeth, and ribs are rarely the focus of burning. Of the five burned long bone fragments, three are from epiphyses. The horse and bison samples are too small to yield reliable information on these issues.

This chapter has provided some basic information on taxonomic composition and skeletal representation in the Saint-Césaire occupations. The next two chapters focus on the taphonomy and seasonality of the assemblages. These chapters are important because they will provide us with a better control on the patterns observed. Consequently, the results are more likely to address the questions motivating this reseach.

CHAPTER 5

TAPHONOMY: FILTERING OUT THE FACTORS THAT STRUCTURED THE ASSEMBLAGES

Significant differences in specimen abundance and taxonomic composition were observed between some of the occupations from Saint-Césaire. Conversely, little change appears to be recorded in skeletal part representation throughout the sequence. However, are these patterns behaviorally meaningful?

From an analytical point of view, at least six families of filters may structure a faunal assemblage. The first group of filter relates to site formation processes. This aspect must be investigated because postdepositional processes might have redistributed archaeological traces over the landscape and across stratigraphic units, hence reorganizing the initial spatio-temporal relationship of the remains. Testing the reliability of the stratigraphic sequence at Saint-Césaire will help to elucidate whether variation in bone counts, skeletal representation, and species composition between the assemblages are diachronically meaningful or spurious byproducts of postdepositional processes. Second, one should determine how recovery and sampling methods affect species and body part representation in the occupations under study. Third, the effects of cultural and natural processes on bone surface preservation and, more importantly, on mark preservation, a critical source of information on site formation, need to be evaluated. Fourth, the agent that created the assemblages, generally humans, carnivores, or a combination of both, should be identified, as well as their relative position in the sequence of accumulation. Fifth, natural and cultural processes can also lead to the selective removal of elements, for instance through differential preservation. These processes can also fragment specimens to a point where they become analytically absent (Lyman and O'Brien 1987). Sixth, identification filters, that is, factors intrinsic to skeletal morphology that enhance or inhibit the identification of some elements or taxa, have to be taken into account.

How these processes shape archaeological interpretation is variable. For instance, as a result of differences in skeletal morphology, some species or elements may have fewer diagnostic landmarks than others and be consistently under-represented. Damaged bone surfaces may hinder the identification of elements with few landmarks and may reduce detection of anthropic marks. In addition, differential preservation and carnivore ravaging may modify body part representation. All these aspects might have come into play and structured the distribution and composition of the Saint-Césaire faunal remains. Therefore, we need to control for these factors of variability in order to produce meaningful results on past cultural behavior. In this chapter, these six families of filters are scrutinized in order to explore how they affect the interpretation of the faunal assemblages from Saint-Césaire.

The chronological grain at Saint-Césaire

Ultimately, any archaeological interpretation is shaped by the history of the samples on which it is based on. Therefore, if we want to make valid and accurate statements about past behavior, it is essential to control the chronological grain of our samples. For instance, how reliable are patterns derived from samples in which multiple layers are combined postdepositionally or analytically? Combining several occupations into a single sample may merge behavioral contexts that differ in their composition, for example as a consequence of "drift" in behavior, changes in demography, climatic conditions, availability and abundance of resources, etc. Indeed, this type of approach produces averages of averages, a situation that suppresses variability. Consequently, the amalgamation of different occupations, sometimes helpful when confronted with small sample size, should be avoided as much as possible. In the study of Saint-Césaire, occupations are examined individually.

However, natural and cultural processes might have resulted in the inclusion of different occupations within a single stratigraphic unit. These contaminations may not be easy to detect in situations in which a relative behavioral stability is documented over a relatively long period of time. For all these reasons, evaluating the chronological and spatial integrity of the assemblages under scrutiny should precede any other step in analysis. This issue is especially relevant for Saint-Césaire given that concerns have been raised concerning the homogeneity of some of its occupations (Bordes 1981; Sonneville-Bordes 1989; Backer 1994; Guilbaud *et al.* 1994).

Based on bone refits on both dry- and green-bone fractures, in addition to data on specimen vertical and horizontal distribution, body part representation, and taxonomic composition, it has been possible to show that occupation mixing is minor at Saint-Césaire (Morin *et al.* 2004). Because this issue is developed in detail elsewhere (Morin *et* *al.* forthcoming), the results from the refitting program carried out during the analysis of the faunal material from Saint-Césaire are only very briefly summarized here.

A total of 2068 specimens has been refitted (considering the NISP sample only). These are distributed into 847 refit sets, for an average of 2.4 specimens per set. Counting only the specimens tentatively refitted across all décapages and levels, it was found that approximately 91% of the refits involve fragments that belong to the same décapage. However, most of these refits are on dry-bone fractures and might have been fragmented postdepositionally, possibly as recently as during the excavation of the site. In contrast, specimens refitted on green-bone fractures became disassociated during, or not long after, being discarded. For this reason, these are most useful when addressing issues of occupation mixing.

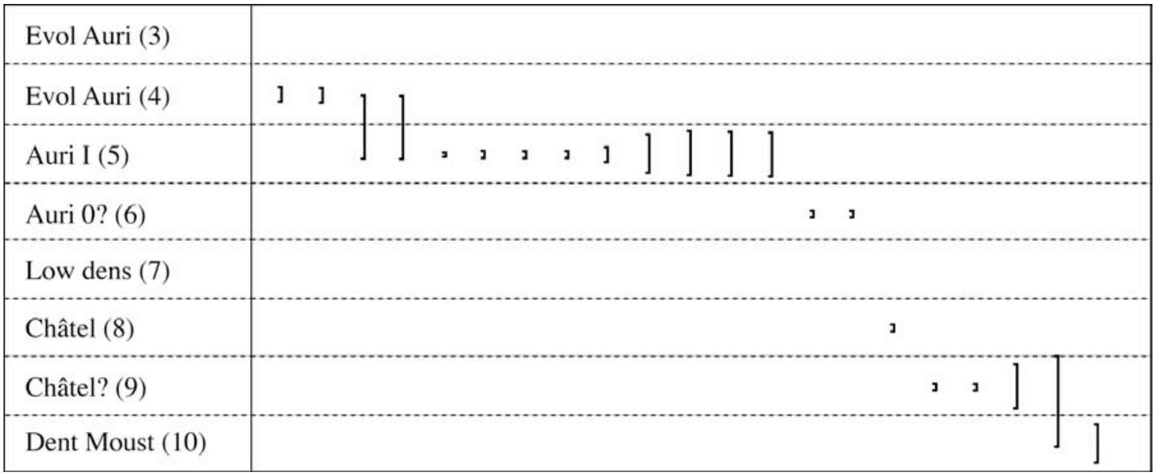

Figure 19. Vertical distribution of all the refits on green-bone fracture from Saint-Césaire.

Using this last category of refits, it is possible to show that Saint-Césaire is characterized by a relatively fine chronological grain (Figure 19). This is supported by the fact that only 3 refit sets out of a total of 18 are indicative of occupation mixing[3]. This low proportion of inter-layer refits suggests that if mixing occurred, the occupations involved were most probably penecontemporaneous from an archaeological point of view. Occupation averaging would therefore be minimized at Saint-Césaire.

Effects of recovery methods on faunal composition

Recently, the impact of recovery methods on body part representation has been hotly disputed (Turner 1989; Klein 1989; Marean and Kim 1998; Bartram and Marean 1999; Outram 2001, Stiner 2002; Pickering *et al.* 2003). A key issue in these debates is the effect that the exclusion of shaft fragments from the analysis, often inescapable because they were discarded during the excavations, has on estimations of skeletal part abundance. This follows several decades of discussion on how recovery methods affect species abundance, especially with respect to small taxa (e.g., Struever 1968; Thomas 1969; Cossette 2000).

As emphasized earlier, sediments were dry sieved at Saint-Césaire using 5 mm and 2 mm mesh screens. This resulted in thorough recovery of the faunal material. However, this mesh size was probably too large for many microfaunal (mouse size or smaller) remains. Therefore, their abundance is probably under-estimated in the samples. It is worth stressing again that, except for the unstudied Mousterian levels and a handful of specimens on exhibit in a museum in the village of Saint-Césaire, the complete sample

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[3] Excluding the reindeer metatarsal, as refitting of this element could not be performed across all occupations (see Chapter 4). This reduces the total of refit sets from 21 to 18. The number of sets documenting occupation mixing remains the same (n=3).

of faunal specimens was made available to the author and studied. Importantly, all fragments with precise stratigraphic information on layer and square of provenience were included in the counts.

Looking at fragment size, it is no surprise to find that small fragments are very abundant in the assemblages, reflecting the thoroughness of the recovery methods (Table 23). Fifty-seven percent of the unburned bones are smaller than 2 cm in a sample of twelve décapages that includes most layers from Saint-Césaire. In the same décapages, this proportion increases to 84% when looking at burned bones. This difference between the burned and unburned samples is highly significant ($t_s = 8.97$, $p < 0.0001$). Overall, burned bones are smaller on average than unburned ones and show a narrower distribution of measurements (Figure 20). These distributions also highlight the fragmentation of the material, given that few specimens are larger than 6 cm. This high degree of fragmentation is not unusual in prehistoric assemblages, however, as similar distributions are documented in several other cultural and carnivore sites (e.g., Gould 1996; Villa *et al.* in press).

	0-1		*1-2*		*2-3*		*3-4*		*4-5*		*5-6*		*6 and +*		*Total*	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
burned	112	23.5	288	60.5	68	14.3	7	1.5	1	0.2	.	.	.	.	476	100
unburned	151	17.2	352	40.1	229	26.1	93	10.6	24	2.7	19	2.2	9	1.0	877	100
total	263	19.4	640	47.3	297	22.0	100	7.4	25	1.8	19	1.4	9	0.7	1353	100

Table 23. Distribution of specimens by size class in twelve décapages from Saint-Césaire. Size classes are in cm. The last size class is open and includes all fragments equal to or larger than 6 cm.

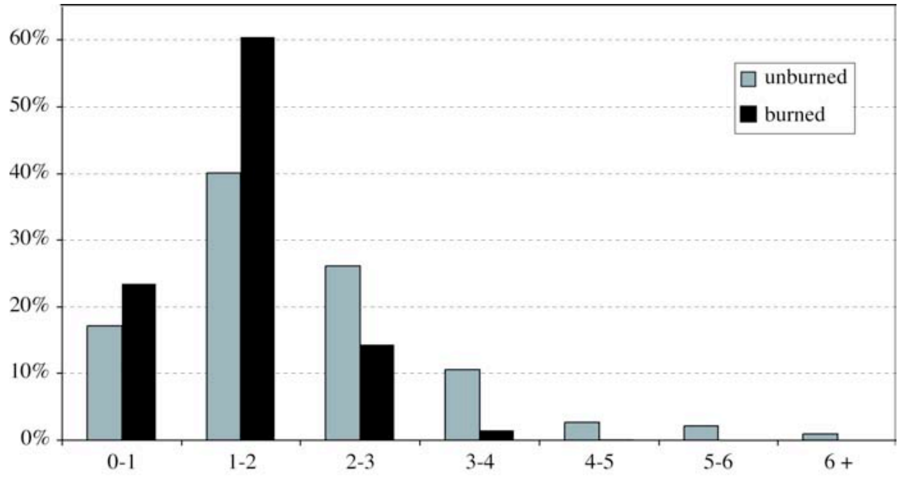

Figure 20. Comparison of the distributions of burned and unburned bones by size classes at Saint-Césaire.

Because fragment size appears to be positively correlated with taxonomic identification (Lyman and O'Brien 1987), and because burning increases fragmentation (Stiner *et al.* 1995; Costamagno *et al.* 1999), burned fragments are expected, holding taxon constant, to be more difficult to identify than unburned specimens.

In sum, biases in recovery and sampling methods have been minimized at Saint-Césaire. Therefore, these factors are unlikely to have affected significantly the composition of the macrofaunal assemblages. Unfortunately, because some sections of the site have been destroyed prior to the excavations, it is impossible to estimate how much of the samples are missing. This should be taken into account when interpreting faunal patterns in the occupations.

Bone surface preservation and abundance of marks at Saint-Césaire

Marks are critical for inferring the role played by humans and carnivores in site formation. However, before interpreting the abundance of marks at Saint-Césaire, it is necessary to estimate their degree of preservation in the occupations. Several factors hindering the interpretation of marks within and between assemblages are scrutinized here. These factors include root etching, weathering, exfoliation, and various types of bone damage (Delpech and Villa 1993). Coding for this type of information was restricted to a sample of 4,639 specimens, mostly long bones.

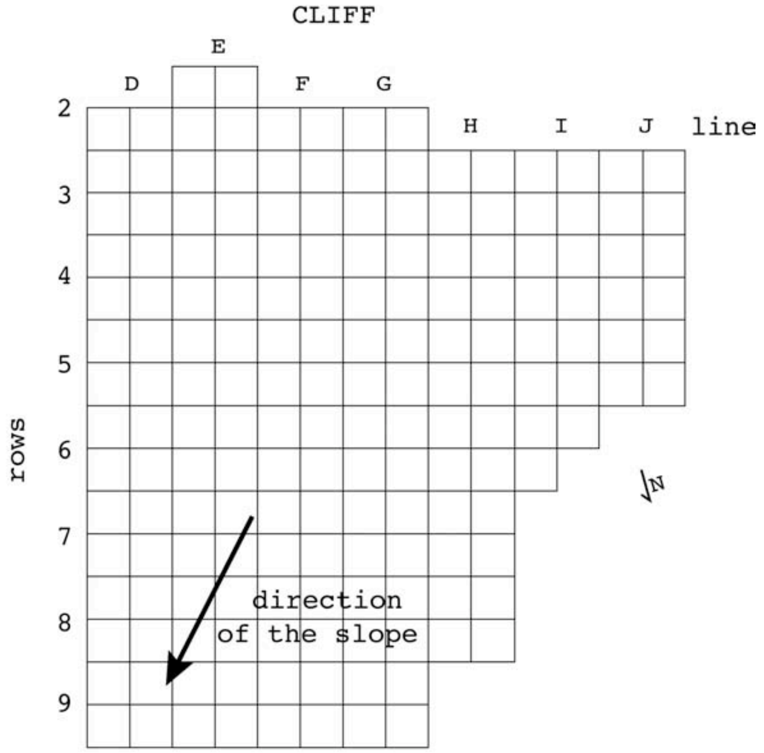

Figure 21. The square grid at Saint-Césaire. Lines B and C truncated by road work, and for this reason excluded from the analysis, are not shown on this figure.

As will become obvious in the next paragraphs, spatial variation is a key factor for understanding bone surface preservation at Saint-Césaire. As noted previously, the excavation grid was set slightly off from the natural slope of the deposit. Employing diagonals being very impractical with a square system, the role that the slope might have played on spatial distribution can be investigated using either rows 2 to 9 or lines D to J (Figure 21). Because the slope seems more accentuated in the former, rows were selected in the analysis of spatial patterning. The use of a single (rows), rather than both (rows and lines) dimensions of space for investigating spatial patterns probably results in a loss of resolution. However, in each case, it was verified whether the same (mirror) pattern could be perceived in lines D to J.

A four-state classification system was implemented in the study of Saint-Césaire to explore mark preservation on bone surfaces. This system, described in Chapter 4, encompasses the whole spectrum of surface preservation from poorly preserved, somewhat damaged, to relatively well preserved, and intact surfaces (see the section on methods in Chapter 4 for more details). Obviously, an intact surface will yield better readings than a poorly preserved surface. In this discussion, it is important to note that with few exceptions (n=10), specimens are rarely coated with calcareous concretions.

Most specimens from Saint-Césaire fall in the middle of the preservation spectrum, few bones having a “poorly preserved” or an “intact” surface (Table 24). This means that although some marks might have been partly or entirely obliterated, this affects only a portion of the material.

Layers	*Poorly Preserved*		*Damaged*		*Slightly Damaged*		*Intact*		*Total*	
	n	%	n	%	n	%	n	%	n	%
Evol Auri (3)	23	8.4	173	63.1	76	27.7	2	0.7	274	99.9
Evol Auri (4)	49	8.3	367	62.5	170	29.0	1	0.2	587	100.0
Auri I (5)	35	2.1	729	43.0	913	53.8	19	1.1	1696	100.0
Auri 0? (6)	7	1.9	167	46.3	186	51.5	1	0.3	361	100.0
low dens (7)	1	2.1	29	61.7	17	36.2	0	0.0	47	100.0
Châtel (8)	38	6.7	317	55.9	206	36.3	6	1.1	567	100.0
Châtel? (9)	11	5.0	86	39.4	115	52.8	6	2.8	218	100.0
Moust (10)	7	1.5	186	39.9	269	57.7	4	0.9	466	100.0
Total	171	4.1	2054	48.7	1953	46.3	39	0.9	4216	100.0

Table 24. Saint-Césaire. Degree of surface preservation by level for a sample consisting mostly of long bones.

No obvious patterning between levels can be perceived, although surfaces tend to show a lower degree of preservation in the Châtelperronian and the Evolved Aurignacian EJM and EJJ assemblages. As we will see, these differences in surface preservation can be attributed to the combination of two factors: spatial distribution of the remains and root etching. This is because at Saint-Césaire, surface preservation decreases generally with distance from the cliff (Table 25). The pattern is, however, not as clear in the bottom of the sequence, that is, from the Denticulate Mousterian to the Châtelperronian, due to small sample size. The same trend can be detected, however, when these last levels are combined (Figure 22).

	Distance Away From the Cliff in Meters											
	2		3		4		5		6		total	
Evol Auri (3)	n	%	n	%	n	%	n	%	n	%	n	%
poorly preserved	2	25.0	2	3.9	3	12.0	10	10.0	6	6.7	23	8.4
damaged	1	12.5	25	49.0	14	56.0	70	70.0	62	69.7	172	63.0
slightly damaged	4	50.0	24	47.1	8	32.0	20	20.0	20	22.5	76	27.8
intact	1	12.5	0	0.0	0	0.0	0	0.0	1	1.1	2	0.7
total	8	100.0	51	100	25	100.0	100	100.0	89	100.0	273	99.9
Evol Auri (4)												
poorly preserved	2	7.1	3	3.1	16	4.8	13	17.3	12	26.7	46	8.0
damaged	13	46.4	59	60.8	206	62.0	52	69.3	31	68.9	361	62.6
slightly damaged	13	46.4	35	36.1	109	32.8	10	13.3	2	4.4	169	29.3
intact	0	0.0	0	0.0	1	0.3	0	0.0	0	0.0	1	0.2
total	28	99.9	97	100.0	332	99.9	75	99.9	45	100.0	577	100.1
Auri I (5)												
poorly preserved	1	0.2	4	0.9	6	2.6	4	8.0	5	10.2	20	1.4
damaged	254	38.4	145	32.7	118	50.4	37	74.0	39	79.6	593	41.2
slightly damaged	401	60.6	284	64.0	109	46.6	9	18.0	5	10.2	808	56.2
intact	6	0.9	11	2.5	1	0.4	0	0.0	0	0.0	18	1.3
total	662	100.1	444	100.1	234	100.0	50	100.0	49	100.0	1439	100.1
Auri 0? (6)												
poorly preserved	1	0.5	3	2.5	2	5.7		0.0	1	6.7	7	2.0
damaged	100	54.6	32	26.9	17	48.6	4	66.7	11	73.3	164	45.8
slightly damaged	82	44.8	83	69.7	16	45.7	2	33.3	3	20.0	186	52.0
intact	0	0.0	1	0.8	0	0.0	0	0.0	0	0.0	1	0.3
total	183	99.9	119	99.9	35	100.0	6	100.0	15	100.0	358	100.1
Châtel (8)												
poorly preserved	1	4.0	1	2.7	9	5.6	9	7.0	1	2.5	21	5.4
damaged	10	40.0	27	73.0	91	56.9	64	50.0	25	62.5	217	55.6
slightly damaged	13	52.0	9	24.3	59	36.9	54	42.2	13	32.5	148	37.9
intact	1	4.0	0	0.0	1	0.6	1	0.8	1	2.5	4	1.0
total	25	100.0	37	100.0	160	146	128	100.0	40	100.0	390	99.9
Châtel? (9)												
poorly preserved	0	0.0	3	8.1	0	0.0	0	0.0	4	11.4	7	4.0
damaged	11	19.3	10	27.0	17	60.7	8	40.0	17	48.6	63	35.6
slightly damaged	40	70.2	24	64.9	11	39.3	12	60.0	14	40.0	101	57.1
intact	6	10.5	0	0.0	0	0.0	0	0.0	0	0.0	6	3.4
total	57	100.0	37	100.0	28	100.0	20	100.0	35	100.0	177	100.1
Moust (10)												
poorly preserved	1	1.6	2	1.5	3	2.9	0	0.0	1	1.4	7	1.6
damaged	22	36.1	43	31.6	37	35.6	43	57.3	35	50.0	180	40.4
slightly damaged	37	60.7	91	66.9	63	60.6	30	40.0	34	48.6	255	57.2
intact	1	1.6	0	0.0	1	1.0	2	2.7	0	0.0	4	0.9
total	61	100.0	136	100.0	104	100.1	75	100.0	70	100.0	446	100.1

Table 25. Saint-Césaire. Degree of bone surface preservation by meter in a sample consisting mostly of long bones.

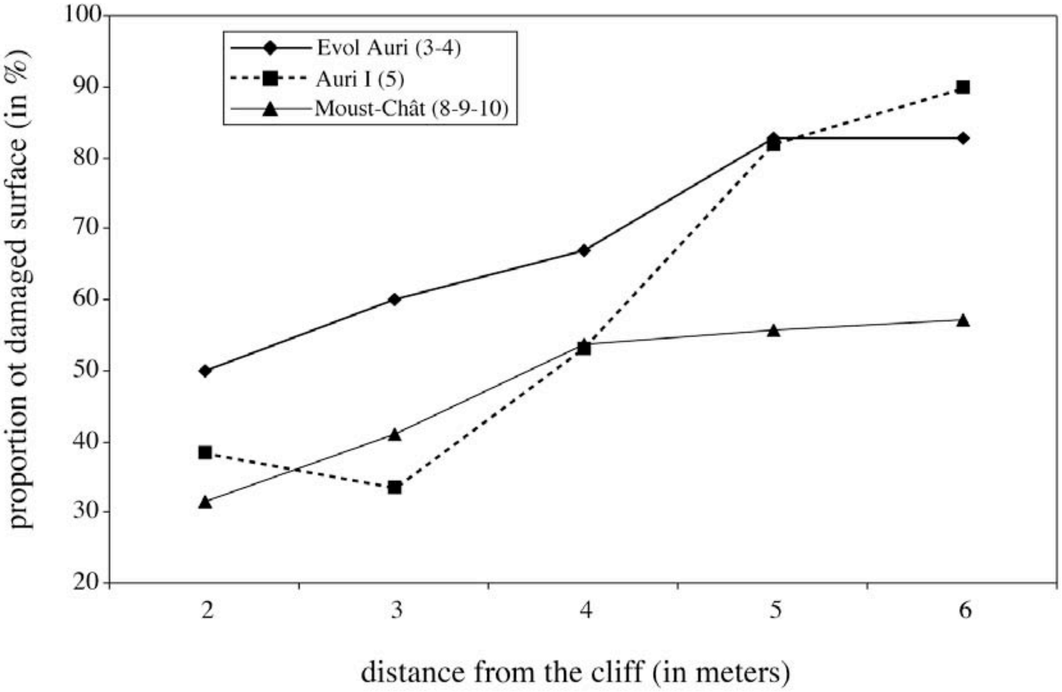

Figure 22. Proportions of bones that have either a damaged or poorly preserved surface by level and distance from the cliff.

	Distance Away From the Cliff in Meters											
	2		3		4		5		6		Total	
	n	%	n	%	n	%	n	%	n	%	n	%
Evol Auri (3)	14	3.3	70	16.5	45	10.6	148	34.9	147	34.7	424	100.0
Evol Auri (4)	45	4.2	146	13.7	653	61.4	133	12.5	86	8.1	1063	99.9
Auri I (5)	1633	46.9	987	28.3	606	17.4	140	4.0	116	3.3	3482	99.9
Auri 0? (6)	212	44.6	161	33.9	67	14.1	18	3.8	17	3.6	475	100.0
Châtel (8)	70	9.5	106	14.5	272	37.1	213	29.1	72	9.8	733	100.0
Châtel? (9)	65	25.9	61	24.3	36	14.3	30	12.0	59	23.5	251	100.0
Moust (10)	119	14.2	270	32.2	197	23.5	127	15.1	126	15.0	839	100.0
Total	2158	29.7	1801	24.8	1876	25.8	809	11.1	623	8.6	7267	100.0

Table 26. Spatial distribution of the abundance of NISP by meter and level at Saint-Césaire.

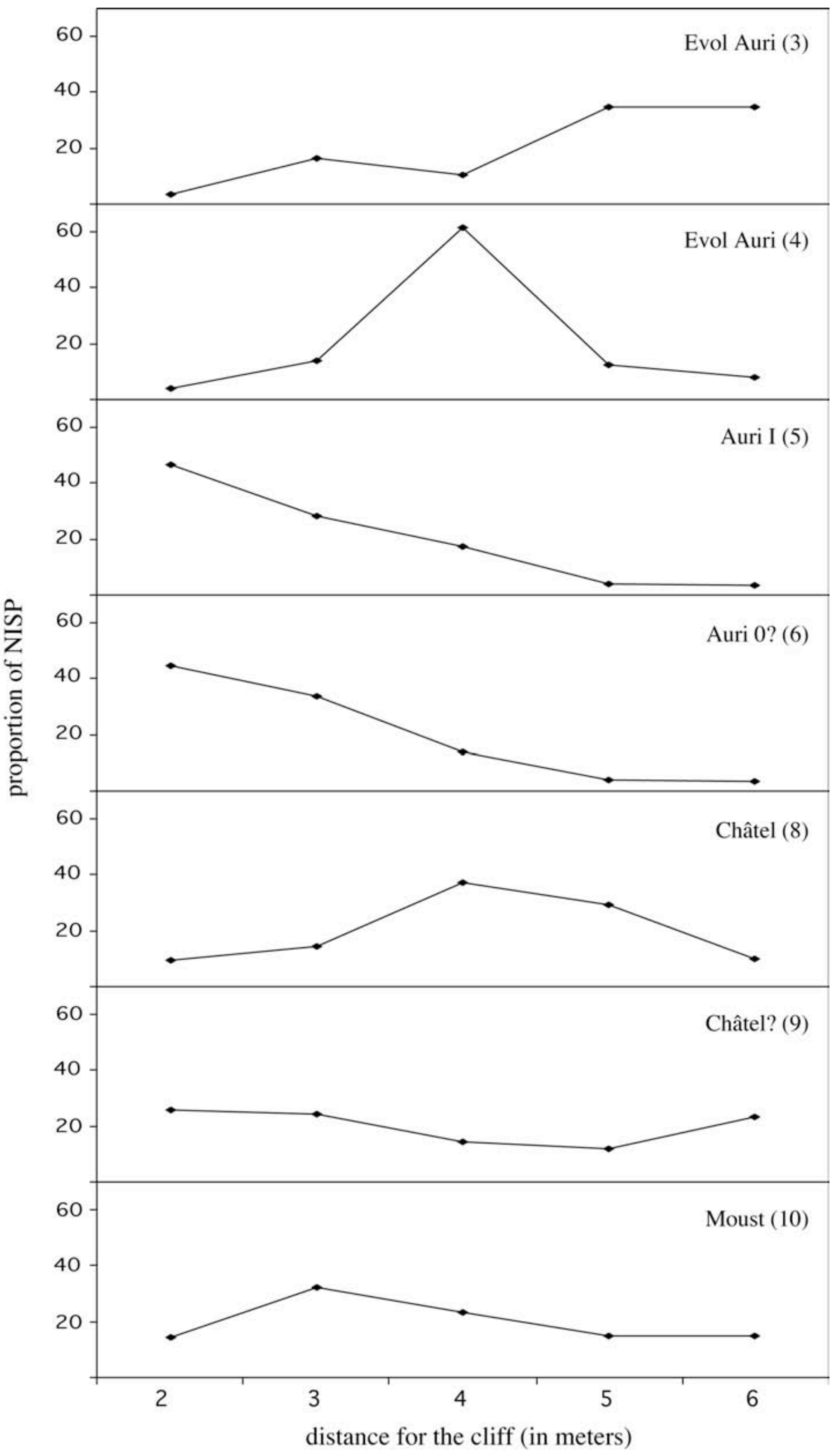

Figure 23. Abundance of NISP by level as a function of the distance away from the cliff. Data from Table 26.

At Saint-Césaire, fragments that have been identified, as measured by NISP counts, vary spatially in abundance (Table 26 and Figure 23). For instance, NISP counts are highest near the cliff in the Aurignacian 0? and Aurignacian I occupations, whereas the highest NISP values are recorded on the slope in the Châtelperronian and Evolved Aurignacian EJJ occupations. The reader should note, however, that spatial patterns in the Evolved Aurignacian assemblages might be biased by the truncation of some of the décapages by road construction. Changes in the stratigraphic framework during the excavations may also affect raw NISP counts for the Châtelperronian? and Châtelperronian assemblages.

The implications of these results are threefold. First, surfaces tend to be poorly preserved on the slope throughout the sequence, especially in the uppermost layers. In general, surfaces are best preserved near the cliff in the lowermost occupations. This means that considering only percentages for total assemblages, as in Table 24, overlooks completely this spatial component. A second implication is that the levels where faunal remains tend to be concentrated on the slope, specifically, the Châtelperronian and the two Evolved Aurignacian occupations, are expected to have more damaged surfaces and fewer marks on average than the other levels. A third implication of the results is that mark percentages may be under-estimated at Saint-Césaire with respect to other sites characterized by better preserved surfaces.

The relationship between surface preservation and mark frequencies can be investigated directly with cutmark data. Despite the use of a hand lens for analyzing the specimens, a reliable method for detecting marks according to Blumenschine *et al.* (1996), an almost perfectly linear decrease in cutmark frequencies is observed, assuming equidistance between the categories, with decreasing surface preservation (Table 27 and Figure 24). This suggests that a significant fraction of the marks are obliterated from the surfaces. Trends appear to be broadly similar across levels.

	All Taxa											
	Poorly Preserved			*Somewhat Damaged*			*Slightly Damaged*			*Intact*		
	ncut	n	%	ncut	n	%	ncut	n	%	ncut	n	%
Evol Auri (3)	0	15	0.0	6	111	5.4	11	48	22.9	0	2	0.0
Evol Auri (4)	1	39	2.6	15	209	7.2	19	104	18.3	0	1	0.0
Auri I (5)	0	20	0.0	42	375	11.2	104	472	22.0	2	8	25.0
Auri 0? (6)	0	4	0.0	4	109	3.7	10	113	8.8	0	1	0.0
low dens (7)	0	0	0.0	0	7	0.0	2	4	50.0	0	0	0.0
Châtel (8)	1	23	4.3	12	154	7.8	39	127	30.7	2	6	33.3
Châtel? (9)	0	5	0.0	4	53	7.5	16	82	19.5	3	5	60.0
Moust (10)	1	5	20.0	15	94	16.0	52	197	26.4	1	3	33.3
Total	3	111	2.7	98	1112	8.8	253	1147	22.1	8	26	30.8

Table 27. Saint-Césaire. Frequency of cutmarks on long bones by level and their relation with bone surface preservation. Long bones only. All species are included, excepting birds and microfauna. *ncut* is the number of cutmarked specimens and *n* is the total number of specimens considered.

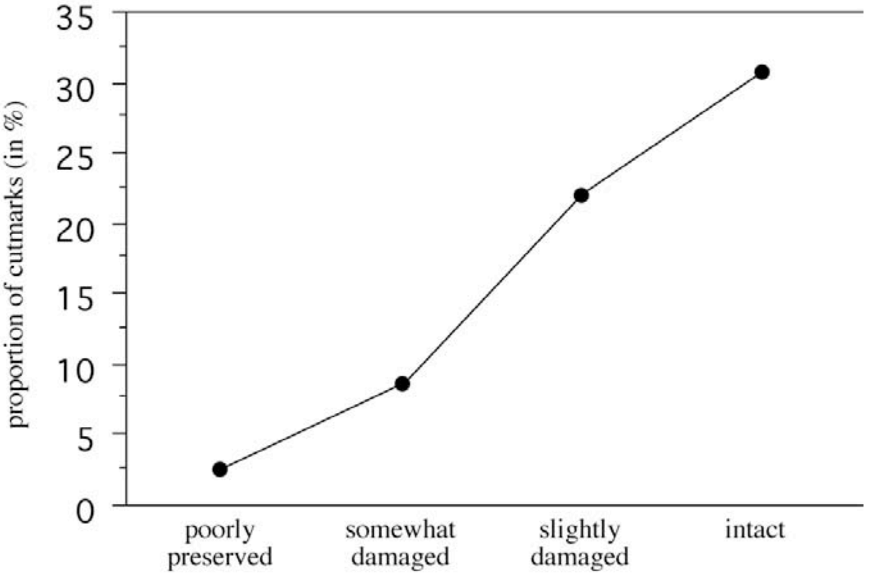

Figure 24. Relation between proportions of cutmarks and degree of bone surface preservation. Data from the Total of Table 27.

These findings lead to the conclusion that some levels, especially the Châtelperronian and the two Evolved Aurignacian occupations, are likely to be more affected by this type of bias than other occupations. Using the total for the intact surface category in Table 27, the proportion of elements with cutmarks at Saint-Césaire can be estimated to have been initially close to 31%, which is more than a 100% increase compared to the mean (15.1%) that combines all surface categories. The same pattern is observed when both species and element are held constant (Table 28 and Table 29). In this case, however, the samples for the poorly preserved and intact surface categories are generally too small to be useful.

	Reindeer: Hind Leg								
	Femur			*Tibia*			*Metatarsal*		
	ncut	total	%	ncut	total	%	ncut	total	%
poorly preserved	0	8	0.0	0	23	0.0		5	0.0
damaged	14	95	14.7	39	220	17.7	8	226	3.5
slightly damaged	21	82	25.6	63	188	33.5	24	293	8.2
intact	0	1	0.0	0	2	0.0	0	0	0.0
total	35	186	18.8	102	433	23.6	32	524	6.1
	Reindeer: Fore Leg								
	Humerus			*Radio-ulna*			*Metacarpal*		
	ncut	total	%	ncut	total	%	ncut	total	%
poorly preserved	0	6	0.0	0	11	0.0	0	2	0.0
damaged	7	57	12.3	7	155	4.5	7	61	11.5
slightly damaged	35	101	34.6	28	142	19.7	24	78	30.8
intact	0	0	0.0	0	0	0.0	1	1	100.0
total	42	164	25.6	35	308	11.4	32	142	22.5

Table 28. Proportions of cutmarks on reindeer long bones and their relation with bone surface preservation at Saint-Césaire.

These observations have broader implications and raise the problem of using raw cutmark percentages in assemblage comparison without taking into account their taphonomic history. Because faunal assemblages tend to move through phases of increasing attrition and decreasing bone surface preservation over time, the pattern highlighted for Saint-Césaire is probably not restricted to this sole location.

	Bison						*Horse*		
	Tibia			*Humerus*			*Tibia*		
	ncut	total	%	ncut	total	%	ncut	total	%
poorly preserved	0	6	0.0	0	1	0.0	0	8	0.0
damaged	7	78	9.0	3	13	23.1	0	21	0.0
slightly damaged	24	113	21.2	7	26	26.9	5	21	23.8
intact	1	2	50.0	5	14	35.7	0	0	0.0
total	32	199	16.1	15	54	27.8	5	50	10.0

Table 29. Proportions of cutmarks on bison and horse elements and their relation with bone surface preservation at Saint-Césaire.

It would be interesting to determine if the same decrease in cutmark abundance with decreasing surface preservation is characteristic of other sites as well. For instance, several interpretations of cutmarks frequencies have been published for FLK Zinj, an important early hominid site from Olduvai Gorge in Tanzania (Binford 1981; Bunn 1981; Bunn and Kroll 1986; Blumenschine 1995; Domínguez-Rodrigo 1997; Selvaggio 1998; Lupo and O'Connell 2002). Cutmark abundance is possibly under-estimated at this site, given that several bone surfaces are damaged (Blumenschine 1995:28). Excluding poorly preserved bones from the sample studied for cutmarks, as done by Blumenschine, might appear as a solution to this problem. However, percentages of cutmarks not only decrease on poorly preserved surfaces at Saint-Césaire, but also on specimens with slight to moderate damage. Therefore, excluding poorly preserved surfaces is only a partial solution to the under-estimation of cutmark abundance in faunal assemblages with damaged surfaces. The use of a microscope in some of the FLK Zinj studies may have, however, alleviated this bias by increasing the number of identified cutmarks.

Coming back to Saint-Césaire, results on surface preservation imply that the spatial distribution of species and skeletal elements in the assemblages may affect the comparability of percentages of cutmarks. These data indicate that taxa and parts that are better represented on the slope are more likely to have lower percentages of cutmarks than those deposited near the cliff. How can we explain this decrease in surface preservation?

		Distance Away From the Cliff in Meters						
		2	*3*	*4*	*5*	*6*	*7*	*Total*
Evol Auri (3)	root	2	23	17	39	32	0	113
	total	8	51	25	100	89	1	274
	%root	25.0	45.1	68.0	39.0	36.0	0.0	41.2
Evol Auri (4)	root	4	48	113	48	26	5	244
	total	28	97	332	75	45	7	584
	%root	14.3	49.5	34.0	64.0	57.8	71.4	41.8
Auri I (5)	root	37	48	59	24	21	22	211
	total	662	444	234	50	49	30	1469
	%root	5.6	10.8	25.2	48.0	42.9	73.3	14.4
Auri 0? (6)	root	2	2	1	3	4	0	12
	total	183	119	35	6	15	0	358
	%root	1.1	1.7	2.9	50.0	26.7	0.0	3.4
Châtel (8)	root	1	0	6	2	5	49	63
	total	25	37	160	128	40	166	556
	%root	4.0	0.0	3.8	1.6	12.5	29.5	11.3
Châtel? (9)	root	0	0	2	0	3	1	6
	total	57	37	28	20	35	12	189
	%root	0.0	0.0	7.1	0.0	8.6	8.3	3.2
Moust (10)	root	0	7	5	3	9	3	27
	total	61	136	104	75	70	19	465
	%root	0.0	5.1	4.8	4.0	12.9	15.8	5.8
total	root	46	128	203	120	100	80	676
	total	1024	921	918	454	343	235	3895
	%root	4.5	13.9	22.1	26.4	29.2	34.0	17.4

Table 30. Incidence of root marks by level and as a function of distance from the cliff (in meters) at Saint-Césaire.

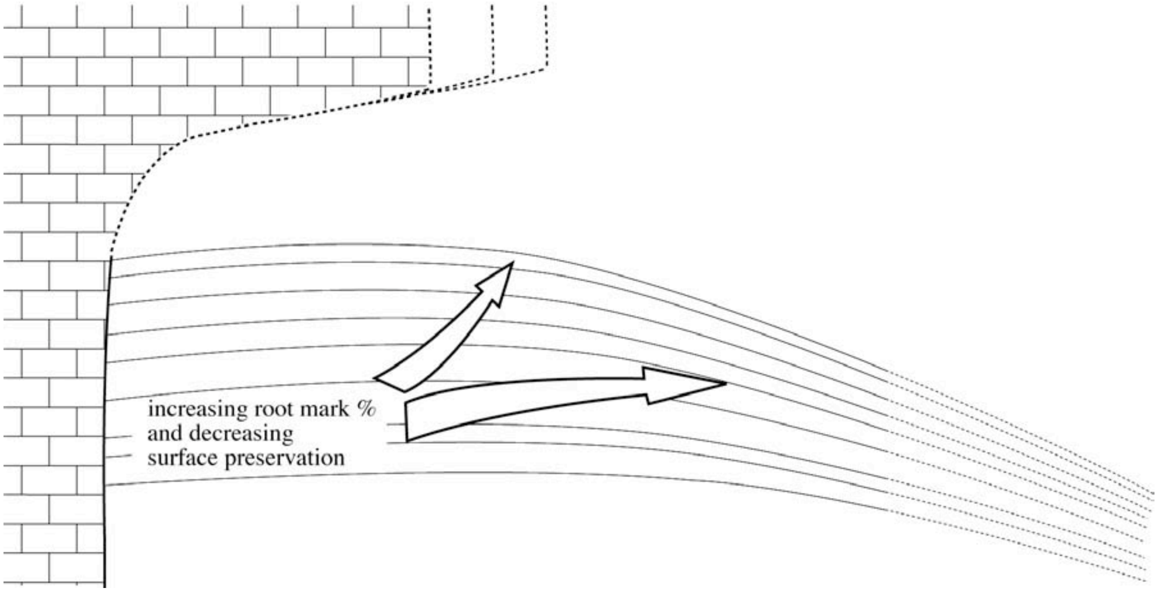

Figure 25. Schematic representation of the distribution of root etching at Saint-Césaire.

Marks left by several natural agents have been identified on bone surfaces at Saint-Césaire. Among these, root etching is the most conspicuous type of damage. In the sequence, root marks are most frequent in the uppermost Evolved Aurignacian EJM and EJJ and, to a lesser extent, the Châtelperronian (Table 30). Integrating the spatial dimension, root marks decrease more or less steadily with depth but increase with distance away from the cliff. In other words, root marks are most common on the slope, with a peak in meters 6 through 8 in the Evolved Aurignacian levels, and lowest near the cliff in the lowermost levels (Figure 25).

These results duplicate the observations derived from bone surface preservation. Therefore, root etching is probably responsible for a significant portion of the variation in bone surface preservation in the assemblages, even though root marks have not been identified on each specimen that has a damaged surface. The fact that root activity increases toward the cliff in the uppermost levels may indicate the evolution and retreat of the cliff throughout the cultural sequence. However, other scenarios (e.g., denser vegetation on the slope during the Holocene) might also explain the spatial pattern in root mark distribution at Saint-Césaire.

Other types of bone damage

Sheeting was identified on some bones from Saint-Césaire. As defined in Chapter 4, sheeting refers to bones that broke down into one or more sheets according to fracture planes that are more or less parallel to the cortical surface, sometimes creating sub-rectangular shaft splinters (Figure 26). Sheeting may decrease mark frequencies and hamper the identification of specimens. Therefore, this aspect may lead to an under-estimation of NISP and cutmarks in an assemblage.

Sheeting is rare in the Saint-Césaire occupations, being recorded on only 2.2% of the long bones. As a result, its effect on specimen identification is probably limited. Moreover, refitting contributed to alleviate this problem at Saint-Césaire. Like root etching, sheeting increases with distance from the cliff (Table 31). Unfortunately the sample of bones indicative of sheeting is too small to evaluate whether this type of damage varies also across levels. It is possible that the increase in sheeting observed toward the slope is related to root activity. If this is indeed the case, we would expect these features to be correlated. Of the bones affected by root marks, 17.9% show evidence of sheeting, a proportion markedly higher than the one (2.2%) that characterizes long bones without root marks. These statistically significant differences ($t_s = 4.26$,

$p < 0.0001$) may indicate that root etching and sheeting are correlated. Although root etching is presumably related to the density and/or type of vegetal cover, as well as, perhaps, many other pedologic and environmental factors, what causes sheeting is not clear and asks for further work. However, this might relate to bone thickness and gradient of change in degree of moisture (see below).

Figure 26. Sub-rectangular shaft splinters on a UNG3-4 long bone resulting from sheeting.

Exfoliation, the desquamation of the first mm of the bone outer surface, is moderately frequent in the assemblages (Table 31). It should be noted that this type of damage is related to ontogenetic age and affects especially fetuses and juveniles. Exfoliation probably occurs following incremental growth layers. In this respect, it is worth noting that incremental growth layers are easy to detect on fetal bones and constitute an extremely useful criterion for their identification (Figure 27).

One may suspect that exfoliation decreases the identification of cutmarks. This problem may be minor at Saint-Césaire, however, cutmarks being statistically as common on exfoliated bones (9.3%) as on non-exfoliated (9.6%) ones ($t_s = 0.21$, $p < 0.84$).

Conversely, the lack of differences between the two samples may simply reflect the possibility that all these bones are, in fact, either exfoliating or already fully exfoliated. Therefore, the possibility that exfoliation decreases the identification of very shallow cutmarks cannot be ruled out.

		Distance Away From the Cliff in Meters								
		1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*Total*
sheeting	with sheeting	0	5	3	12	11	13	13	4	61
	total bones	124	700	562	494	336	258	206	61	2741
	% sheeting	0.0	0.7	0.5	2.4	3.3	5.0	6.3	6.6	2.2
exfoliation	exfoliated	14	65	51	44	26	18	17	6	241
	total bones	124	700	562	494	336	258	206	61	2741
	% exfoliation	11.3	9.3	9.1	8.9	7.7	7.0	8.2	9.8	8.8
cracks	with cracks	12	49	51	77	34	30	31	8	292
	total bones	124	700	562	494	336	258	206	61	2741
	% with cracks	9.7	7.0	9.1	15.6	10.1	11.6	15.0	13.1	10.6

Table 31. Proportions of long bones with evidence of sheeting, exfoliation, and cracks by meter at Saint-Césaire.

Figure 27. Incremental growth layers on a fetal bone from Saint-Césaire.

Edge abrasion can be useful for understanding postdepositional processes. At Saint-Césaire, edge abrasion is slight and very homogeneous, given that 98% of the bones have slightly abraded edges. Thus, edge damage is very limited at Saint-Césaire.

Agents of accumulation: carnivores as commensal neighbors?

Several lines of evidence were used to study mark preservation at the site. It was found that marks are generally less well preserved on the slope, especially in the uppermost occupations from Saint-Césaire. Taking this information into account, the agents that caused the accumulations, as well as their position in the sequences of accumulation, are examined in the next paragraphs based on marks preserved.

Evidence of human activity at Saint-Césaire is corroborated by the large lithic assemblages recovered and indication of bone tool manufacture and hearth maintenance (Lévêque *et al.* 1993; Backer 1993, 1994; Guilbaud *et al.* 1993; Patou-Mathis 1993). However, it is central to our discussion to examine whether humans produced *all* of the *bone* accumulations or only some or a fraction of them. Indeed, carnivores appear to have contributed to these accumulations as well, as evidenced by the presence of gnawed bones and nonhuman coprolite fragments in the assemblages. Therefore, it is necessary to disentangle the respective role of these agents in the formation of the faunal assemblages from Saint-Césaire.

There is little doubt that the faunal accumulations from Saint-Césaire were produced primarily in the course of human activities. One line of argument supporting this interpretation is the abundance of bones yielding cutmarks (Figure 28). On average, between 5 and 16% of the bones are cutmarked in the occupations. This is particularly revealing of the intensity of human activity at Saint-Césaire, given that roots and other natural agents might have obliterated as much as half of them (see discussion above). As shown in Chapter 4, most cutmarks are found on long bones. One should note that burned fragments, teeth, and the very abundant antler fragments were excluded from the calculation of cutmark percentages.

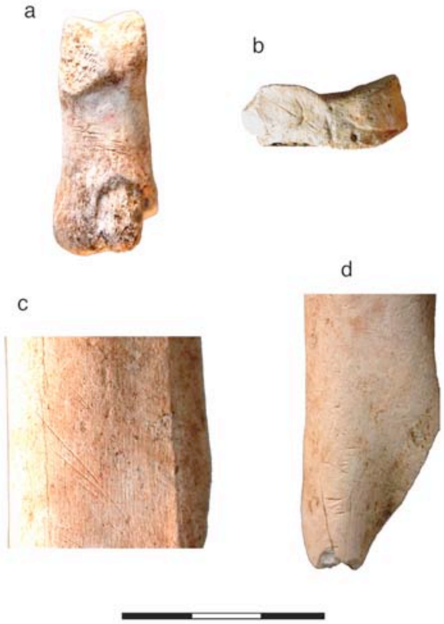

Figure 28. Cutmarks on a reindeer a) greater cuneiform, b) second phalanx, c) tibia, d) humerus. Cm scale.

Burning, an unambiguous marker of human activity, is documented on approximately 35% of the faunal remains from Saint-Césaire. Burned specimens are common in all of the occupations, although they are less salient in the small EJO inf sample (Table 32). This high level of burning is not exceptional in Paleolithic assemblages from southern France and characterizes the Mousterian sites of La Quina

(Chase 1999), La Chaise (Costamagno *et al.* 1999), and Chez Pinaud, Jonzac (Villa *et al.* 2002), as well as Upper Paleolithic sites like Cuzoul de Vers (Castel 1999a), Castanet (Villa *et al.* 2002), Combe Saunière (Castel 1999a), Chez Pinaud 2, Jonzac (Airvaux *et al.* 2003), and Saint-Germain-la-Rivière (Costamagno *et al.* 1999).

	Cutmarks			*Burned Bones*			*Retouchers*			*Percussion Notches*		
layers	cut	$NISP_1$	%	burned bones	total sample	%	retou-chers	total NISP	%	notch	$NISP_1$	%
Evol Auri (3)	20	258	7.7	1240	4066	30.5	2	426	0.5	11	258	4.3
Evol Auri (4)	42	673	6.2	2119	7613	27.8	.	1083	0.0	31	673	4.6
Auri I (5)	269	3013	8.9	13524	38296	35.3	10	4102	0.2	154	3013	5.1
Auri 0? (6)	16	345	4.6	1178	5453	21.6	.	480	0.0	15	345	4.3
low dens (7)	4	44	9.1	85	751	11.3	.	83	0.0	1	44	2.3
Châtel (8)	63	514	12.3	7544	28004	26.9	18	966	1.9	25	514	4.9
Châtel? (9)	27	196	13.8	3497	9241	37.8	5	331	1.5	14	196	7.1
Moust (10)	79	500	15.8	7148	20436	35.0	.	867	0.0	19	500	3.8
Total	520	5543	9.4	39757	113860	34.9	35	8338	0.4	270	5543	4.9

[1] excluding burned specimens, teeth, and antlers.

Table 32. Proportions of bones modified by humans in the Saint-Césaire occupations. *cut* is the total of specimens on which at least one cutmark was recorded. *notch* is the total of specimens on which at least one percussion notch is present.

Most burned bones at Saint-Césaire are black or brown in color, suggesting moderate fire temperature, while bones with white, blue, green, and gray colors, possibly indicative of higher fire temperature (Shipman *et al.* 1984; Stiner *et al.* 1995; Costamagno *et al.* 1999), were rarely encountered. It is worth pointing out that this observation applies to both the NISP and debris samples (proportions of burning colors may differ between these samples, given that high-fired bones are less likely to be identifiable than low-fired ones).

In addition to those that did not preserve, the assemblages include probably far more anthropic marks, as percussion notches (Figure 29) had to be excluded from the list of culturally diagnostic marks due to some overlap in notch morphology between humans and carnivores (Binford 1981). Some differences in percussion notch measurements recorded in experimental context between humans and hyenas are said to be discriminating in this regard (Capaldo and Blumenschine 1994). It remains to be shown, however, whether the statistical differences noted by these authors can be extended to include the robust hyena of the European Paleolithic (Ballesio 1979; Brugal *et al.* 1997; Fosse 1997). Nonetheless, because percussion marks are rarely associated with gnaw marks at Saint-Césaire, a single case being documented, it is suggested that most percussion marks were made by humans. Therefore, these are presented along with other anthropic marks in Table 32 with the above reservations.

Figure 29. Long bone shaft fragments with percusion notches from Saint-Césaire. Above is shown a percussion flake refitted with a UNG 3-4 shaft fragment. The lowermost specimen, probably from a reindeer, shows two overlapping percussion flakes still attached to a shaft fragment.

In comparison, retouchers are not as abundant (Table 32). As described in the previous chapter, retouchers are specimens with zones of linear marks that are distributed more or less perpendicular to the specimen axis. Importantly, these marks are found only on the outer (cortical) face of the specimen. Because retouchers are rare in the assemblages and sometimes look superficially like gnawed bones, one could make the argument that this type of surface modification lays at one extreme of the carnivore damage spectrum. This is the opinion of Binford (1981) who reinterpreted the retouchers identified by Henri-Martin (1907) as byproducts of carnivore activity. The current evidence suggests that this alternative can be ruled out.

Excluding the marks interpreted as the outcome of knapping activities, none of the retouchers show marks typically associated with carnivore ravaging like grooves, scooping, deep punctures, or evidence of digestion. In opposition to carnivore marks, retouching marks are never found on the fracture planes or the inner (medullary for long bones) face of the retouchers. More decisive is the fact that cutmarks (26.3%) and percussion marks (10.5%) are very abundant on retouchers. The same marks are absent or very rare on unambiguously ravaged specimens (cutmarks = 0%; percussion marks = 2.5%). These differences are significant or nearly significant (cutmarks: $t_s = 5.11$, $p < 0.0001$; percussion notches: $t_s = 1.85$, $p < 0.07$). Further, cutmarks and retouching marks often overlap on the same fragments. Clearly, ravaged specimens and retouchers are derived from two different populations.

It is hypothesized here that the high incidence of cutmarks on the retouchers of Saint-Césaire, many of which are scrape marks, is consistent with the removal of the periosteum on fresh bones prior to the use of the specimens in stone tool retouching. Further, there seems to be an intentional selection of long bones from UNG3-4, as evidenced by the fact that reindeer is under-represented in the retoucher sample (6/38 or 15.8%), even though the latter is the most abundant taxon (62.0) at Saint-Césaire. This difference in specimen selection is highly significant ($t_s = 6.12$, $p < 0.0001$). Because retouchers appear to be *ad hoc* tools produced at the end of a behavioral *chaîne opératoire* in which fresh bones (as indicated by the presence of periosteum on the bones) are recycled, these objects were included in the analysis of body part representation.

These conclusions on retouchers are corroborated by other studies. For instance, it has been suggested that the cross-section of retouching marks differs in morphology from those associated with gnawing (Chase 1990; Giacobini and Patou-Mathis 2002). Additionally, experiments have demonstrated that retoucher marks are compatible with the use of long bone shafts for retouching stone tools (Chase 1990; Armand and Delagnes 1993). Similar marks observed on phalanges, teeth, and long bone epiphyses might also be produced in stone tool retouching (Henri-Martin 1907; Valensi 2002a, 2002b). Another interpretation, not incompatible with the previous one, is that some of these marks were produced through heavy contact with an anvil, perhaps during marrow-cracking activities. Interpreting retoucher marks as being the outcome of stone tool edge modification is reasonable. Indeed, there is little reason to believe that antler has been the only raw material used as soft hammers during prehistory. In fact, only fifteen soft hammers made of antler were recorded by Averbouh and Bodu (2002) for the Paleolithic of Europe. All of these belong to the Upper Paleolithic with a peak during the Solutrean. This finding may indicate that antler hammers are relatively recent and were not characteristic of the Lower and Middle Paleolithic dominated, perhaps, by bone retouchers. It remains to be seen, however, if this generalization will stand the test of time. Visibly, although the context in which retouching marks have been produced is not totally unambiguous and calls for further work, most of the retouchers from Saint-Césaire are seemingly unrelated to carnivore ravaging and are best attributed to human behavior.

Evidence of carnivore activity

As we have seen, carnivores are rare at Saint-Césaire and never comprise more than 6.7% of the samples. In the presentation of the fauna (Chapter 4), it was also stressed that nonhuman producers of bone accumulations like hyena, wolf, cave lion, and cave bear are only marginally represented at Saint-Césaire, the carnivore cohort being dominated by fox. This picture is comparable to the one reconstructed by Castel (1999b) for Combe-Saunière, an Upper Paleolithic site also located in southwestern France.

The low proportion of large carnivore remains, 0.4% of the total NISP, may lead one to conclude that carnivore activity was insignificant at Saint-Césaire. These percentages can be misleading, however, given that some European assemblages with unambiguous indication of intense carnivore activity (Guadelli *et al.* 1988; Stiner 1994; Fosse 1997; Villa *et al.* in press) have relatively low carnivore NISP, although this situation tends to be more typical of African hyena dens (Klein and Cruz-Uribe 1984). For instance, carnivores account for only 8.6% of the NISP in the layer 2 of Bois-Roche, even though these are said to be primarily responsible for the faunal assemblage formation (Villa *et al.* in press). A similar situation characterizes the hyena den of Camiac where carnivores correspond to only 9.1% of the assemblage (Guadelli 1987, Guadelli *et al.* 1988). Thus, relative abundance of carnivores should be used with caution.

Despite this reservation, Saint-Césaire fall outside the range of European assemblages attributed to carnivores, as listed by Fosse (1997).

A more decisive source of information for determining the role played by carnivores in an assemblage comes from marks left on bones (Binford 1981; Bunn 1981; Potts and Shipman 1981; Blumenschine 1986; Marean and Spencer 1991; Selvaggio 1994; Domínguez-Rodrigo 1997).

Gnawing marks and digested bones are rare at Saint-Césaire, providing persuasive evidence that carnivores contributed minimally to the bone assemblages (Table 33). The relative abundance of gnawed bones at Saint-Césaire is more than an order of magnitude lower than at hyena dens like Bois-Roche (between 74 and 87% of the remains depending on the calculation method, Villa *et al.* in press). Bones with gnaw marks largely outnumber those with marks of digestion, represented by only four identified specimens: a horse first phalanx illustrated in Figure 30 and three teeth, two of which are from carnivores (lynx and fox).

Layer	*Gnawed and Digested*	*Total NISP*	*% of Gnawed and Digested*
	n	n	%
Evol Auri (3)	1	426	0.2
Evol Auri (4)	1	1083	0.1
Auri I (5)	23 *(2)*	4102	0.6
Auri 0? (6)	4	480	0.8
low dens (7)	2	83	2.4
Châtel (8)	16 *(2)*	966	1.7
Châtel? (9)	3	331	0.9
Moust (10)	1	867	0.1
Total	51	9114	0.6

Table 33. Frequency of gnawing and digestion marks by level at Saint-Césaire. Numbers of digested bones are shown in italics.

Figure 30. Saint-Césaire. Elements with evidence of carnivore activity. The uppermost specimen is a thoroughly gnawed bison metatarsal (Aurignacian I). The lower left specimen is a bison rib with puncture marks (Aurignacian I). Grooves are found on the lower right specimen, a horse scapula head (Evolved Aurignacian EJJ).

	Grooves		*Pits*		*Digested*		*Total*	
	n	%	n	%	n	%	n	%
reindeer	14	77.8	4	22.2	.	.	18	100.0
horse	9	64.3	4	28.6	1	7.1	14	100.0
bison	12	100.0	.	.	.	.	12	100.0
red deer	2	66.7	1	33.3	.	.	3	100.0
rhinoceros	1	50.0	.	.	1	50.0	2	100.0
fox	.	.	2	100.0	.	.	2	100.0
lagomorph	.	.	1	100.0	.	.	1	100.0
hare	1	100.0	.	.	.	.	1	100.0
lynx		.	.	.	1	100.0	1	100.0
wild boar	.	.	.	.	1	100.0	1	100.0
UNG3-4	.	.	1	100.0	.	.	1	100.0
Total	39	69.6	13	23.2	4	7.1	56	100.0

Table 34. Types of carnivore damage by species in the Saint-Césaire assemblages.

Grooves are the most frequent type of gnawing marks, followed by pits. These marks reach their highest frequencies on bison, horse, and reindeer (Table 34). Carnivore marks are usually confined to a single part of the bone (Table 35). Conversely, bones covered with carnivore marks are rare. The low occurrence of ravaged bones in the NISP sample does not seem to result from an identification bias, carnivore marks also being rare in the indeterminate sample.

	Marginal		*Limited to One Section*		*Covered*		*Total*	
	n	%	n	%	n	%	n	%
Evol Auri (3)	.	.	1	100.0	.	.	1	100.0
Evol Auri (4)	.	.	.	.	1	100.0	1	100.0
Auri I (5)	7	35.0	9	45.0	4	20.0	20	100.0
Auri 0? (6)	.	.	.	.	4	100.0	4	100.0
low dens (7)	.	.	2	100.0	.	.	2	100.0
Châtel (8)	5	35.7	7	50.0	2	14.3	14	100.0
Châtel? (9)	.	.	1	33.3	2	66.7	3	100.0
Moust (10)	.	.	1	100.0	.	.	1	100.0
Total	12	26.1	21	45.6	13	28.3	46	100.0

Table 35. Extent of ravaging marks on bone surfaces in the level of Saint-Césaire.

Intense carnivore activity is commonly associated with prolific abundance of coprolites (Binford 1981). Unfortunately, this type of archaeological trace has not been collected systematically during the excavations. Nevertheless, the fact that some coprolite fragments were found in soil samples by the author confirms the presence of active carnivores during the site formation.

According to Binford (1981), bone cylinders are more frequent in hyena dens than in assemblages accumulated by humans. However, the disparity between these two classes of sites appears to be less clear-cut than previously thought, as very small specimens (<2 cm) were rarely collected in earlier excavations of hyena dens (Villa *et al.* in press). At Saint-Césaire, the proportion of cylinders in the assemblages is very low (17/2745 or 0.6%), in line with other human assemblages presented by Villa *et al.* (in press), but much less than at the hyena den of Bois Roche layer 2 (8%). These authors also suggest that fragment length would be a better criterion for discriminating assemblages made by carnivores from those accumulated by humans. It should be noted, however, that sites might not be fully comparable due to different levels of postdepositional breakage. Keeping this reservation in mind, the assemblages from Saint-Césaire cluster clearly with assemblages accumulated by humans (Table 36).

	Bison Long Bones		*Horse Long Bones*	
	n	mean length	n	mean length
Saint-Césaire:				
Evol Auri (3)	13	88.1	7	76.2
Evol Auri (4)	18	96.0	27	91.6
Aurignacian I	25	102.0	67	78.5
Châtelperronian	178	85.6	18	84.5
Châtelperronian?	53	88.1	13	88.7
Dent Mousterian	87	80.5	38	89.9
Combe Saunière				
level IV	44	76.4	134	74.9
Jonzac				
level 22	81	83.0	.	.
Bois Roche				
layer 2	**173**	**148.7**	**43**	**156.0**

Table 36. Mean fragment length of bison and horse long bones for a series of assemblages. Values for sites other than Saint-Césaire are from Villa *et al.* (in press). Data for the carnivore assemblage of Bois Roche, layer 2 are shown in bold.

Age profiles have been used to discriminate human from carnivore-made assemblages (e.g., Stiner 1990). Due to small sample size, information is very limited on carnivore age profiles at Saint-Césaire. Only two immature individuals, both represented by deciduous teeth, were identified. One of these teeth belongs to a hyena (found in EJOP) and the second to a wolf (found in the Aurignacian 0? assemblage). Most of the other individuals are young adults, based on use-wear and stage of epiphyseal fusion. One atrophied phalanx may signal the presence of a senile hyena. The lack of very young individuals in the assemblages appears to confirm that the site has not been used as a nursery.

In addition to traces of carnivore activity, some marks similar to those produced by porcupines (Rabinovich and Horwitz 1994) were observed in the assemblages. However, these marks are very rare (n=9) and the agent of modification is unclear for most of them.

In sum, information on burning, cut marks, taxonomic composition, bone fragmentation, and carnivore marks, combined with the small amount of data available on age profiles, is compatible with the hypothesis of occasional scavenging by carnivores of assemblages created by humans. It should be noted that these observations are in agreement with previous conclusions on the role played by carnivores in the Châtelperronian occupation (Patou-Mathis 1993).

These results do not rule out the possibility that carnivores have contributed sporadically to these assemblages with kills. However, it is clear from these data that most of the faunal remains uncovered at Saint-Césaire were accumulated by humans. In that view, carnivores might have been no more than commensal neighbors. However, it is also possible that some of the carnivores were brought into the site by humans. This issue is addressed in Chapter 7. Nevertheless, attrition due to carnivore ravaging appears to have been marginal at Saint-Césaire. Yet, other factors of attrition might also have affected the faunal assemblages. These factors include analytical underrepresentation and burning.

Comparability of elements and identification filters in shaft-dominated assemblages

Taxonomic identification of skeletal elements and species is central to the study of subsistence strategies. Obviously, this depends on a combination of factors, including properties relating to the inherent identifiability of the species in question, the degree of preservation and completeness of the material, one's expertise and experience identifying faunal remains, the quality of the comparative collection that is available, and many other factors as well. One issue —the differential identifiability of specific skeletal elements (e.g., the shaft of the tibia compared to the shaft of the femur)— has only received due attention recently (Lyman and O'Brien 1987; Lyman 1994; Marean and Kim 1998; Bartram and Marean 1999; Grayson *et al.* 2001). Yet, this topic remains poorly developed despite the attention that it should deserve. Differential identifiability is a key issue in faunal analysis because it can result in the analytical underrepresentation of certain specific element or taxa. Because faunal studies of differential preservation often rely on identified specimens (see below), understanding this source of bias may be critical to our knowledge of attrition processes.

In this section, the differential identifiability of *skeletal elements*, especially shaft portions, is explored. This will be followed in the next section by a discussion of the differential identifiability of *taxa*. However, before proceeding to the discussion of differential identifiability, it is necessary to highlight the differences between analytical underrepresentation and differential preservation.

Analytical underrepresentation is easily confused with differential preservation, even though these two concepts refer to distinct, yet complementary, aspects of attrition. Differential preservation is associated with the deletion of skeletal parts from the archaeological record through the physical and chemical breakdown of bone structure, whereas analytical underrepresentation characterizes situations in which natural or cultural factors fragment elements to a point where some or most of the resulting pieces become taxonomically unidentifiable, without implying that specimens have vanished or been destroyed beyond recognition. In other words, differential preservation monitors destruction of parts, while analytical underrepresentation relates to specimens that are recognizable as bone but taxonomically unidentifiable due to their degree of fragmentation (Lyman and O'Brien 1987).

An example will illustrate this. Extraction of marrow from long bones results typically in the production of several splinters and spongy pieces, most of which are taxonomically unidentifiable. However, the process rarely ends in the complete destruction of the bone fragments. In contrast, the production of bone "cakes" (Binford 1978) from long bone epiphyses and other parts is more likely to be associated with attrition because many specimens will, in all probability, disappear from the archaeological record and be transformed into another form of energy. To recapitulate the argument, in spite of some bone destruction, it should still be possible to infer marrow-cracking, based on the preserved specimens, even though analytical underrepresentation may obscure interpretation. In contrast, the unraveling of bone cake production is likely to be eclipsed by two factors: analytical underrepresentation and, most importantly, attrition.

Degree of fragmentation, morphological variation, and identifiability of skeletal elements

Problems of identification might be minor in sites where fragmentation, burning, and carnivore ravaging are slight, and in which the material is well preserved. This is because complete or nearly complete bones are generally easy to identify to skeletal element and body size class in mammal-dominated assemblages. The problem is different, however, for moderately to highly fragmented specimens, a situation typical of most prehistoric sites.

However, is analytical underrepresentation simply a factor of degree of fragmentation? Are all elements similarly identifiable? This is debatable. For instance, some limb bone shafts (e.g., tibia) appear to be easier to identify than others (e.g., femur). Other elements like ribs and vertebrae are often reported to be difficult to identify to the genus or species level when fragmented (e.g., Bouchud 1962; Poplin 1976; Speth 1983; Grayson 1989; Stiner 1995). This identification filter may represent a very important source of patterning that needs to be taken into account when exploring patterns in body part representation.

An important early concern with this issue is illustrated by Bouchud's (1961, 1966, 1966, 1975) attempt to explain variations in the abundance of skeletal elements in Paleolithic assemblages from southwestern France. These variations were argued by him to reflect differences in resilience to breakage and differential identifiability of anatomical elements rather than past economic decisions. Although Bouchud's assumption that reindeer carcasses were transported as complete units to the cave sites he studied may be questionable, there remains the very real possibility that differential identifiability affect skeletal element representation. Interestingly, this might also include many studies of faunal assemblages accumulated by living hunter-gatherers in which skeletal parts were identified in lab conditions some time after the fieldwork (e.g., Bartram 1993).

Refitting has been presented as a solution to this problem (e.g., Marean and Kim 1998; Bartram and Marean 1999). However, elements may not have been transported complete. Moreover, some bone fragments may not be preserved or might have been dispersed over a large area as a result of behavior, post-depositional processes, sampling, recovery techniques, all situations that prevent refitting. Moreover, damaged edges may prevent the refitting of fragments. Although it may help to minimize the problem, refitting alone is unlikely to eliminate fully the effects of bias of identification.

Is the NISP sample representative of the animal populations deposited at Saint-Césaire?

Contrasting skeletal representation between the NISP and the NSUTS (number of specimens of uncertain taxonomic status) samples might be a productive approach for exploring analytical underrepresentation at Saint-Césaire. Indirectly, what is examined here is the assumption that body part representation is represented accurately by NISP counts. The relation between differential identifiability of species, taxonomic composition, and NISP counts is discussed afterward.

In general, a skeletal element characterized by strong analytical underrepresentation is expected to be rare or absent in the NISP sample, somewhat more common in the NSUTS sample, and most common in the faunal debris (Figure 31). This reflects the fact that identifiability decreases with degree of fragmentation, holding taxon constant.

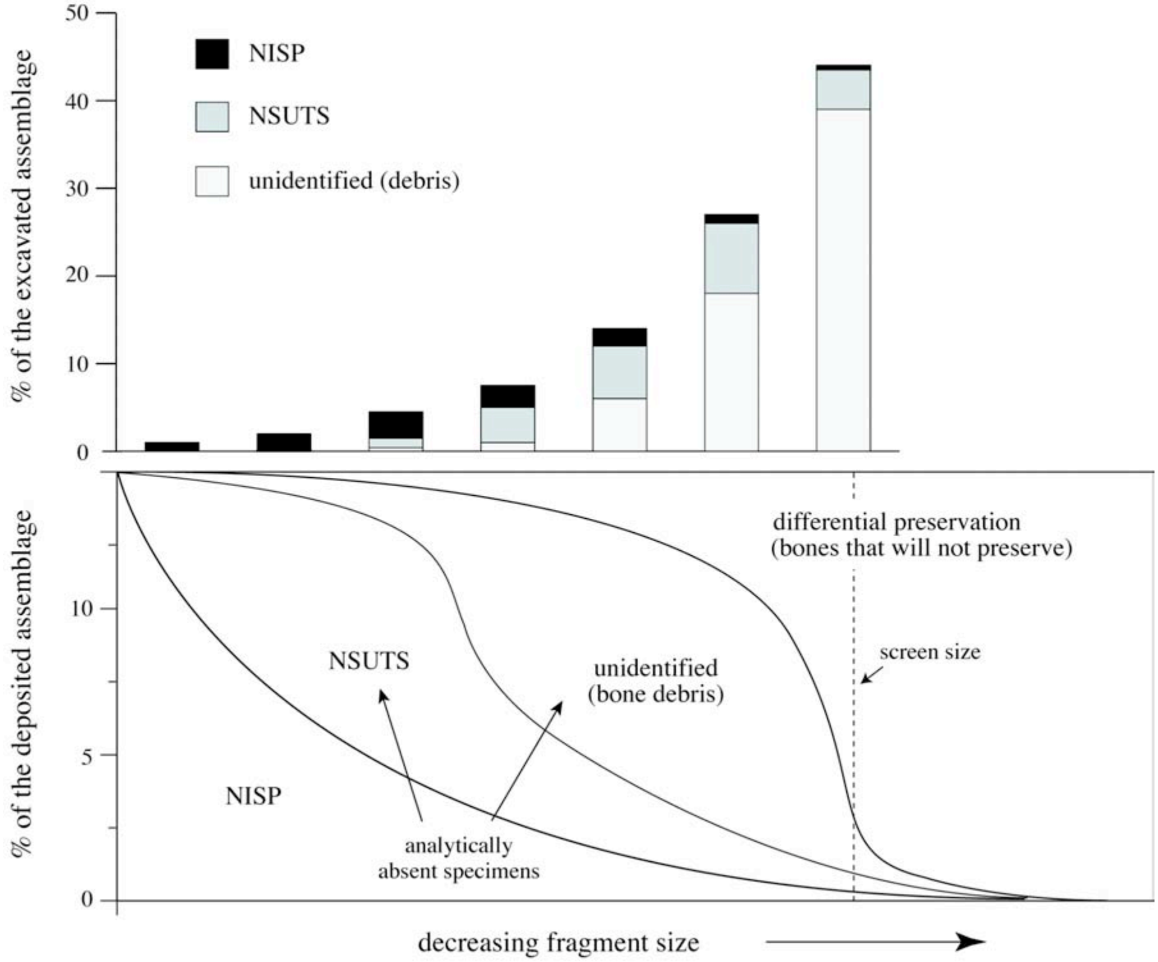

Figure 31. Hypothetical model of the relation between identifiability and degree of fragmentation in a deposited versus excavated assemblages.

Proportions of skeletal elements at Saint-Césaire are presented in Table 37 according to different levels of identification. In this table, all of the occupations are combined. If elements are comparably identifiable at Saint-Césaire, one expects the NISP

	NISP		*NSUTS*		*%Difference*
	n	%	n	%	%
antler	1406	15.4	0	0.0	15.4
horncore	30	0.3	0	0.0	0.3
cranial	**90**	**1.0**	**189**	**5.3**	**-4.3**
mandible/maxillary	**256**	**2.8**	**226**	**6.3**	**-3.5**
tooth	**1476**	**16.2**	**725**	**20.3**	**-4.1**
hyoid	7	0.1	5	0.1	0.0
atlas	11	0.1	0	0.0	0.1
axis	3	0.0	0	0.0	0.0
cervical	**25**	**0.3**	**19**	**0.5**	**-0.2**
thoracic	**49**	**0.5**	**57**	**1.6**	**-1.1**
lumbar	26	0.3	10	0.3	0.0
sacrum	6	0.1	4	0.1	0.0
caudal	**1**	**0.0**	**7**	**0.2**	**-0.2**
vertebrae	**10**	**0.1**	**131**	**3.7**	**-3.6**
ribs	**1161**	**12.7**	**2008**	**56.1**	**-43.4**
sternum	8	0.1	1	0.0	0.1
scapula	**102**	**1.1**	**60**	**1.7**	**-0.6**
humerus	271	3.0	18	0.5	2.5
radius/radio-ulna	525	5.8	13	0.4	5.4
scaphoid	14	0.2	0	0.0	0.2
lunatum	9	0.1	0	0.0	0.1
hamatum	9	0.1	0	0.0	0.1
capitatum	13	0.1	0	0.0	0.1
pisiform	9	0.1	0	0.0	0.1
triquetrum	6	0.1	0	0.0	0.1
metacarpal	250	2.7	0	0.0	2.7
pelvis	71	0.8	12	0.3	0.5
femur	259	2.8	23	0.6	2.2
patella	10	0.1	1	0.0	0.1
tibia	915	10.0	59	1.6	8.4
malleolus/fibula	19	0.2	0	0.0	0.2
talus	28	0.3	0	0.0	0.3
calcaneum	34	0.4	0	0.0	0.4
greater cuneiform	14	0.2	0	0.0	0.2
smaller cuneiform	3	0.0	0	0.0	0.0
cubo-navicular	19	0.2	0	0.0	0.2
metatarsal	1498	16.4	0	0.0	16.4
metapodial	195	2.1	3	0.1	2.0
vestigial metapodial	42	0.5	0	0.0	0.5
phalanges	172	1.9	8	0.2	1.7
vestigial phalanges	17	0.2	0	0.0	0.2
sesamoids	45	0.5	0	0.0	0.5
Total	9114	100.0	3579	100.0	0.0

Table 37. Proportions of skeletal elements at Saint-Césaire. All taxa and levels combined. The last column was calculated by subtracting %NSUTS from %NISP. Values in bold are elements that are over-represented in the NSUTS sample.

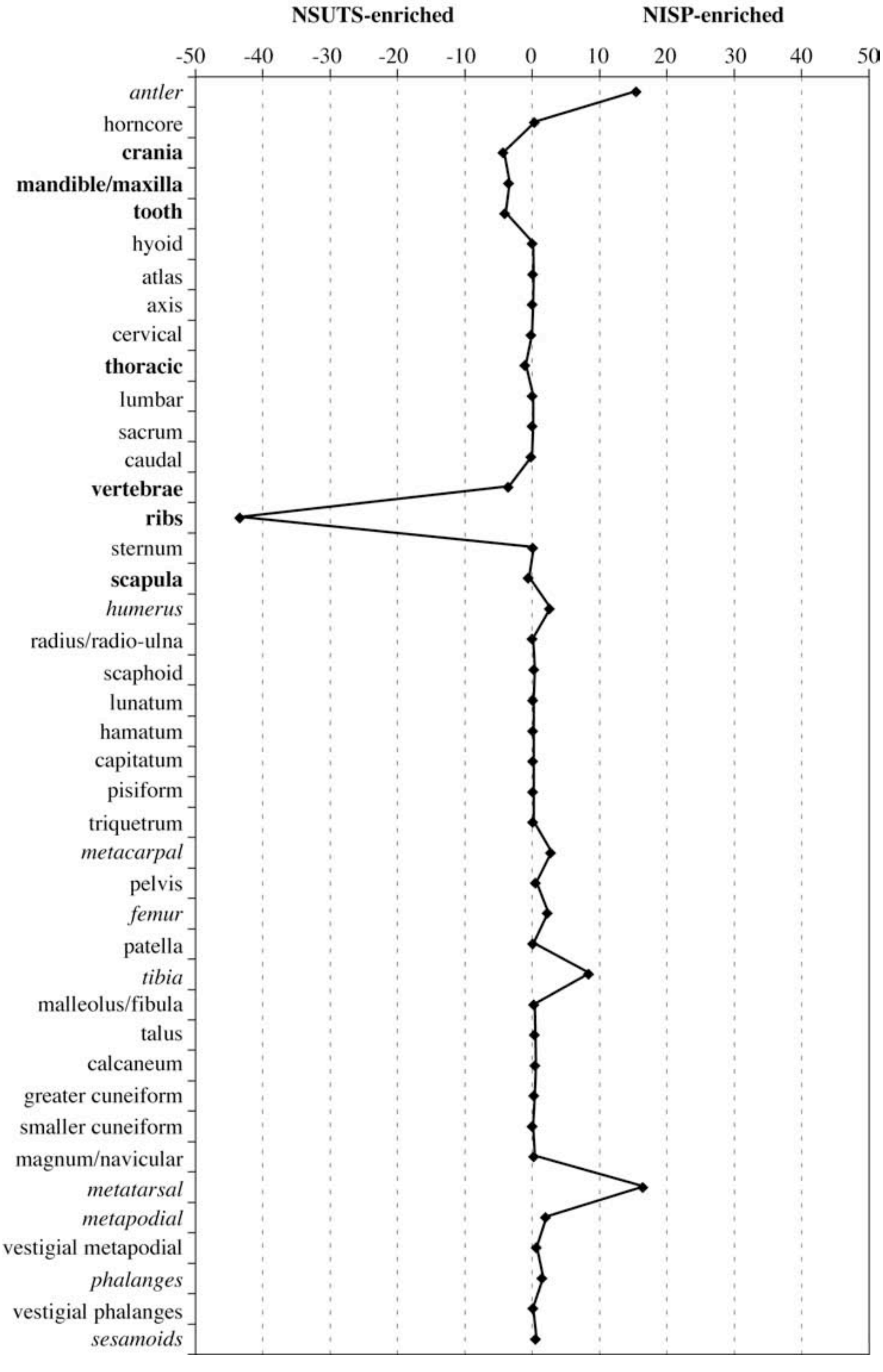

Figure 32. Saint-Césaire. Proportions of skeletal elements in the NSUTS and NISP samples. All occupations are combined. Values in bold are elements that are over-represented in the NSUTS sample, whereas values in italics are elements that are over-represented in the NISP sample.

and NSUTS samples to be more or less similar with respect to body part representation. If this is true, the line in Figure 32 should be straight and vertical, that is, the proportion of each class of skeletal elements should remain approximately stable when moving from one sample to the other.

Clearly, this is not the case at Saint-Césaire. For instance, parts like antler and phalanges are over-represented in the NISP sample. This is also the case for long bones. However, fragments from rib, scapula, mandible/maxillary, crania, tooth, and vertebra are all over-represented in the NSUTS sample (Figure 32). Does this mean that the NISP sample is a skewed reflection of body part representation in the assemblages?

In fact, because these elements are generally associated with fragile portions not incorporated in the calculation of MNI and MNE, their analytical underrepresentation is relative and does not have detrimental effects on interpretations of element composition. For instance, most scapula fragments in the NSUTS sample are from the blade and border regions, whereas in most cases, it is the glenoid cavity that provided the minimum number of individuals and elements for this bone. Additionally, as it appears unlikely that the past occupants of Saint-Césaire partitioned deliberately the scapula, the analytical underrepresentation of blade fragments in the NISP sample should not affect its representation seriously.

The abundance of mandibles and maxillaries, typically represented by alveolar bone in the NSUTS sample, are probably accurately, although indirectly, estimated by teeth counts. Many cranial fragments are found in the NSUTS sample. In this case, counting maxillary teeth and petrosals should provide a reliable approximation of the frequency of cranium in the assemblages.

Regarding tooth fragments, most of the specimens found in the NSUTS sample are small fragments detached from crowns and roots. It seems reasonable to argue that the tooth from which these fragments were isolated have been successfully identified, teeth being particularly diagnostic (Klein and Cruz-Uribe 1984). Indeed, their texture, characteristic morphology, and resilience to postdepositional processes increase identification to skeletal element and taxon relative to other parts. All these factors might inflate head representation in fragmented assemblages. We will see that this bias might be critical in interpretations of skeletal representation.

Vertebrae are notably difficult to identify at a precise taxonomic level due to significant inter-individual variability, reduced inter-species variation, complex morphology, and their fragility; the processes and neural arch are easily fragmented and dissociated from the body. For the same reasons, they are also difficult to refit. As a result, the abundance of vertebrae may be underestimated at Saint-Césaire. Numerically speaking, however, vertebrae are not abundant in any of the samples, representing no more than 2.8% of all the material identified at least anatomically, and are notably rare in the Châtelperronian and the Mousterian. Moreover, vertebral bodies being easy to identify to skeletal element, these probably represent a small portion of the faunal debris. Therefore, the scarcity of vertebrae in the assemblages does not appear to be explained by analytical underrepresentation. A more likely reason for their low occurrence at Saint-Césaire is burning, as will be shown below.

With respect to ribs, their initial abundance is much harder to assess. Many rib fragments were identified to skeletal element, but many other were not, due to their degree of fragmentation. Unlike the other parts, identification to species is considered more tentative concerning this element, given that there is significant variation within and across ribs, and between individuals. Additionally, there is much overlap in rib morphology between closely related species of roughly similar size. Because of these problems, estimating the initial abundance of ribs in the assemblages is difficult. In this case, analytical underrepresentation is likely to be important.

Long bone elements are abundant in the samples. With respect to epiphyses, their relative absence in the assemblages cannot be attributed to analytical underrepresentation, these being *less* common (6% versus 14.3%) in the NSUTS sample than in the NISP sample. This difference is statistically significant ($t_s = 2.97$, $p \leq 0.003$). Looking at even less precisely identified fragments, that is, specimens that could not be identified to skeletal element and taxon, a large quantity of unidentified long bone fragments was found in the indeterminate sample. However, the vast majority of them (estimated to be over 95%) are, again, shaft fragments. Therefore, this sample probably does not provide an explanation for the lack of epiphyses in the assemblages. There remains the possibility that epiphyses are characterized by very severe analytical underrepresentation and are so fragmented that most went unidentified. In fact, many epiphyseal fragments appear to be present in the debris sample as burned specimens. Unfortunately, it is not possible to quantify this proportion accurately.

In sum, even though the NISP and the NSUTS samples differ and signal small biases of identification, only ribs and vertebrae might be significantly under-represented in the former sample. For all these reasons, it can be concluded that the abundance of most skeletal elements is probably accurately predicted in the NISP samples. Although long bone epiphyses are affected by underrepresentation at Saint-Césaire, this does not seem to be the case for shaft portions, as will be shown below.

Analytical underrepresentation of long bones at Saint-Césaire

At Saint-Césaire, some parts and portions are affected by analytical underrepresentation and are over-represented in the NSUTS and debris samples. These biases were discussed in relation to the whole site. With few exceptions, the skeletal representation in the NSUTS sample does not alter the picture that can be inferred based on NISP.

Epiphyses, the long bone's most diagnostic parts, are significantly under-represented in the Saint-Césaire occupations. As a result, NISP and MNE values for this location were largely based on shaft fragments. Saint-Césaire is not an exception in that respect. In fact, shaft-dominated Paleolithic assemblages are not rare and are expected to become increasingly common with the improvement of our recovery techniques and analytical methods (Bunn and Kroll 1986; Turner 1989; Bartram and Marean 1999; Pickering *et al.* 2003). Because shaft portions vary in morphology, this raises the question: are some specific long bone elements underrepresented with respect to other long bone elements? If the answer is yes, how does this affect the interpretation of skeletal representation? These important issues are developed below.

As argued by Bouchud (1962, 1966) and, more recently, by Marean and Kim (1998), shaft fragments may not all be comparably identifiable, in contrast to epiphyses. Experience suggests that some bone portions, the femur shaft for instance, are more difficult to identify than others. In theory, it would be possible to verify these assertions by conducting blind tests using experimentally fragmented skeletal elements. One could simply compare the percentage of correct identifications for each element in the experiment. This is beyond the scope of this study. An alternative is to look at refit data.

All else being equal, more easily identified elements should result in higher probabilities of refitting than elements that are difficult to identify. Controlling for fragment size is critical here because a fragile element is more likely to become fragmented than a robust one and, thereby, be harder to identify, as fragment size and identifiability are positively correlated (Lyman and O'Brien 1987). Therefore, if fragment size is held constant, high percentages of refits should be indicative of greater identifiability. Conversely, elements with low refitting values should be associated with lower likelihood of identification. This is expected whether the elements were originally carried complete to the site or not. However, patterns of fragmentation may favor the refitting of some bones over other.

Because the kind and number of potentially diagnostic landmarks may vary between taxa, proportions of refits are most productive when presented by species. Despite some morphological variation, analogous elements in closely related taxa (e.g., red deer and reindeer) are expected to show similar biases with respect to identification. Variation with respect to skeletal element identifiability can be explored using data from Saint-Césaire.

Table 38 shows percentages of refitted fragments for reindeer long bones, based on NISP counts. Degree of fragmentation is controlled, to a certain degree, by assigning each fragment to one of three size classes. These size classes were produced based on surface area estimated by multiplying the maximum length of the fragment by its maximum width.

Proportions of Refitted Long Bone Fragments by Size Class in Reindeer

	0-500 (mm^2)			500-1000 (mm^2)			1000-1500 (mm^2)			All		
	refit	n	%	refit	n	%	refit	n	%	refit	n	%
metatarsal	146	671	21.8	123	589	20.9	21	127	16.5	311	1553	20.0
radio-ulna	17	98	17.3	20	146	13.7	16	83	19.3	64	400	16.0
metacarpal	10	40	25.0	11	102	10.8	4	39	10.3	27	218	12.4
tibia	13	58	22.4	22	192	11.5	19	213	8.9	71	693	10.2
humerus	2	9	22.2	6	63	9.5	8	66	12.1	18	186	9.7
femur	2	19	10.5	6	78	7.7	3	44	6.8	18	196	9.2
Total	190	895	21.2	188	1170	16.1	71	572	12.4	509	3246	15.7

Table 38. Saint-Césaire. Proportions of refitted long bone fragments by size class in reindeer. All of the assemblages are included. The category *all* includes fragments ≥ 1500 mm^2. Proportions of refits were calculated by subtracting the number of specimens refitted from the pre-refit NISP counts.

The data indicate a statistically significant over-representation of the metatarsal and radio-ulna relative to the femur, tibia, and humerus (femur/radio-ulna: $t_s = 2.37$, $p < 0.02$; femur/metatarsal: $t_s = 4.10$, $p < 0.0001$; humerus/radio-ulna: $t_s = 2.14$, $p < 0.04$; humerus/metatarsal: $t_s = 3.79$, $p \leq 0.0002$; tibia/radio-ulna: $t_s = 2.75$, $p \leq 0.006$; tibia/metatarsal: $t_s = 6.07$, $p < 0.0001$; based on all fragments). Underrepresentation is most conspicuous across size classes for the femur, whereas overrepresentation is most apparent for the radio-ulna and metatarsal (Figure 33). The metacarpal, and tibia tend to have intermediate values. These results suggest that raw NISP counts probably underestimate, often significantly, the abundance of the femur in reindeer. Conversely, the metatarsal and radio-ulna in particular would be over-represented.

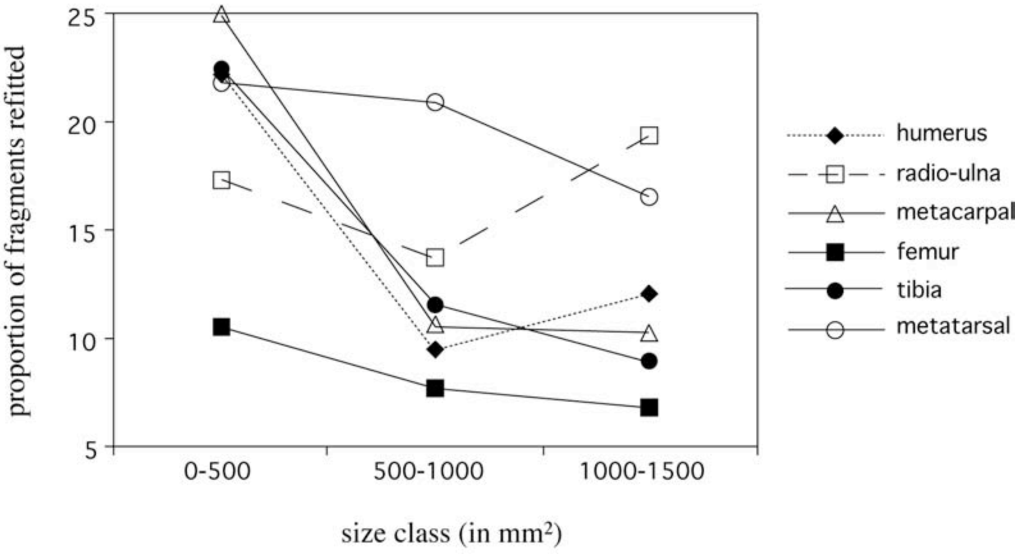

Figure 33. Proportions of refitted reindeer long bones by size class (in mm^2). Data from Table 38.

Refit data are also available for bison. In this case, however, the sample is small and cannot be partitioned into size classes. It is very important to note that raw percentages for bison are not comparable with those of reindeer. The enormous quantity of material available for reindeer limited refitting to fewer elements and categories of fragments than was true for bison (see discussion in Chapter 4). Therefore, comparison should be limited here to ranking of elements within a single taxon.

As in reindeer, the bison femur is not refitted as often as the radius, humerus, and tibia (Table 39). Yet, none of these differences are statistically significant (results not shown), perhaps due to small sample size. In contrast to reindeer, however, bison metatarsals are rarely refitted and are underrepresented compared to tibiae, a difference that is statistically significant ($t_s = 3.10$, $p < 0.002$). This result makes intuitive sense, as the metatarsal is relatively featureless in bison and lack the anterior groove characteristic of the reindeer metatarsal. The bison metacarpal may also be underrepresented compared to other skeletal elements, although the sample is very small for the former. In sum, these results suggest that a proportionately larger fragment is necessary, on average, to identify bison metapodials than, for instance, tibiae. Thus, a low abundance of bison metapodials in an assemblage may be partly an artifact of their lower identifiability.

Proportions of Refitted Long Bone Fragments by Size Class in Bison

	refit	n	%refitted
tibia	168	309	54.4
radius	24	45	53.3
humerus	39	77	50.6
femur	27	56	48.2
metatarsal	38	103	36.9
metacarpal	8	25	32.0
Total	304	615	49.4

Table 39. Saint-Césaire. Proportions of refitted long bone fragments in bison. All of the assemblages are included. Proportions of refits were calculated by subtracting the number of specimens refitted from the pre-refit NISP counts.

Differential identifiability and difficulties in estimating abundance

It might be argued that the identification biases inferred based on refit data are limited to NISP counts and that other counting methods, MNE or MNI for instance, would be unaffected by these biases. The problem with this argument is that we do not know *a priori* which portion of the element, with diagnostic landmarks or not, is best represented in an assemblage (Bunn and Kroll 1986; Todd and Rapson 1988; Marean 1991; Morlan 1994). In a situation where there is differential transport of proximal versus distal parts, a bias may be introduced if the landmarks are not distributed evenly between the proximal and distal shaft portions.

More important is the observation that MNE counts are *usually derived based on the NISP sample.* Therefore, biases in identification will affect both counting methods. For instance, shaft fragments with distinctive landmarks may be reconstructed more fully, enhancing identifiability. On the other hand, failure to recognize a specific landmark on a highly diagnostic fragment may be buffered by the detection of another distinct landmark on the same specimen. This will contribute to raise the identifiability of this part with respect to other parts. Failure to identify a specific landmark may occur due to erosion, weathering, breakage, burning, carnivore ravaging, age of the animal at death (muscle attachments are often faint in juveniles), or simply because it is lacking (e.g. the *foramen nutricium*, usually located on the anterior side of the bison femur, may be misplaced or absent in some individuals). Therefore, shaft NISP and MNE values are expected to increase with the number of landmarks on an element, even when sample size is held constant (Grayson 1984). This means that MNE is also likely to be affected by the analytical underrepresentation of the shaft of specific skeletal elements.

It is generally difficult to produce reliable MNI and MNE values when landmarks are few and uniform over the length of the shaft, as is the case with metapodials and ribs. The reindeer metatarsal provides an illustration of this problem. As pointed out above, the groove on the anterior side of the reindeer metatarsal is highly diagnostic. Yet, because this landmark is relatively uniform over the length of the shaft, identifying *precisely* where, and from which side, a shaft fragment comes from is difficult. This is true of the reindeer metacarpal as well, and, in fact, may be characteristic of ungulate metapodial shafts in general.

To counter these problems, a counting method based on length measurements was adopted (see Chapter 4). It is worth emphasizing that summing fragment lengths is a conservative approach prone to produce underestimates. This is because length measurement methods adopt an assumption that probably does *not* characterize the assemblages: fragments do not overlap. This assumption is specific to the summed length method and probably depresses MNE estimates. Indeed, traditional MNE counts rely on the identification of the same diagnostic landmark on a number of specimens and it is this property that allows one to estimate the minimum number of elements present. In contrast, the summed length methods assume that no fragments overlap in order to provide a reliable MNE value, despite the fact that some fragments probably *did* overlap on the original complete specimen. In other words, the difficulty with the summed length method is that the lack of landmarks diagnostic of a restricted portion of the total shaft area makes it impossible to identify fragments as part of distinct elements.

It is possible to assess, although indirectly, this proposition. MNE counts were produced for the reindeer radio-ulna with both the traditional and summed length methods. The large reindeer assemblages of the Aurignacian I and Evolved Aurignacian EJM occupations were selected for this. In the first sample, the length-based MNE represents only 60.5% (26/43) of the traditional MNE, obtained on the basis of the frequency of fragments preserving the area immediately distal to the radius foramen. A similar percentage of 62.5% (5/8), obtained using the same landmark, characterizes the second sample. Although the evidence is indirect and rely on small samples, the summed length method produces MNE values that are depressed, perhaps significantly, compared to the more traditional methods. Despite these difficulties, we can expect biases in summed length MNE estimates to be relatively constant across the Saint-Césaire sequence, given that the same methodology was adopted in the study of the remains. Therefore, even though they may produce underestimates compared to more traditional methods, MNE values derived with summed length methods are useful when comparisons focus on the same element compared in different samples and for which the abundance was estimated using the same methodology.

These results raise an interesting problem. The reindeer metatarsal may be over-estimated by NISP, but under-estimated by MNE at Saint-Césaire, possibly more so than when calculated with traditional counting methods. In bison, metapodials are expected to be slightly underrepresented. This might be true of horse metapodials as well. Finally, the reindeer radio-ulna and tibia may be over-estimated in NISP counts compared to most other long bones. In this case, however, MNE counts provide what are believed to be relatively accurate estimates of initial abundance.

With respect to non-limb elements, MNI and MNE can be estimated fairly accurately for most elements. There are some exceptions, however. For ribs, MNI and MNE were all derived from rib heads or based on the summed length method. However, because rib slabs are frequently broken off above the heads and transported as such (Binford 1978; Oliver 1993; Bartram 1993), rib head MNE may be poor estimators of the original abundance of rib slabs, but rather be indicative of the number of thoracic vertebral segments that were transported to the site. Unfortunately, ribs are sometimes extensively fragmented, which may skew MNE and MNI counts. Nevertheless, as stressed above with respect to long bones, abundance of ribs can be compared across samples in situations in which the counting method was held constant.

The problem is somewhat different with antlers. Antlers are relatively fragile and prone to fragmentation. Consequently, antlers are more likely than analogous parts in non-cervids species (e.g., horns) to inflate head NISP counts. In addition, contrary to other cervids, antlers are developed by both sexes in reindeer (Bergerud 1976). This causes an over-representation of the head in reindeer with respect to other cervids. Further, as in many contemporaneous sites (Liolios 1999; Julien *et al.* 2002), antlers were used for toolmaking in the Upper Paleolithic occupations from Saint-Césaire (pers. observ., Lévêque *et al.* 1993). This is not unanticipated, as antlers are known ethnographically to serve multiple functions, including use as drying facilities, seal breathing-hole probes, etc. (Birket Smith 1959; Balikci 1970). But use of antler for toolmaking is not documented in the Mousterian levels at Saint-Césaire nor in other Middle Paleolithic assemblages (White 1982; Mellars 1996). For all these reasons, antlers were not included in the analysis of body part representation. However, it is worth stressing that antlers, at least during the Upper Paleolithic, may well have increased the utility of reindeer heads.

Species comparability and scalar effects in identification

Differential identifiability has been reviewed in the previous section with respect to skeletal elements. This section constitutes the logical extension of this problem and, this time, deals with differential identifiability across taxa.

Compared to African assemblages, the identifiability of taxa is enhanced in Paleolithic assemblages from southwestern France. This is because taxa are generally well graded in body size (Grayson and Delpech 2003). Indeed, identification is dependent on the diversity of species present in the region—comparatively low in Late Pleistocene Europe, very high in Late Pleistocene sub-Saharan Africa (Klein and Cruz-Uribe 1984).

In addition to problems of identifiability related to the diversity of species present, there seems also to be a scalar effect in taxonomic identification of fragmented specimens. Specifically, it can be hypothesized that biases in element identifiability increases with body size, as fragments from large animals like bison and horse are likely to sample a proportionately smaller area of the complete skeletal element compared to fragments derived from smaller taxa. However, this proposition relies on the assumption that there are significant differences in fragmentation as a function of body size class, which remains to be demonstrated. We will see that this assumption seems to be supported by the Saint-Césaire data.

Differential fragmentation is difficult to monitor, as cultural decisions may structure its numerical behavior. In the literature, a common tool used to assess this problem is the NISP/MNE ratio (Klein and Cruz-Uribe 1984). This measure is not totally satisfactory, however, because NISP increases linearly in an assemblage but MNI and MNE do not (Grayson 1984; Lyman 1994). As a result, large samples can be expected to have higher NISP/MNE ratios than smaller samples. Furthermore, it is not clear how identification affects this ratio. Instead, Grayson and his colleagues (2001) use taxon-specific ratios of diaphysis to epiphysis limb bones. At Saint-Césaire, this method is not helpful because burning of epiphyses has been a standard practice.

Another way to explore differential fragmentation between taxa is by contrasting proportions of elements in assemblages with similar skeletal representation but dominated by species from different body size classes. At Saint-Césaire, the percentages of elements identified (Table 40) are consistently lower in the samples dominated by large ungulates (Mousterian and Châtelperronian occupations) than in those dominated by reindeer (Aurignacian occupations). Differences between reindeer-dominated and large ungulate-dominated assemblages are all highly significant (at the 0.0001 level, results not shown). Costamagno (1999:412) also found a similar pattern in the Magdalenian assemblages she studied. Therefore, differential fragmentation may indeed be responsible for the lower identification of large ungulates relative to reindeer at Saint-Césaire.

This issue can be explored further. Excluding the low-density occupation, Table 41 shows that despite some variation, the proportion of long bones identified to taxon relative to other identified parts is relatively constant across the sequence. In marked contrast, the proportion of *unidentified* long bones in the indeterminate sample is approximately two to three times lower in the large ungulate-dominated assemblages compared to the reindeer-dominated assemblages. This pattern may reflect the possibility that more blows and energy are necessary to crack the robust large ungulate long bones than is the case with bones from smaller taxa, as suggested by ethnoarchaeological data (Oliver 1993). What is implied here is that marrow-cracking in large ungulates may result in the production of proportionately smaller fragments relative to reindeer, which decreases identifiability.

Layer	*NISP*	*Total Specimens*	*NISP/Total*
	n	n	%
Evol Auri (3)	426	4182	10.2
Evol Auri (4)	1083	7906	13.7
Auri I (5)	4102	39636	10.3
Auri 0? (6)	480	5567	8.6
low dens (7)	83	781	10.6
Châtel (8)	**966**	**28665**	**3.4**
Châtel? (9)	**331**	**9409**	**3.5**
Moust (10)	**867**	**20975**	**4.1**
Total	8338	117121	7.1

Table 40 Proportion of NISP versus total specimen counts by level at Saint-Césaire, excluding birds and microfauna. Assemblages dominated by large ungulates are shown in bold. NISP are post-refit counts. The low-density EJO inf assemblage comprises comparable proportions of medium-sized (reindeer) and large-sized taxa (bison and horse). Post-refit counts.

	NISP (only)			*Unidentified*		
layer	identified long bones	total identified	%long bones	unidentified long bones	total unidentified	%long bones
Evol Auri (3)	180	426	42.2	877	3641	24.1
Evol Auri (4)	468	1083	43.2	1636	6530	25.1
Auri I (5)	2053	4102	50.0	7857	34202	23.0
Auri 0? (6)	228	480	47.5	821	4973	16.5
low dens (7)	13	83	15.7	58	668	8.7
Châtel (8)	**356**	**966**	**36.9**	**1738**	**27045**	**6.4**
Châtel? (9)	**164**	**331**	**49.5**	**858**	**8911**	**9.6**
Moust (10)	**323**	**867**	**37.2**	**1711**	**19569**	**8.7**
Total	3785	8338	45.4	15556	105539	14.7

Table 41. Percentages of long bones in the NISP and unidentified samples. Assemblages dominated by large ungulates are shown in bold. NISP are post-refit counts. The unidentified sample excludes NSUTS. The low-density EJO inf assemblage comprises comparable proportions of medium-sized (reindeer) and large-sized taxa (bison and horse).

The higher proportion of unidentified long bones in the large ungulate-dominated assemblages from Saint-Césaire may also indicate structural differences in how bones from animals of different body size classes react to postdepositional processes. In that respect, the presence of cracks on bones may be used to investigate the relation between body size and resilience to postdepositional processes. More specifically, this variable may be used to test Klein's (1989) proposition that postdepositional breakage would be more prevalent, in general, on large versus small ungulates.

Controlling for spatial variation as much as possible, the incidence of cracks on long bones in the best-preserved rows of Saint-Césaire is much greater for horse and bison than for reindeer (Table 42). These differences with reindeer are significant (horse: $t_s = 6.75$, $p < 0.0001$; bison: $t_s = 6.14$, $p < 0.0001$, mean of meter 2 and 3), but not between horse and bison ($t_s = 0.83$, $p < 0.41$). These data imply that horse and bison bones would be more likely to crack and break, possibly as a result of scaling effects, and therefore more difficult to identify, than those of reindeer. One such effect might be associated with bone thickness and differential moisture. Because the gradient of moisture appears to be greater in large animal bones than in smaller ones (D. Fisher, pers. com. 2003), fiber contraction and dilatation might be increased in the bone walls of the former taxa, which would promote cracking.

Whatever is the cause of this increased fragmentation, these results suggest that large ungulate limbs may be under-identified relative to those of reindeer at Saint-Césaire. This finding has another important implication. Because teeth are highly diagnostic, this part is more likely to be over-represented with respect to limbs in large ungulates than in smaller taxa. This might explain why head parts are so abundant in some assemblages dominated by large ungulates (e.g., Klein 1989).

	Distance Away From The Cliff In Meters					
	2			3		
	with cracks	total bones	% with cracks	with cracks	total bones	% with cracks
reindeer	27	1180	2.3	22	702	3.1
horse	9	39	23.1	12	35	34.3
bison	9	35	25.7	11	53	20.7

Table 42. Incidence of cracking on long bones for three different species in the best preserved lines of Saint-Césaire.

Differential fragmentation across the Saint-Césaire sequence?

Bones from large ungulates appear to be proportionately more fragmented at Saint-Césaire compared to reindeer. This may decrease the representation of the former in the assemblages. However, are patterns of fragmentation constant across the Saint-Césaire sequence?

During the analysis, maximum fragment length was measured on most identified long bone specimens. Mean fragment length can be used to contrast patterns of fragmentation in a species across assemblages. Shaft fragments are very useful here because they are mechanically resistant, usually abundant in assemblages, and are less likely to be modified once discarded save for those used as retouchers (Bunn and Kroll 1986; Blumenschine 1988; Marean and Spencer 1991). In addition, shaft fragments are less likely to be burned because they have low grease content (Costamagno *et al.* 1999; Villa *et al.* 2002).

Three reindeer elements, the tibia, metatarsal, and rib, were studied in that purpose, as they are abundant in the samples (Table 43). Mean fragment length suggests a slight increase of fragment mean length in the upper part of the Saint-Césaire sequence

(Figure 34). In contrast, mean length of rib fragments seems to be more uniform across layers. In general, these results may indicate that bones in the lowermost layers are slightly more fragmented than those from the Aurignacian levels. However, these patterns are weak as many samples are small.

Differential fragmentation across the Saint-Césaire sequence may ultimately affect the interpretation of cutmark frequencies. Indeed, the relative abundance of cutmarks increases quasi-linearly with fragment size at Saint-Césaire (Figure 35). In fact, this pattern is probably characteristic of most sites. As a result, if patterns of fragmentation do differ between the Saint-Césaire occupations, cutmarks might be expected to be slightly over-represented in the Aurignacian assemblages relative to the older occupations save, perhaps, for the Denticulate Mousterian.

	Reindeer									*Bison*		
		tibia			metatarsal			rib			tibia	
	n	mean	σ	n	mean	σ	n	mean	σ	n	mean	σ
Evol Auri (4)	76	55.7	19.3	141	43.5	20.9	43	36.3	11.8	5	105.0	40.4
Auri I (5)	379	59.0	20.7	755	42.5	17.8	384	37.7	18.5	9	85.6	39.7
Auri 0? (6)	47	52.5	17.1	96	38.0	17.9	46	38.4	18.6	1	55.3	-
Châtel (8)	15	54.1	28.2	17	31.5	12.3	34	29.1	7.9	52	90.5	32.9
Châtel? (9)	14	44.6	19.8	27	32.0	14.7	6	29.3	5.3	16	86.5	24.4
Moust (10)	31	52.6	18.2	65	40.1	17.1	8	31.0	6.9	36	75.7	34.2
total	562	57.2	20.4	1101	41.7	18.2	521	36.8	17.3	119	85.3	33.5

Table 43. Mean fragment length of reindeer and bison bones across the stratigraphic sequence of Saint-Césaire.

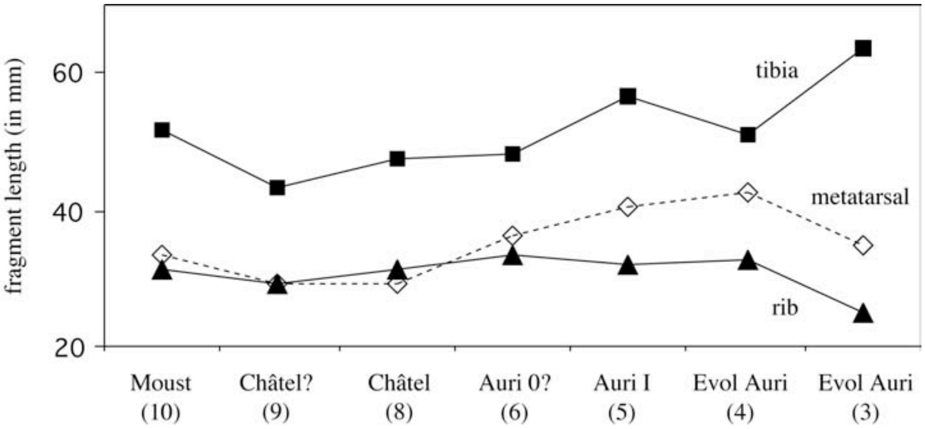

Figure 34. Mean length of reindeer tibia, metatarsal, and rib fragments in the Saint-Césaire occupations.

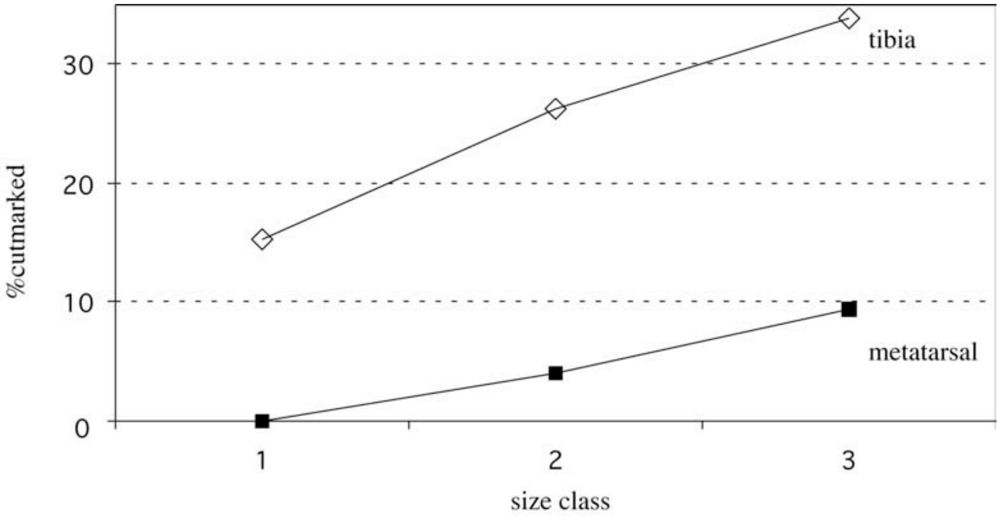

Figure 35. Proportion of cutmarked tibia and metatarsal specimens in reindeer for three size classes. Size classes are based on fragment maximum length. For the tibia, the size classes are 0-40 (21/137), 40-80 (106/404), and 80-120 mm (25/74). For the metatarsal, the size classes are 0-30 (0/339), 30-60 (30/757), and 60-90 mm (15/159).

In summary, elements might be slightly more fragmented at Saint-Césaire in the Châtelperronian? and Châtelperronian occupations relative to the Aurignacian assemblages. However, it is believed that these differences are too small to have detrimental effects on the interpretations of the faunal assemblages. However, identification biases appear to exist between certain specific elements. These identification biases are important and need to be taken into account when assessing patterns in body part representation in fragmented assemblages.

The complex interplay between burning and analytical underrepresentation

We have seen that a large quantity of burned bones was recovered in the assemblages from Saint-Césaire. This is worthy of note as burning might affect body part representation. Unfortunately, burned bones are rarely discussed as a separate class of data, except for occasional reference to the intensity of burning, generally assessed by change in bone color. This may potentially remove a significant dimension of variability out of the picture. This study, as well as a number of recently published ones (Castel 1999a; Costamagno *et al.* 1999; Villa *et al.* 2002), stresses the importance of studying the effects of burning on body part representation.

Burned specimens are generally small and damaged, which complicate considerably the task of identification (Stiner *et al.* 1995). This is reflected in the higher proportions of burned bones in the NSUTS sample relative to the NISP sample in four large assemblages from Saint-Césaire (Table 45 to Table 48), and, as we have seen, within the debris sample where burning affects between 13 and 39% of the specimens (Table 44). The reader should note that in order to enhance comparability, all taxa are combined in these tables.

Figure 36. Reindeer tali recovered in the Aurignacian I assemblage from Saint-Césaire. Only the three specimens to the left in the bottom row are not burned.

Results indicate that there is an increase in abundance of burned specimens with decreasing degree of identification at Saint-Césaire. This means that it is not possible to get a complete picture of this phenomenon using NISP only. Looking at the NSUTS and debris allows one to make interpretations that are more accurate concerning the prevalence of burning in an assemblage and the parts involved. To use a metaphor, what is resounding noise in the debris sample becomes an almost silent whisper in the NISP sample.

Figure 37. Reindeer cubo-navicular recovered in the Aurignacian I assemblage from Saint-Césaire. Only one specimen (left, bottom row) is not burned.

	NISP			*NSUTS*			*Unidentified Fragments*		
	Burned	*NISP*	*%Burned*	*Burned*	*NSUTS*	*%Burned*	*Burned*	*Indet*	*%Burned*
Evol Auri (3)	10	426	2.3	4	116	3.4	1226	3641	33.7
Evol Auri (4)	22	1083	2.0	13	293	4.4	2084	6530	31.9
Auri I (5)	150	4102	3.7	114	1340	8.5	13260	34202	38.8
Auri 0? (6)	17	480	3.5	3	114	2.6	1158	4973	23.3
Low dens (5)		83	0.0		30	0.0	85	668	12.7
Châtel (8)	2	966	0.2	25	661	3.8	7517	27045	27.8
Châtel? (9)	13	331	3.9	4	168	2.4	3480	8911	39.1
Moust (10)	16	867	1.8	45	539	8.3	7087	19569	36.2
Total	230	8338	2.8	208	3261	6.4	35897	105539	34.0

Table 44. Proportions of burned specimens in the assemblages as a function of level of identification. Indeterminate specimens exclude specimens from the NSUTS sample.

	NISP			*NSUTS*			*Difference*
	burned	total	%burned	burned	total	%burned	%difference
	n	n	%	n	n	%	%
horn/antler	1	28	3.6	.	.	.	3.6
cranial fragment	**2**	**27**	**7.4**	**22**	**78**	**28.2**	**-20.8**
mandible/maxillary	2	41	4.9	3	92	3.3	1.6
tooth	**8**	**353**	**2.3**	**19**	**173**	**11.0**	**-8.7**
hyoid	0	3	0.0	0	3	0.0	0.0
vertebrae	0	10	0.0	0	25	0.0	0.0
ribs	0	32	0.0	0	127	0.0	0.0
sternum	0	5	0.0	.	.	.	0.0
scapula	**0**	**10**	**0.0**	**1**	**17**	**5.9**	**-5.9**
humerus	0	25	0.0	0	8	0.0	0.0
radio-ulna	0	31	0.0	0	1	0.0	0.0
capitatum	0	2	0.0	.	.	.	0.0
hamatum	0	2	0.0	.	.	.	0.0
pisiform	0	2	0.0	.	.	.	0.0
triquetrum	0	1	0.0	.	.	.	0.0
metacarpal	0	24	0.0	.	.	.	0.0
pelvis	1	5	20.0	0	3	0.0	20.0
femur	0	19	0.0	0	1	0.0	0.0
tibia	0	91	0.0	0	10	0.0	0.0
malleolus/fibula	2	7	28.6	.	.	.	28.6
talus	0	1	0.0	.	.	.	0.0
calcaneum	0	1	0.0	.	.	.	0.0
greater cuneiform	0	1	0.0	.	.	.	0.0
smaller cuneiform	0	1	0.0	.	.	.	0.0
navicular	0	1	0.0	.	.	.	0.0
metatarsal	0	96	0.0	.	.	.	0.0
metapodial	0	15	0.0	0	1	0.0	0.0
vestigial metapodial	0	10	0.0	.	.	.	0.0
sesamoids	0	9	0.0	.	.	.	0.0
phalanges	0	12	0.0	.	.	.	0.0
vestigial phalanges	0	2	0.0	.	.	.	0.0
Total	16	867	1.8	45	539	8.3	-6.5

Table 45. Saint-Césaire. Bodypart representation in the NISP and NSUTS samples in the Denticulate Mousterian (EGPF) occupation. Values in bold are elements that are over-represented in the NSUTS sample.

	NISP			*NSUTS*			*Difference*
	burned	total	%burned	burned	total	%burned	%difference
	n	n	%	n	n	%	%
horn/antler	0	145	0.0	.	.	.	0.0
cranial fragment	0	6	0.0	0	4	0.0	0.0
mandible/maxillary	**0**	**29**	**0.0**	**1**	**18**	**5.6**	**-5.6**
tooth	**2**	**313**	**0.6**	**20**	**256**	**7.8**	**-7.2**
hyoid	0	1	0.0	0	1	0.0	0.0
vertebra	0	13	0.0	0	26	0.0	0.0
ribs	**0**	**96**	**0.0**	**4**	**276**	**1.4**	**-1.4**
scapula	0	21	0.0	0	26	0.0	0.0
humerus	0	40	0.0	0	3	0.0	0.0
radio-ulna	0	41	0.0	0	8	0.0	0.0
hamatum	0	1	0.0	.	.	.	0.0
metacarpal	0	12	0.0	.	.	.	0.0
pelvis	0	5	0.0	0	1	0.0	0.0
femur	0	31	0.0	0	10	0.0	0.0
patella	0	2	0.0	.	.	.	0.0
tibia	0	102	0.0	0	23	0.0	0.0
malleolus/fibula	0	1	0.0	.	.	.	0.0
talus	0	1	0.0	.	.	.	0.0
calcaneum	0	4	0.0	.	.	.	0.0
greater cuneiform	0	2	0.0	.	.	.	0.0
cubo-navicular	0	2	0.0	.	.	.	0.0
metatarsal	0	62	0.0	.	.	.	0.0
metapodial	0	11	0.0	0	2	0.0	0.0
vestigial metapodial	0	7	0.0	.	.	.	0.0
sesamoids	0	4	0.0	.	.	.	0.0
phalanges	0	13	0.0	.	.	.	0.0
vestigial phalanges	0	1	0.0	.	.	.	0.0
Total	2	966	0.2	25	654	3.8	-3.6

Table 46. Saint-Césaire. Bodypart representation in the NISP and NSUTS samples in the Châtelperronian (EJOP sup) occupation. Values in bold are elements that are over-represented in the NSUTS sample.

In the NISP sample, burning affects principally long bones, the malleolus, pelvis, vertebrae, carpals, and tarsals (Figure 36 and Figure 37). Conversely, the NSUTS sample provides us with a somewhat different picture, teeth, cranial, and vertebral fragments being most commonly burned. Despite the small samples of identified burned specimens, similar patterns are found across the sequence.

	NISP			*NSUTS*			*Difference*
	burned	total	%burned	burned	total	%burned	%difference
	n	n	%	n	n	%	%
horn/antler	1	643	0.2	.	.	.	0.2
cranial fragment	3	34	8.8	3	67	4.5	4.3
mandible/maxillary	0	95	0.0	0	52	0.0	0.0
tooth	**5**	**250**	**2.0**	**23**	**84**	**27.4**	**-25.4**
vertebrae	**8**	**61**	**13.1**	**61**	**104**	**58.6**	**-45.5**
ribs	**9**	**692**	**1.3**	**24**	**995**	**2.4**	**-1.1**
sternum	0	1	0.0	0	1	0.0	0.0
scapula	0	33	0.0	0	11	0.0	0.0
humerus	6	120	5.0	0	3	0.0	5.0
radio-ulna	23	303	7.6	0	1	0.0	7.6
scaphoid	2	9	22.2	.	.	.	22.2
lunatum	1	8	12.5	.	.	.	12.5
capitatum	0	7	0.0	.	.	.	0.0
hamatum	0	1	0.0	.	.	.	0.0
pisiform	2	3	66.7	.	.	.	66.7
triquetrum	0	2	0.0	.	.	.	0.0
metacarpal	0	135	0.0	.	.	.	0.0
pelvis	12	39	30.8	0	4	0.0	30.8
femur	**10**	**133**	**7.5**	**1**	**1**	**100.0**	**-92.5**
patella	1	6	16.7	.	.	.	16.7
tibia	**24**	**421**	**5.7**	**1**	**4**	**25.0**	**-19.3**
malleolus/fibula	4	5	80.0	.	.	.	80.0
talus	12	19	63.2	.	.	.	63.2
calcaneum	5	13	38.5	.	.	.	38.5
greater cuneiform	1	3	33.3	.	.	.	33.3
smaller cuneiform	0	1	0.0	.	.	.	0.0
cubo-navicular	6	10	60.0	.	.	.	60.0
metatarsal	10	856	1.2	.	.	.	1.2
metapodial	1	76	1.3	.	.	.	1.3
vestigial metapodial	0	13	0.0	.	.	.	0.0
sesamoids	0	18	0.0	.	.	.	0.0
phalanges	**3**	**84**	**3.6**	**1**	**5**	**20.0**	**-16.4**
vestigial phalanges	1	8	12.5	.	.	.	12.5
Total	150	4102	3.7	114	1332	8.6	-4.9

Table 47. Saint-Césaire. Bodypart representation in the NISP and NSUTS samples in the Aurignacian I (EJF) occupation. Values in bold are elements that are over-represented in the NSUTS sample.

	NISP			*NSUTS*			*Difference*
	burned	total	%burned	burned	total	%burned	%difference
	n	n	%	n	n	%	%
cranial fragment	**1**	**250**	**0.4**	**1**	**14**	**7.1**	**-6.7**
horn/antler	0	6	0.0	.	.	.	0.0
mandible/maxillary	0	36	0.0	0	15	0.0	0.0
tooth	**0**	**125**	**0.0**	**1**	**15**	**6.7**	**-6.7**
vertebrae	**1**	**12**	**8.3**	**7**	**17**	**41.2**	**-32.9**
ribs	**0**	**123**	**0.0**	**4**	**227**	**1.8**	**-1.8**
scapula	0	12	0.0	0	2	0.0	0.0
humerus	1	31	3.2	.	.	.	3.2
radio-ulna	5	72	6.9	.	.	.	6.9
scaphoid	0	1	0.0	.	.	.	0.0
hamatum	0	1	0.0	.	.	.	0.0
capitatum	0	2	0.0	.	.	.	0.0
pisiform	0	1	0.0	.	.	.	0.0
metacarpal	0	26	0.0	.	.	.	0.0
pelvis	0	9	0.0	.	.	.	0.0
femur	2	28	7.1	.	.	.	7.1
patella	0	2	0.0	.	.	.	0.0
tibia	0	97	0.0	0	3	0.0	0.0
malleolus/fibula	1	1	100.0	.	.	.	100.0
talus	1	1	100.0	.	.	.	100.0
calcaneum	3	6	50.0	.	.	.	50.0
greater cuneiform	1	2	50.0	.	.	.	50.0
cubo-navicular	2	3	66.7	.	.	.	66.7
metatarsal	4	166	2.4	.	.	.	2.4
metapodial	0	45	0.0	.	.	.	0.0
vestigial metapodial	0	5	0.0	.	.	.	0.0
sesamoids	0	3	0.0	.	.	.	0.0
phalanges	0	16	0.0	.	.	.	0.0
vestigial phalanges	0	1	0.0	.	.	.	0.0
Total	22	1083	2.0	13	293	4.4	-2.4

Table 48. Saint-Césaire. Bodypart representation in the NISP and NSUTS samples in the Evolved Aurignacian (EJM) occupation. Values in bold are elements that are over-represented in the NSUTS sample.

It was suggested in Chapter 4 that epiphyses are less abundant than shaft fragments in reindeer, bison, and horse. Table 49 supports this assertion, as the MNE values for the epiphyses are almost an order of magnitude lower than those for the shaft portion in the Saint-Césaire occupations. Importantly, proportions of shafts are very similar between the occupations and none of the small differences found are statistically significant (results not shown). As we will see, burning appears to be responsible for the under-representation of long bone epiphyses in the assemblages.

	Total MNE Proximal		*Total MNE Shafts*		*Total MNE Distal*		*Total MNE*	
	n	%	n	%	n	%	n	%
Evol Auri (3)	6	11.3	43	81.1	4	7.5	53	99.9
Evol Auri (4)	19	14.7	100	77.5	10	7.8	129	100.0
Auri I (5)	65	14.9	328	75.4	42	9.7	435	100.0
Auri 0? (6)	12	20.7	43	74.1	3	5.2	58	100.0
Châtel (8)	18	17.3	80	76.9	6	5.8	104	100.0
Châtel? (9)	6	15.0	33	82.5	1	2.5	40	100.0
Moust (10)	15	17.6	63	74.1	7	8.2	85	99.9
Total	141	15.6	690	76.3	73	8.1	904	100.0

Table 49. MNE-based counts of proximal epiphyses, distal epiphyses, and shafts at Saint-Césaire. Reindeer, bison, and horse combined. Specimens that could not be identified more precisely than "metapodials," as well as the ulna, when isolated from the radius, are excluded.

Although the sample of burned specimens that are identified is often small, it is relatively clear that long bone epiphyses are burned extensively at Saint-Césaire, in marked opposition with the trend observed for shafts (Table 50). It is interesting to note that burning decreases the further we move from the articulations and is lowest at midshaft. This decrease is statistically significant (epiphyseal/near-epiphyseal fragments $t_s = 5.12$, $p < 0.0001$; near-epiphyseal/shaft fragments: $t_s = 11.01$, $p < 0.0001$; based on total). In fact, abundance of long bone skeletal portions, as measured by MNE, is inversely correlated with level of burning (Figure 38), a pattern best expressed in the Aurignacian I assemblage. These observations suggest that spongy extremities are burned preferentially. Furthermore, the relatively low level of burning in the sample of unidentified diaphyses confirms that the inverse relationship noted between percentage of burning and abundance cannot be explained by the analytical underrepresentation of burned shafts (Table 51).

	Epiphyses Only			*Epiphyses and Near-Epiphyseal Shafts*			*Shafts*		
	burned	total	%burned	burned	total	%burned	burned	total	%burned
Evol Auri (3)	3	4	75.0	3	12	25.0	2	168	1.2
Evol Auri (4)	2	9	22.2	5	35	14.3	7	430	1.6
Auri I (5)	40	82	48.8	46	190	24.2	30	1852	1.6
Auri 0? (6)	4	9	44.4	4	21	19.0	2	205	1.0
low dens (7)	0	1	0.0	0	4	0.0	0	9	0.0
Châtel (8)	0	9	0.0	0	48	0.0	0	297	0.0
Châtel? (9)	1	3	33.3	1	15	6.7	2	149	1.3
Moust (10)	0	6	0.0	0	24	0.0	0	297	0.0
Total	50	123	40.6	59	349	16.9	43	3407	1.3

Table 50. Percentages of burning on diaphyses and epiphyses at Saint-Césaire based on NISP. All taxa combined.

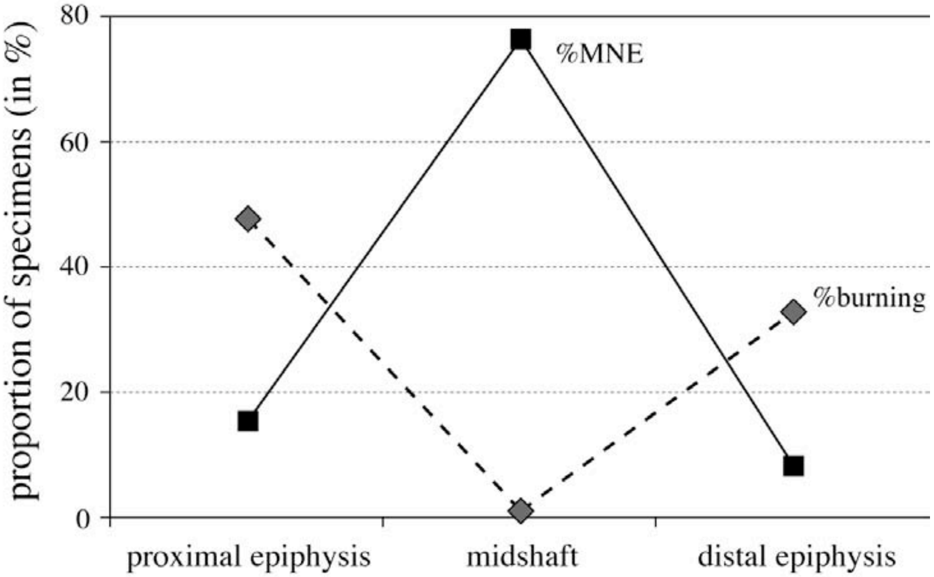

Figure 38. Proportions of burned proximal epiphyses, midshafts, and distal epiphyses versus the abundance of the same portions in the assemblages from Saint-Césaire. Data for %burning are 31/65 (proximal), 43/3407 (shaft), and 19/58 (distal) and are based on NISP. %MNE are derived from the pooling of the MNE values for reindeer, horse, and bison long bones (Table 49). Complete long bones excluded.

	Unidentified UNG2 Shafts			*Unidentified UNG3-4 Shafts*			*Total Unidentified Shafts*		
	burned	total	%	burned	total	%	burned	total	%
Evol Auri (3)	96	716	13.4	7	161	4.3	103	877	11.7
Evol Auri (4)	220	1483	14.8	18	153	11.8	238	1636	14.5
Auri I (5)	1318	7385	17.8	93	472	19.7	1411	7857	18.0
Auri 0? (6)	37	755	4.9	5	66	7.6	42	821	5.1
Low dens (5)	1	9	11.1	0	49	0.0	1	58	1.7
Châtel (8)	6	330	1.8	5	1408	0.4	11	1738	0.6
Châtel? (9)	11	308	3.6	11	550	2.0	22	858	2.6
Moust (10)	14	538	2.6	74	1173	6.3	88	1711	5.1
Total	1703	11524	14.8	213	4032	5.3	1916	15556	12.3

Table 51. Percentages of burning on UNG2 and UNG3-4 long bones in the Saint-Césaire occupations.

In summary, it can be concluded that burning is not distributed randomly in the assemblages from Saint-Césaire and appears to affect certain specific skeletal elements. Obviously, this reduced the number of elements for which reliable estimates of abundance can be produced. Although abundance cannot be estimated reliably for the pelvis, long bone epiphyses, malleolus, vertebrae, carpals, and tarsals, MNE values obtained for the other elements of the skeleton, including long bone shafts, can be expected to be representative of the excavated assemblage.

Differential preservation, burning, and bone mineral density

The previous sections focused on various families of filters that may mediate the interpretation of faunal remains. The evidence reviewed for Saint-Césaire suggests the existence of some biases with respect to the identifiability of some specific shaft portions.

Specifically, the relation between identifiability and degree of fragmentation was investigated. Burning was also shown to affect some specific classes of elements. In this section, we now turn our attention to the problem of differential preservation.

Attrition of skeletal elements can be mediated by at least three distinct factors, all potentially correlated with bone density: carnivore ravaging, differential preservation, and burning. Among these, carnivore ravaging is well understood at Saint-Césaire and was shown to be slight. More complex, however, is the identification of differential preservation, a widespread source of patterning in fossil assemblages with detrimental effects on archaeological inference. This process is usually dissected by looking at the relation between bulk density and abundance of skeletal elements (e.g., Brain 1967, 1969; Binford and Bertram 1977; Lyman 1984, 1985, 1993; Grayson 1989; Kreutzer 1992; Lyman *et al.* 1992; Brink 1997; Lam *et al.* 1998, 1999, 2003; Munson 2000).

Qualitatively speaking, the faunal assemblages from Saint-Césaire offer the full range of preservation, from modern-looking bones to completely shattered specimens. All types of bones are represented in the assemblages and no obvious bias in preservation could be perceived during the study of the material. Deciduous teeth are exceptions to this rule, as some of them, especially those from artiodactyls, are usually more fragmented than permanent teeth. Refitting contributed to alleviate this problem (Morin *et al.* 2004). It was also noted that bone surfaces from juvenile individuals were not as well preserved as those from adults.

Despite these small biases, the list of identified specimens includes several fragile elements, for instance fetal bones (n=39), hyoid (n=12), sternum and costal cartilage (n=9), and antlers (n=1406). Additionally, numerous teeth with attached mandible fragments were uncovered. In sum, this *a priori* appraisal of the material suggests relatively good preservation of the fauna, despite the extent of postdepositional fragmentation in the occupations. However, this kind of qualitative evaluation typically suffers from its heavy reliance on subjectivity, and, perhaps, optimism. Therefore, other types of information are needed to validate or falsify these interpretations.

Over the years, several methods were developed in an attempt to measure accurately bone "true" and "bulk" density[4] (e.g., Brain 1967, 1969; Binford and Bertram 1977; Lyman 1984; Kreutzer 1992; Lyman *et al.* 1992; Lam *et al.* 1998, 1999, 2003). These efforts were directed toward the building of an analytical frame for evaluating whether an assemblage is correlated, but not necessarily causally related, with density-mediated processes, notably differential preservation.

In general, the task consists of comparing mineral density values derived from modern skeletons with the proportion of archaeological elements that "survived" destruction (Brain 1969, 1976). A positive correlation between these two factors may be taken to indicate that differential preservation occurred in an assemblage when causality can be demonstrated. Correlations between density and skeletal element abundance are often presented as evidence of differential preservation or cultural behavior. Because a correlation between two factors does not imply causality, other methods are necessary to determine the agent responsible for the pattern uncovered (Grayson 1989; Lyman 1994).

Yet, an assemblage is generally said to be *un*affected by differential preservation when there is a lack of correlation between density and skeletal part abundance.

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[4] In fact, because "true" mineral density does not change much across a single bone (Shipman *et al.* 1984), what seems to be measured is bone porosity rather than mineral density, that is, the proportion of pore spaces in a specimen. The most porous bones or bone regions (e.g., vertebrae, epiphyses) are those that give consistently lower values in "density" studies (e.g. Lam *et al.* 1999).

However, the inferences that can be drawn from these types of correlations are relatively limited, as several scenarios, involving differential preservation or not, can produce similar correlations (Grayson 1989; Lyman 1994; Rogers 2000). For example, differential preservation may reduce the abundance of vertebrae in a site in which they were initially abundant, as might be expected at Nunamiut kill sites (Binford 1978). Vertebrae being characterized by low density values (Lam *et al.* 1999), differential preservation should affect them more extensively than more durable parts like long bone shafts. Comparison with density values may indicate a lack of correlation with skeletal element abundance, despite the fact that the assemblage is known to have suffered from differential preservation. This is because a sufficient number of "soft" elements might have survived to preclude a correlation with density. In other words, the probability of making Type I (rejecting a hypothesis that should be accepted) and Type II (accepting a hypothesis that should be rejected) errors is relatively high. As a result, these types of correlation should be used with considerable caution.

A solution to this problem may be to look for direct evidence of differential preservation by exploring the level of mineral change in the assemblages (e.g., Schiegl *et al.* 2003). Unfortunately, no such studies could be undertaken at Saint-Césaire due to time and budget constraints. Another way to explore this problem is to compare the abundance of different portions of an element characterized by heterogeneous density values (Lyman 1994). Long bones are good candidates in that respect, epiphyses being in general significantly less dense than shaft parts (Lam *et al.* 1998).

Because a proximal epiphysis is unlikely to have been transported without the proximal region of the shaft, contrasting their respective abundance should provide far more meaningful interpretations about differential preservation than correlations between density and complete assemblages. However, because burning reduced the abundance of long bone epiphyses at Saint-Césaire, it is not possible to examine differential preservation using long bone portions. Therefore, it is difficult to determine how differential preservation affected the occupations. The solution adopted here is a conservative one: rather than using all skeletal elements, the interpretation of body part representation is limited to those parts that have comparable density values (see Chapter 7).

Beyond attrition and analytical biases

Degree of fragmentation, morphological variation, and body size stand out as critical factors affecting identifiability. These factors are important as they potentially decrease comparability of skeletal elements within and across species. These problems are not limited to archaeological assemblages and may include actualistic studies. For instance, modern hunter-gatherer kill site assemblages collected immediately after the event (e.g., Binford 1978; Bunn *et al.* 1988; O'Connell *et al.* 1988) can be expected to be much less affected by identification biases than ethnoarchaeological studies of cooking debris in which pot-sizing, marrow-cracking, grease-rendering and other fragmentation processes occurred (e.g., Oliver 1993). As a result, behavioral interpretations based on fragmented assemblages cannot be made without taking into account these analytical biases.

The fact that the abundance of some specific elements has been shaped by attrition-based processes at Saint-Césaire may appear to limit the possibility of reconstructing Neandertal and modern human subsistence strategies accurately. For instance, it was shown that the outcome of the analytical absence of certain parts is to produce under-estimations of their abundance in the assemblages. In most cases, however, analytical underrepresentation is restricted to the fragile portion of the elements. Analytical underrepresentation is, however, more acute for ribs, as postdepositional processes appear to break ribs into two halves following parasagittal and transverse fractures, an outcome that reduces identifiability. Large ungulates are probably slightly under-represented relative to smaller taxa, but these biases might be relatively constant throughout the sequence, as the same taxa are found in the occupations.

Burning is a more serious problem. Specifically, burning decreased considerably the abundance of the vertebrae, pelvis, malleolus, carpals, and tarsals at Saint-Césaire. Therefore, it might be more productive to eliminate these parts from the analysis of skeletal part representation. One of the most robust patterns in the assemblages is the consistent burning of long bone epiphyses. However, shafts were rarely burned and a considerable amount of time has been devoted to identify them. Therefore, using shaft MNE should alleviate biases induced by burning and provide accurate approximations of the initial abundance of long bone elements at Saint-Césaire.

CHAPTER 6: BIRTHING SYNCHRONY, SEASONALITY, AND SPECIES PROCUREMENT

During most of the late Pleistocene, the annual weather of southwestern France appears to have been colder in general and seasonally more contrasted, especially in the region north of the Pyrénées and west of the Rhône, than it is today. This condition is indicated by the abundance of cold-adapted species like reindeer in faunal assemblages (Delpech 1983; Grayson and Delpech 1998; Castel 1999a; Costamagno 1999; Fontana 2000; this study), the type of microfauna recorded (Chaline 1972; Marquet 1993), and pollen and ice-core data (Sãnchez Goñi 1994).

Reindeer, bison, and the horse are the dominant taxa in many Middle and Upper Paleolithic assemblages from southwestern France. In addition, other large ungulates, red deer and *Megaceros* for example, were exploited by Paleolithic foragers as well. Holding cultural adaptation constant, the availability of a wide spectrum of large-bodied ungulates probably increased the carrying capacity of the environment in late Pleistocene France and sustained densities of human populations that *might* have been higher relative to those of historic hunter-gatherers living in the Subarctic belt of North America and the northern plains of Eurasia, where the ungulate spectrum is narrower. However, we have seen that there is evidence that in spite of this potential, foragers experienced food stress periodically. The fact that reindeer, bison, and horses occupy different ecological niches might have contributed to the leveling of seasonal fluctuations in resource abundance.

Failure of one resource might have been offset, to a certain degree, by falling back on other taxa. However, scheduling was probably not an easy task in Paleolithic France, as those species have slightly different nutritional requirements, gestation length, birthing seasons, and migratory patterns. For instance, horses can live on coarser food than reindeer or bison (Slade and Godfrey 1982), while the reindeer is one of the few species to assimilate lichens efficiently (Kelsall 1968).

In this type of environment, resource stress would have been highest in the season of lowest predictability, that is, from the onset of winter to the end of spring. Taking reindeer as an illustration, several ethological studies confirm that its distribution and aggregation can be relatively unpredictable in some winters and sometimes changes from one year to the next. Winter distribution in any one year is largely dictated by prevailing environmental conditions (Kelsall 1968; Parker 1972; Roby 1979; Boertje *et al.* 1988; Helle 1979). Major factors include snow cover (depth, hardness, and density) and thickness and extent of icing in, on, or under the snow pack, which all influence extent of accessible grazing. Also, the frequency of wild fires on the summer range and the type and density of large carnivores present on different sections of the winter range will all influence wintertime distribution of reindeer and other ungulates. Fat levels vary throughout the year in reindeer. Males are usually fat-depleted in winter and start gaining weight in spring, whereas females maintain their weight in winter but begin losing weight in spring and reach their nadir about 1 July (Kelsall 1968; Reimers 1979; Thing and Clausen 1979; Syroechkovskii 1995). The same general loss of weight during or at the end of the cold season is also characteristic of bison (Reynolds *et al.* 1982; DelGiudice *et al.* 1994), and horse (Berger 1986). With respect to reindeer, the period of lowest predictability ends with the spring migration when the animals aggregate and move to the calving grounds. These springtime migrations tend to be roughly predictable in both path and timing (Banfield 1951; Kelsall 1968; Burch 1972; Helle 1979). In late summer, after the post-calving aggregation and mid-summer migration, reindeer and caribou can be more dispersed and, therefore, more difficult to find (Helle 1979; Parker 1972). Archaeologists have neglected the routine occurrence of mid-summer migrations in the repertoire of *Rangifer* movement patterns. Most, if not all, populations, make a mid-summer southward migration, followed by an August dispersal prior to the better-known fall migration (Kelsall 1968; Parker 1972; Miller 1974; Bergerud 1976). Although the actual migration path used in mid-summer is variable from year-to-year, the use of major water crossing sites during those migrations is highly predictable, as witnessed by the remains of longtime native encampments at those crossing sites (Gordon 1988).

Less information is available on migratory patterns of bison and horse. Most ungulates would have been easier to find and kill in summer and fall, a period in which animals are gaining weight, preparing for the rut, and initiating the shift to the winter range. However, migratory shifts for wood and plains bison (see below), and, more specifically for horses, are not as predictable as for reindeer. At the end of the summer, bison aggregate in preparation for the rut (Berger and Cunningham 1994). In contrast, large aggregations are not typical for horses, whose basic social unit is the harem (Slade and Godfrey 1982). As a result of these patterns, it is hypothesized that diversity and abundance of available plant and ungulate resources probably increased during summer and fall in late Pleistocene France. In contrast, winter and spring were seasons of lowest predictability in resource procurement.

Synchrony of birthing and migration patterns in reindeer, bison, and horse

Reconstructing seasons of ungulate procurement is a necessary step for interpreting Neandertal and modern human subsistence strategies. Data on fetal development, the annual antler cycle, epiphyseal fusion, and dental eruption and wear are used here for assessing whether the assemblages from Saint-Césaire were accumulated during the season of lowest predictability in resource availability.

Any determination of season of procurement, whether based on cementum annuli, tooth eruption or epiphyseal fusion relies on the assumption of birth synchrony and a single calving season per year. For reindeer, these assumptions are very well supported. Calving occurs once a year in late spring and seems to be tightly related to plant phenology (Post *et al.* 2003). There seems to be little variation in the time of the peak period of the calving season in a given population, usually only ≤1 week, less seldom 1–2 weeks, and rarely 2–3 weeks. This variation in the peak calving period within a population over time is most likely caused by annually occurring positive (favorable) or negative (unfavorable) changes in grazing conditions. Favorable conditions promote an earlier initiation of calving and thus an earlier peak period. Unfavorable conditions cause a delay in the onset of calving, and thus a later peak in calving (Reimers 1979). In general, the peak of the calving season takes place between early May and the end of June and varies primarily as a function of location, overall condition of the herd, and latitude. Skoog (1968) and Parker (1972) have noted that 90 to 95% of the births occur within a 2-week period in, respectively, the Nelchina (Alaska) and Kaminuriak (west of

Hudson Bay, Canada) barren-ground caribou herds. Kelsall (1968:177) reported that 75% of the calf crop was born over a single week in the Beverly barren-ground caribou herd of north-central mainland western Canada. According to Syroechkovskii (1995:127), 90% of the calves in the Taymir area (Siberia) are born within a 10-day period at the end of June. The same author indicates that calving takes place somewhat earlier (mid-May to end of May) in Yakutia, the Trans-Baikal region, and the Chukchi Peninsula. The calving season is also very restricted for three wild reindeer populations of southern Norway, given that 90% of the calves are born within a 10-day period between early May and the end of the same month, depending on the herd (Holthe 1975).

Various explanations have been offered to explain this tight clustering of births. One of the arguments often put forward is that birth synchrony is an adaptation to highly contrasted seasons and winter predation. Calves born in early spring then use the relatively warm and mostly snow-free season to grow, build up fat reserves, and learn how to survive and to become accepted into their mother's social unit. At the beginning of the winter in favorable years, calves are stronger, fatter, more vigilant, and, therefore, more likely to survive the harsh season than if they were born later in the brief summer. Because birthing is highly synchronous in reindeer, some developmental features, especially fetal bones, are likely to be very accurate predictors of season of procurement. Spiess (1979:77) suggested mid-May as the peak of the calving season in Pleistocene France. Ethological data on Eurasian herds (Holthe 1975; Syroechkovskii 1995) are in agreement with his claim. However, this would be true only if the climate in Pleistocene France has been broadly similar to the one described by the last authors. In addition, it should be noted that wild reindeer populations are found farther north in areas with shorter day length compared to the Pleistocene herds of southwestern France. This might have affected the reproduction cycle.

In spite of controversy among biologists regarding the number of extant subspecies, most authors recognize two different types of reindeer/caribou: the *woodland* and *tundra caribou* (Banfield 1951). Many woodland caribou and wild forest reindeer living in forested areas tends to migrate on a small scale, while those living in mountainous areas often make predominantly vertical migrations (elevation displacement) higher up to alpine settings. In contrast, the barren-ground caribou and tundra reindeer are more prone in general to migrate over greater distances, often in the range of 300 to 600 km (Kelsall 1968). As pointed out by Spiess (1979), however, significant variation is found in migratory patterns within these types, some populations of barren-ground caribou migrating over small distances, whereas some woodland caribou are known to migrate on large distances. For instance, the large Canadian herds of woodland caribou that live east of Hudson Bay use both forested areas and tundra ranges to make relatively long linear migrations (horizontal displacements). *Importantly, within a single herd, not all caribou participate to migration*. Kelsall (1968) and Parker (1972) noted that pregnant females are usually at the forefront of the spring migration, the non-breeding portion of the population lingering behind. However, it is common for adult males to linger on winter range, moving northward more slowly than the parturient females and young animals, and not participate to the spring migration (Helle 1979; Parker 1972). Sexual segregation can also be observed in the early summer (Parker 1972). As a result, we should not expect the annual cycle in reindeer procurement to be perfectly dichotomized in terms of seasonal presence/absence in archaeological assemblages. Rather, sites that are focal locations in the landscape are more likely to be dominated by one or two seasons of kills, reflecting *modal* seasons of procurement. Additional individuals that linger behind major migrations could be taken sporadically later in that season or during other seasons when most of the herds had moved away to new range. A persistent problem in seasonality studies is that it is often difficult to identify unequivocally minor seasons of procurement. That is because it is generally unclear whether these out-of-phase kills depict real episodes or are an analytical artifact. This is true for all methods used by archaeologists for estimating seasons of procurement, including cementum annuli (Lubinski and O'Brien 2001; Stutz 2002). For reindeer, aging fetal bones is probably the method least affected by this problem and the most precise.

Despite several decades of research, it is still unclear how many reindeer subspecies were present in Paleolithic France (Bouchud 1954a, 1954b, 1966, 1975; Lacorre 1953; 1956; Guillien and Perpère 1966; Spiess 1979; Delpech 1983; Gordon 1988; Guadelli 1990; Fontana 2000). It also is unclear whether populations moved to higher or lower elevations to calve and temporarily escape predators or to seek relief from the rigors of winter or whether they move relatively short or long linear distance to achieve the same ends. Yet, seasonality data provided by Spiess (1979), Gordon (1988), Costamagno (1999), Castel (1999a), and Fontana (2000) show that most of the Upper Paleolithic sites sampled in southwestern France document winter/spring procurement of reindeer in the snow-covered season. However, Enloe and David (1997) have demonstrated convincingly that Verberie and Pincevent, two penecontemporaneous open-air sites located in the Paris basin, were occupied during the fall season. The existence of other reindeer populations making shorter migrations has been suggested by Delpech

(1983) for the Pyrénées. Concerning this last suggestion, studying sex ratios, in addition to biometric data, may allow the testing of this proposition.

For bison, the situation is more complicated. Although bison herds have been well studied in the wild in America (e.g., Meagher 1973; Reynolds *et al.* 1982; Berger and Cunningham 1994), European populations are usually smaller and kept in semi- or full captivity (Krasinska *et al.* 1987; Pucek *et al.* 2003). North America has two subspecies of bison: the wood bison (*Bison bison athabascae*)[5] and the plains bison (*Bison bison bison*) (Reynolds *et al.* 1982). Most studies have focused on the plains bison, while there is far less information on the wood bison that almost went extinct during the twentieth century (Mitchell and Gates 2002). The European bison or wisent (*Bison bonasus*) is found mostly in the Bialowieza forest of Poland and in reserves in Caucasia. According to Brugal (1983, 1999), the late Pleistocene form of bison found in France is *Bos priscus*, which is argued to have evolved anagenetically from *Bos schoetensacki*. It is unclear, however, whether *Bos priscus* was most closely related to the current European bison, or to the wood bison, now restricted to North America.

Birthing is less synchronous in bison than in reindeer. Typically, calving in plains bison begins in mid-March or early April, but appears to occur 2 weeks later in northern populations (Reynolds *et al.* 1982). After synthesizing data from three national reserves in North America, Berger and Cunningham (1994) concluded that 80% of births are spread over a 23- to 69-day period in spring. While most births are completed by the end

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[5] There is debate on the taxonomic status of the wood and plains bison. Although some have argued that these populations are no more than ecotypes and do not belong to different subspecies (Geist 1991), the traditional terminology is used here, the issue being unsettled (Mitchell and Gates 2002). Both taxa are grouped under a single genus in the text, as recent genetic studies suggest their close relationship. The fact that hybrids of bison and cattle, called cattaloes and beefaloes, are viable supports this interpretation.

of June, some calves are delivered in October and November, and, sometimes, even later (Reynolds *et al.* 1982). From an archaeological point of view, this results in some calves being "out-of-phase" (Frison and Reher 1970). Moreover, it has been argued that, in the same population, the calving period may be delayed up to a month depending on the year (Meagher 1973). Unfortunately, there is very little information on the birthing schedule of bison from northern latitudes. In wood bison, mostly restricted to Canada, most calves are born in May to early June (Mitchell and Gates 2002). Calving in wisent herds occurs mostly in May and June, with some individuals giving birth later, sometimes as late as October (Pucek *et al.* 2003). As a consequence of this relative spread of births, and of inter-annual variation, predicting the season of occupation in archaeological contexts cannot be more than 2 or 3 months precise, with, perhaps, as much as 10% of the estimates being even less precise. Berger and Cunningham (1994) have stressed that females in good condition "adjust" gestation in order to give birth in synchrony. Nutritionally-stressed females, however, do not and may give birth later. This suggests that poor forage may lead to less synchronized birthing. This is important given that in some archaeological sites of North America, it has been suggested that bison had experienced severe nutritional stress as indicated by high level of enamel hypoplasia (Niven 2001). In these assemblages, estimates of season of bison procurement are possibly less precise than those derived from better-fed populations. In summary, estimates of season of procurement derived from bison are unlikely to be as precise as those for reindeer, especially when based on nutritionally-stressed populations.

Few studies provide data on seasons of bison procurement for Paleolithic sites of southwestern France. Mauran is a late Mousterian open-air site located in Haute-

Garonne. A sample of D_4 from this site has been interpreted as indicating a summer to early fall occupation (David and Enloe 1993). A cementum annuli analysis of three bison teeth from the site of Pech de l'Azé I has suggested to Armand *et al.* (2001) deaths in late fall/early winter and late winter/early spring. Bison fetal bones in the Aurignacian level VII of Arcy-sur-Cure are said to be associated with winter procurement (David and Poulain 2002).

Behavioral information on the wild horse is very limited, compared to what is available for its domesticated form (*Equus caballus*). Today, all the "feral" horse populations living in North American reserves are, in fact, derived from domestic horse and pony stock. Przewalski's horse (*Equus ferus*) is the only surviving wild horse (Groves 1994). Although efforts are now being directed to reintroducing this species into its natural habitat (Bouman *et al.* 1994), Przewalski's horse is today mostly confined to zoos and small reserves. The domestic horse and Przewalski's horse differ genetically, the former having only 64 chromosomes, while the latter has 66 (Ryder 1994). This validates a species distinction between the two forms. If the horses of the Upper Paleolithic are more closely related to the Przewalski's horse, it may be legitimate to refer to the former as *E. ferus* as done by Olsen (1989), and Burke (1995). In spite of these genetic differences, the domestic horse and Przewalski's horse produce fertile hybrids and are very similar in reproduction physiology and general behavior (Berger 1986). Importantly, this similarity is also expressed in gestation length and timing of the foaling season. In captivity, 75% of the Przewalski's horse mares that are pregnant give birth between April and July (Montfort *et al.* 1994). Foaling is somewhat more restricted in time in feral populations. Berger (1986) noted that 75% of births in a feral population in Nevada occurred in April and May and 85% from April through June. However, it is likely that birthing is more synchronous in the wild, as one of the consequences of captivity is the relaxation of selective pressures on birthing. Like bison, births may occur much later, for instance in November and December or even in February, in some populations of feral horses (Berger 1986). In this last case, however, the reserves in which these horses are found are located in regions in which the climate is not as seasonal as is the case in more temperate climates. It is reasonable to assume, based on latitude and the character of the faunal assemblages (Delpech 1983), that foaling would have been slightly more synchronous in the cold and seasonally-contrasted environment of late Pleistocene France. Seasonal indicators of horse procurement cannot, like bison, be more precise than within 2 to 3 months on average, because the birthing season is not as strictly synchronous as for reindeer.

Much of the information on seasons of horse procurement in Pleistocene France derives from the work of Olsen (1989), and Burke (1995; Burke and Castanet 1995). According to these authors, the horse is generally associated with summer and winter procurement in the Magdalenian, with more data supporting the importance of the former season. In contrast, procurement in fall and spring is less common. Unfortunately, little data are available on the season of horse procurement for episodes earlier than the Magdalenian. Horse would have been procured in spring/summer in the Aurignacian of Solutré, with few individuals obtained in late summer/fall (Olsen 1989). Fetal bones indicate early to mid winter deaths in the Aurignacian of Arcy-sur-Cure, an observation confirmed by dental data (David and Poulain 2002).

Methods used in this study for deriving seasonality data

In the 1950's and 1960's, antlers, teeth, and fetal bones were increasingly utilized for determining seasons of procurement in Paleolithic assemblages from France (e.g., Bouchud 1954a, 1959; 1962, 1966; Lacorre 1953, 1956; Guillien and Perpère 1966). These determinations, based almost exclusively on reindeer remains, were produced in a period of more limited information on ungulate biology and, as a result, shortcomings were noted in methods and results (Binford 1973; Guillien and Henri-Martin 1974; Spiess 1979). In reaction, some authors like Spiess (1979) advocated the replacement of these methods by cementum analyses, reputed more reliable. Other studies, however, have corroborated the relative accuracy of tooth eruption and wear in reindeer for predicting the season of death of individuals younger than 24 months (Kelsall 1968; Miller 1974), and of wear in general for constructing age profiles (Spinage 1973; Klein *et al.* 1981; Pike-Tay *et al.* 2000). Methods based on cementum annuli are very useful and may be as accurate, or even more, accurate than the previous methods (Miller 1974; Gordon 1998; Pike-Tay 1991, 1995; Burke 1995; Burke and Castanet 1995; McKinley and Burke 2000). Analysis of cementum annuli is not without problems, however, because it involves the destruction of the specimens, does not produce perfectly consistent results in blind tests, and can be affected by diagenesis (Stutz 2002; Lubinski and O'Brien 2001; McKinley and Burke 2000). Nevertheless, when these problems are addressed properly, cementum analysis is a useful complement to other methods of season determination. For various reasons, this method was not used in this study. Therefore, the discussion focuses mostly on fetal bones, epiphyseal fusion, eruption and wear of the mandibular teeth, and antler development. Some points about methodology need to be first raised in order to address issues of seasonality in the assemblages from Saint-Césaire.

Tooth eruption and wear

Reindeer

A common problem with aging methods based on eruption and wear of mandibular teeth is that inter-individual variability may be significant (Miller 1974; Klein *et al.* 1981; Pike-Tay *et al.* 2000; Whittaker and Enloe 2000). For instance, Skogland (1988) and Kojola *et al.* (1998) argue that the quality of standing crops of terrestrial lichens in winter ranges significantly influences dental wear in reindeer. Poor crops, often due to overgrazing, would enhance particle ingestion and, ultimately, tooth wear. Although variability may be significant in young individuals, it is nonetheless possible to determine seasons of procurement, especially for individuals in their first or second year (e.g., Enloe 1997).

When investigating archaeological assemblages, two categories of data, crown height, sequence of tooth eruption, and patterns of wear are frequently combined for making predictions on seasons of procurement. The same approach was adopted here. Most studies (detailed in Miller 1974) are in general agreement about the sequence and timing of tooth eruption in reindeer, especially concerning the eruption of the M_1 (3 to 5 months) and M_2 (between 10 and 13 months). The range of variation in eruption being relatively small, the development of these teeth can be considered reliable indicators of season of death. Variation in the eruption of the M_3 is too large, however, up to a year, for it to be of any use in seasonality studies. Because the Saint-Césaire assemblages include many mandibles and dental series, we can expect inferences of seasonality to be more accurate than if relying only on isolated teeth. In order to limit subjectivity, the numerous plates provided by Miller (1974), in which variation of wear is presented for various age classes, were used for comparison. Ten arbitrary age classes, detailed in (Table 52) were created after examining this variation. The pooling of males and females in this classification affects the results only slightly, as both sexes show similar levels of wear until approximately 6 or 7 years of age, when the male's teeth begin to be increasingly more worn than those of females (Miller 1974), perhaps, as a result of frequent sexual segregation in the distribution of adults over the range and differences in forages (Parker 1972). Miller (1974:30) offers an alternate hypothesis and attributes this pattern to the fact that males eat more food than females to produce and maintain a heavier body. This means that older age classes may be skewed depending on the sex ratio, a piece of evidence that has been overlooked in discussions of age profiles. The fact that the last two age classes (IX and X) of Table 52 are very wide should alleviate this problem.

Seasons of reindeer procurement can be explored using the first six age classes (classes I to VI) of Table 52, which correspond to age increments smaller than or equal to 6 months. Because there are many rapid and dramatic changes in reindeer dentition prior to and during the first 6 months of life, age classes II and III are more precise than subsequent ones. Estimates of season of reindeer procurement were produced for Saint-Césaire based on the aging system presented in Table 52. In addition to this method, crown height was measured, when possible, on the protoconid, that is, on the buccal side of the mesial lobe, of all d_3 (dP_3) and dP_4 (dP_4) identified in the assemblages and compared with equivalent data from Pincevent (David and Enloe 1993) and Verberie (Enloe and Audouze 1997; Enloe 1997). Pooling of d_3 and d_4 was necessary due to small sample size, but was limited to teeth attributed to different individuals. The pooling of these teeth is probably not an unreasonable decision, crown height being highly correlated on contiguous teeth (Pike-Tay *et al.* 2000).

Comparisons with Verberie and Pincevent are of interest because the existence of a single season (fall) of procurement has been demonstrated convincingly for these sites. It is important to stress that these comparisons assume that the peak of the calving season, as well as patterns in wear of the deciduous dentition, were relatively stable in southwestern France throughout the second half of the late Pleistocene.

If these assumptions are correct, the time span separating Verberie and Pincevent from Saint-Césaire should not affect the results. Contrasts in distributions of crown height between these sites should therefore indicate differences in seasons of reindeer procurement. However, this type of comparison needs to be made very carefully because it can lead to self-reinforcing cycles of season determination. Although the method is far from perfect, we will see that some of the levels of Saint- Césaire differ in season of procurement from Pincevent and Verberie. This information compared to data derived

Number	Age Class	Correspondence with Miller's Plates: Cutoff Points
I	fetus to neonate	fetus *to* pp. 38: left column, 1st mandible from the top
II	0.25-3 months	pp. 38: left column, 1st mandible from the top *to* pp. 38: left column, 4th mandible from the top
III	3-5 months	pp. 38: left column, 4th mandible from the top *to* pp. 38: left column, 5th mandible from the top
IV	5-12 months	pp. 38: left column, 5th mandible from the top *to* pp. 39: left column, 2nd mandible from the top
V	12-17 months	pp. 39: left column, 2nd mandible from the top *to* pp. 39: right column, 8th (last) mandible from the top
VI	17-24 months	pp. 39: right column, 8th (last) mandible from the top *to* pp. 41: right column, 6th mandible from the top
VII	24-36 months	pp. 41: right column, 6th mandible from the top *to* pp. 43: right column, 6th mandible from the top
VIII	36-72 months	pp. 43: right column, 6th mandible from the top *to* pp. 45: right column, 5th mandible from the top
IX	72-123 months	pp. 45: right column, 5th mandible from the top *to* pp. 47: right column, 9th mandible from the top
X	123 months and over	wear greater than p. 47: right column, 9th mandible from the top

Table 52. Arbitrary age classes used in the analysis of the reindeer teeth of Saint-Césaire. Classification based on data from Miller 1974.

from the aging system developed in Table 52 should avoid or at least markedly reduce circularity by anchoring the interpretations to individuals of known estimated ages[6].

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[6] F. L. Miller (pers. comm., 2003) has pointed out that none of the 999 caribou (943 from the Kaminuriak population and 56 from the Beverly population) in the sample used by Pike-Tay (1995) were animals "tagged at birth." Rather, the "age composition of the Kaminuriak Population was estimated from tooth eruption and replacement, by linear dental measurements, and by microscopic examination of annuli in the cementum of mandibular teeth, prepared histologically" (Miller 1974:6). He believes, however, that precise and accurate age estimates were generated for animals between 1 and 39 months old by comparing information on season of capture, sex, antler development, body size, tooth eruption, dental wear patterns, and counts of cementum annuli. His position is that age estimates resulting from the above process are exact for all caribou between 1 and 24 months of age and for most animals between 25 and 39 months old. However, he believes that ages assigned to older caribou should have at least a ± 1-year associated with each age estimate to better reflect the probable limitations (lack on consistency) of the composite approach and the histological examination of dental cementum.

Importantly, the results derived from both methods are congruent. This is expected, given that both aging methods use, among other, crown height for producing age estimates. However, the fact that the samples may differ for each method and that the visual age classification uses criteria other than crown height (e.g., type of wear; eruption and wear of adjacent teeth) shows that the two systems are only partially redundant.

Horse

Horse incisors are commonly used by breeders and biologists for aging live individuals (e.g., Garrott *et al.* 1991, 1991b), and more rarely, for interpreting archaeological material (Guadelli 1998). Unfortunately, horse incisors are rarely numerous in Paleolithic assemblages. To address this problem, Levine (1979) devised an aging system that includes premolars and molars, usually much more abundant than incisors in archaeological samples. This method has been influential, although it has been criticized for being not totally reliable, especially concerning the age estimation of old individuals (Guadelli 1998). Seasons of horse procurement can be determined with some accuracy, given that the deciduous cheek teeth in the mandible are replaced over a relatively short period of time in the mandible by the permanent dentition. Moreover, in contrast to bison, horse deciduous teeth appear to be fairly resistant to damage. The timing of these changes, as well as the evolution of wear with age, is detailed by Levine (1979). These data are in general agreement, especially for the juveniles, with the observations synthesized by Guadelli (1998). Both studies were used for interpreting the faunal samples of Saint-Césaire. Because of the relatively small number of horse remains in the assemblages, the discussion here focuses more specifically on seasonal indicators and less on age profiles.

Bison

There is surprisingly little data on the eruption and wear of mandibular teeth in living bison, which is in disparate proportion with the large amount of archaeological studies discussing bison age profiles. It has been observed that captive bison fed in winter by humans show lighter wear compared to free-ranging animals, possibly as a result of differences in amount of silica ingested (Wasilewski 1967). Soil types and degree of vegetal cover are other factors that are said to shape dental wear in bison (Haynes 1984). Again, wear on incisors has been used by biologists for aging live individuals (e.g., Fuller 1959). However, as acknowledged by these specialists, incisors are often rapidly disarticulated from the body of dead animals (Berger and Cunningham 1994:61), which may explain why these teeth are often found isolated in archaeological assemblages. A more useful system for the archaeologist is the method provided by Reher and Frison (1970, 1980), which focuses on cheek teeth. This aging system, widely used in North America, has been criticized recently for its small modern sample and the lack of information on how the age classes were derived (Whittaker and Enloe 2000). A new analysis of tooth eruption and wear has been published based on modern bison (Gifford-Gonzalez 1991). Unfortunately, as noted by Whittaker and Enloe (2000), these results, apparently based on the same small comparative collection examined by Frison and Reher, are not readily applicable to archaeological assemblages. That is, the fit between age and crown height is poor, when measured with the quadratic formula developed by Klein *et al.* (1981). In general, it can be concluded that because the eruption sequence is slower in bison relative to the horse and reindeer, which appears to increase inter-individual variation, it is more difficult to determine season of procurement for this taxon. Moreover, bison deciduous cheek teeth are relatively fragile compared to those of ungulates of roughly comparable size (e.g., horse; rhinoceros) and tend to be fragmented in archaeological assemblages. Despite its shortcomings, the system presented by Reher and Frison (1980) has been adopted here for aging individuals younger than 2 years. However, the age estimates should be considered more tentative than for the reindeer and the horse.

Sex ratios

Sex ratio can also be used to check for internal consistency between season of procurement and economic strategies. This is because sex ratios vary seasonally, spatially (males may not be found with females in some seasons), and across age cohorts in gregarious species. For instance, Enloe (1991; Enloe and David 1997) noted that similar proportions of male and female reindeer at Pincevent are consistent with the herd composition during the fall migration, in agreement with their seasonal estimates based on tooth wear. Binford (1978), Spiess (1979), Speth (1983), and Weinstock (2000) investigated sex ratios to explore whether there is preferential selection of individual animals and body parts in relation to nutritional condition in various ungulate species. However, relying on sex ratios for interpreting seasons of procurement in non-kill sites like the Abri Pataud or Saint-Césaire is thorny for many reasons. For example, because male parts, particularly skulls and antlers, might be discriminated against during transport because they are bulky and heavy (Binford 1978). The age of the animal, quality of the skin, the taste of the part, and body fat are other factors known to affect selection and transport. However, if the part under consideration varies little in weight or size between sexes, yet still shows sexual dimorphism in osteometric measurements, sex ratios may yield valuable information on herd structure and subsistence strategies. In this case, nutritional condition may be the primary structuring factor of sex ratios in transport.

In Paleolithic research, antler measurements have been used to derive sex ratios in reindeer (e.g., Sturdy 1975). In addition to the possible bias noted above against the transportation of male heads, another problem plagues the interpretation of antler-based sex ratios. This is that some reindeer females lack antlers. Females without one or both antlers are rare in barren-ground caribou, but appear to be more frequent in woodland caribou (Reimers 1993; Whitten 1995). Bergerud (1976) reported that the proportion of antlerless females was sometimes very high (between 28 and 93%!) in some woodland caribou populations of Newfoundland. This is not an isolated phenomenon. Syroechkovskii (1995) pointed out that in several regions of Eurasia (Altai, Yakutia, Siberia), as many as 25 to 33% of the females lack antlers. The frequency of this feature may also vary through time within a single herd, as a function of nutrition, snow cover, population density, etc. (Espmark 1971; Reimers 1993). In contrast, antlers are seldom absent in males and little variation is recorded between subspecies (Whitten 1995; Bergerud 1976). Because the proportion of antlerless females is high in some living populations, antlers recovered in archaeological assemblages cannot be used unambiguously to infer sex ratios. That is, the number of females may have been dependent upon the characteristics of the prehistoric population and, thus, would be systemically underestimated (see also Weinstock 2000). This means that it should be made clear that sex ratios derived from this part may differ from the sex ratio of the death assemblage, which may itself be different from the one of the living population or of the "transported" population. Therefore, several factors (e.g., season of procurement, hunting strategies, number of carriers, etc.) are likely to structure sex-ratios. Unfortunately, because epiphyses tend to be burned at Saint-Césaire, which are generally used to generate sex ratios in archaeological studies, it is not possible here to address these issues.

Antler development and cycle

Unlike other cervids, antlers are grown and shed by both sexes in reindeer. The annual cycle of antler development and casting is regulated primarily by alkaline phosphatase, an hormone which varies in level as a function of age and sex (Bubenik *et al.* 2000). Other hormones like estradiol and IGF–1 (insulin-like growth factor 1) are also involved in these processes (Blake *et al.* 1998).

It has been hypothesized that antlers would give females a selective advantage over bulls during the winter season (Henshaw 1969), and would enhance the fitness of pregnant versus barren females after parturition (Espmark 1971). The role of antlers in establishing dominance in a group is, however, controversial (Henshaw 1969; Bergerud 1973; Barrette and Vandal 1990; Gagnon and Barrette 1992). The following is a summary of data provided by various authors on the details of the annual antler cycle (Kelsall 1968; Espmark 1971; Bergerud 1976; Reimers 1993; Whitten 1995).

For most individuals, antler growth begins in winter or spring and is completed just before or during the rut season in Fall. In males, large bulls start growing their antlers in late March-early April and lose them at the end of the rut between late October and the end of December. Shedding of antlers in younger bulls is more spread but is usually completed by February/March. In some cases, shedding occurs only in April or May.

The schedule is different for females. Antlers are cast by most parturient and maternal pregnant females just before, during or after parturition from late May to mid June. However, some few pregnant females drop their antlers as early as April or May. New growth is usually initiated a few days after the antlers are cast, although slight departure from these patterns has been reported (Gagnon and Barrette 1992). Most likely, depending mainly upon if the animal is in a reasonably good nutritional state. Conversely, barren females can shed their antlers anytime from April to a few days or weeks *before* the peak of the calving season. Calves lose their small antlers at approximately the same time as barren females. One should note, however, that shedding of both antlers is rarely perfectly synchronized in an individual. Both antlers may be shed on the same day, but often this occurs days or, more rarely, weeks apart (Bergerud 1976). Furthermore, healthy populations are more prone to lose their antlers a little earlier than less healthy ones (Bergerud 1976; Gagnon and Barrette 1992). In summary, breeding females are growing antlers in velvet or carrying hard antlers for virtually the entire year. They are usually antlerless for only a couple of weeks, depending on their nutritional state. Nonpregnant adult females either could follow the above annual cycle, or they can shed their antlers as early as March/April and begin new growth shortly thereafter. Female yearlings and 2-year-old females can exhibit patterns similar to either nonpregnant or pregnant adult females. Prime bulls usually begin antler growth in March, but this could be delayed until April if the animal is in poor condition. They usually begin stripping velvet from their antlers after late August and continue to do so through September. They then carry their hard polished antlers until they finish their rutting activities, usually October-November. Prime bulls who were vigorous breeders may become 'spent' before the rut is completely over, and may cast their antlers immediately. Most other breeding bulls cast their antlers soon after the rut is over, sometimes between late November into December. Young males, from one to four years old, can retain their hard antlers from October through March and some into April before shedding them and starting to grow their new pair. Sometimes, young males carrying their last year's antlers into May or even June, and can be seen among the cows and young females on the calving grounds. On the other hand, the period in which adult males lack antlers is much longer, up to three months. The most significant trends of the antler cycle are summarized in Figure 39.

The interpretive potential of these annual patterns was seized upon by Bouchud (1966, 1975), who examined thousands of prehistoric antlers with the goal of identifying the type (woodland versus barren-ground) of reindeer present, and of inferring season of occupation and herd structure. The classification system proposed by Bouchud, and adopted by others (e.g., Sturdy 1975), relies on the assumption that sexes and age groups can be discriminated without difficulty by focusing on antler size and morphology. Although innovative, Bouchud's method of aging and sexing antlers was, however, shown to be flawed, one of the reasons being that it downplays sexual and developmental variation (Spiess 1979). A more recent attempt at interpreting site seasonality and procurement strategies based on antlers was made by Bonnissent (1993) in her study of the antlers of La Madeleine, the type site of the Magdalenian. The arguments put forward by Bonnissent are better supported than those of earlier analysts, because variation in sexes and age groups is emphasized and guide the interpretation of the material. Although Bonnissent's reasoning is sound, little comparative data from modern reindeer populations were included in her study. Consequently, the factors of variation in antler

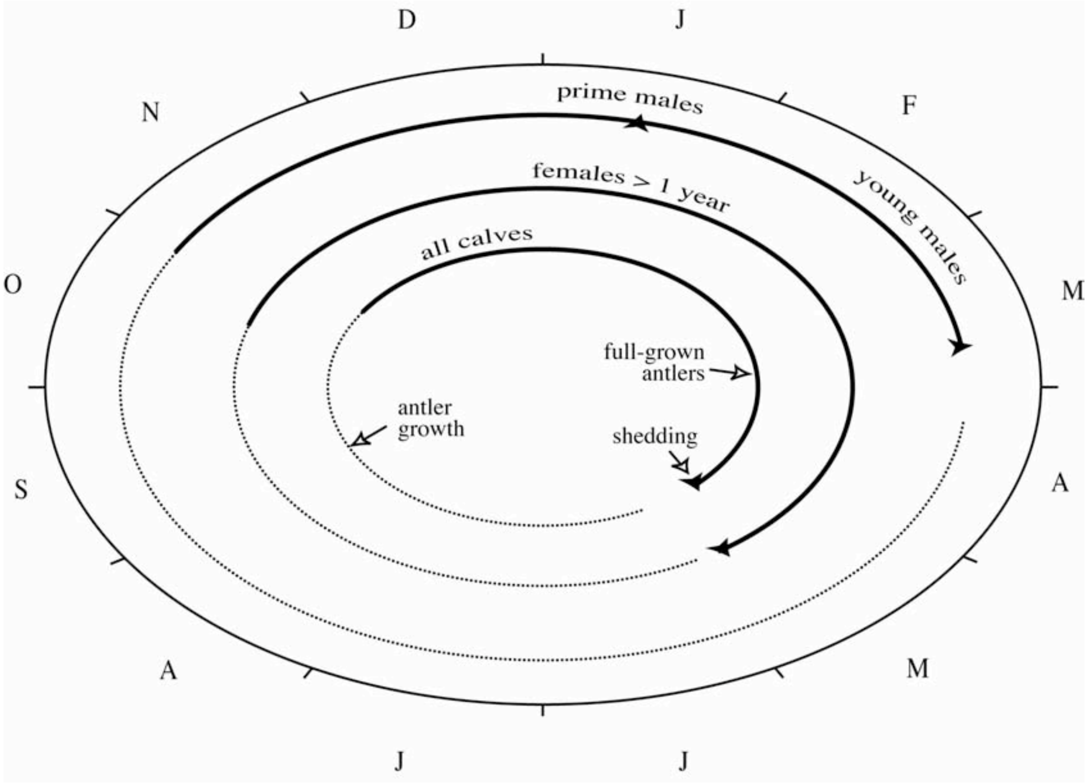

Figure 39. A simplified summary of the annual antler cycle in reindeer.

size and morphology need to be better understood before her results can be assessed more fully.

Shed and unshed antlers have different implications for seasonality. The fact that reindeer heads have a reduced "consumption window," much shorter than the one for rib slabs for instance, and rapidly spoil in the warm season (Binford 1978), strengthens the association between unshed antlers and the period of procurement. In contrast, shed antlers can be picked up on the ground at any time of the year. Therefore, a tight relationship between the season in which antlers are shed and the season of procurement does not necessarily exist. Unshed antlers may generally be transported to the site as *riders*. They might also have been sought after in societies that use antler in toolmaking or heads for ritual purposes. In this case, it can be inferred that this would increase the utility of the head part. In contrast, we can assume that shed antlers are purposefully collected for specific use.

Once dropped, shed antlers weather rapidly and are sometimes gnawed on by rodents, wolves, carnivores, and especially foxes, ungulates. This list includes reindeer. According to F. Miller (pers. comm. 2004), gnawing would be more frequent on the tips of the antlers, because the tips of the tines are more assessable on the living animal when other caribou gnaw on them and perhaps because tines are often sticking up when the antlers are lying on the ground. Also, the base of antler is too large for rodents and arctic foxes to chew on or, at least, inconvenient for them to do so. The adaptive significance of this behavior is stressed by Reimers (1993:1323), who noted that "the fact that reindeer frequently chew on cast antlers during summer (Wika 1982) and that almost all animals killed during winter in Snøhetta and Hardangervidda had antlers that were heavily gnawed (unpublished data) may indicate that minerals are part of the food-limitation complex." Spiess (1979) observed some well-preserved specimens in the Canadian Arctic that were 48-months old. However, the same author concedes that in quantity, shed antlers might be meaningful indicators of season of procurement. However, also in the Canadian Arctic, F. Miller (pers. comm. 2004) has had caribou antlers around his camps, which he knows were on the ground for 10 to 20 years and remained in good shape with minimal deterioration or chewing on them and apparently would have been usable for toolmaking. He believes what makes the main difference in how long a cast antler remains in good shape is whether if falls on a dry site with good drainage or on a wet site where it becomes water-logged and the breakdown process is speeded up. Although unshed antlers are said to be more reliable for investigating site seasonality, the "scavenging" of antlers from dead carcasses cannot be excluded, especially when it involves Upper Paleolithic assemblages, a time period in which the antler is known to have been valued for making bone tools. In sum, unshed antlers are more tightly connected to the season of occupation than shed antlers and should be favored in analyses of seasonality.

We have seen that seasons in which antlers are carried and shed depend on several factors. Sex is a critical structuring component of the antler cycle and needs to be identified if one wants to probe seasons of procurement in archaeological samples. At Saint-Césaire, antler fragments are extremely abundant (total NISP=1406, total MNI=121). Very few of these specimens bear evidence of gnawing. This might suggest that antlers were collected most probably during the shedding season or not long after the death of the animal carrying them for those that are unshed. However, given the possible variability on this theme, it is a weak assumption. The next task, then, is to determine whether the antlers are from females or males and the age class of those animals.

Despite contrary claims in archaeology, antlers other than those from prime adult males are not easily amenable to sexing. In fact, depending on the feature considered, the overlap between young males and females for some antlers variables can be significant. Also, little difference is found between antlers of male and female calves (Høymork and Reimers 2002). However, calves from both sexes can be separated without difficulty from older individuals because they: “have small and distinctive straight, tine-less antlers, which are not easily confused with adults” (Høymork and Reimers 2002:81). These are generally referred to as “spikes” (*daguets*). It is important to note, however, that some calves do not grow antlers (Bergerud 1976), and that some yearlings, especially females, may also carry spike antlers (F. Miller, pers. comm. 2004).

In contrast, males older than 2.5 years have antlers that are as a rule larger than those of females (Høymork and Reimers 2002). Male antlers peak in size at around 6 or 7 years of age and then tend to regress somewhat with age. In this case, however, antlers never regress to the point where they could be confused with those of females (Reimers pers. com. 2003). Therefore, antler measurements may allow one to isolate males older than 2.5, and with greater confidence, 3.5 years from all females. Sexing juveniles is much more challenging, however, as their antlers are not easy to distinguish from those of adult females (Høymork and Reimers 2002).

Recently, Høymork and Reimers (2002) investigated age and sex determination based on antler measurements in a semi-domesticated herd from central Norway. Unfortunately, many of the measurements examined by those authors, for instance, antler height, maximum inter-antler width, and number of tines, were designed for biologists and cannot be applied to fragmented antlers. However, one measurement, the circumference of the burr (the base of the antler), is pertinent to prehistoric material and has been documented by archaeologists (e.g., Bouchud 1966; Bonnissent 1993). The results collected by Høymork and Reimers suggest that male and female calves have similar burr circumferences, with a slightly larger mean for males. There appears to be little overlap in this measurement between calves and older individuals of both sexes. Concerning young adults, even though there are differences in burr circumference between females and males, the overlap in the distribution of the measurements is significant. Based on their Figure 2 (Høymork and Reimers 2002:78), non-calf antlers with a burr circumference smaller than 80 mm are most probably from females. The mean circumference is slightly smaller for yearling males relative to the 2.5 year-old males, but the distributions almost fully overlap. It seems that very few females have a burr circumference larger than 120 mm. Therefore, thicker antlers would represent males. No measurements are available for older males, although their antlers are known to be larger than those of young males (Bergerud 1976). In summary, the analysis conducted by Høymork and Reimers highlights three findings: i) Calves are easy to identify both morphologically and metrically, although some female yearlings may be confused with them. ii) Non-calf burr circumferences smaller than 80 mm are probably females. iii) Those larger than 120 mm are almost certainly males. These threshold values are, of course, limited by the fact that they are derived from a single modern herd that may not be representative of prehistoric reindeer populations in southwestern France. As argued, calves are relatively easy to identify, even when dealing with Paleolithic assemblages. Comparing the measurements of the Norwegian calf sample with those taken on the spike antlers of Saint-Césaire should help clarify whether both populations are similar.

Høymork and Reimers (2002:79) observed mean burr circumferences of 52 and 56 mm for female and male calves, respectively. These values are slightly larger than the mean for the spike antlers from Saint-Césaire (48.5 mm on 10 individuals). This may suggest that the Saint-Césaire population is a bit smaller than the one analyzed by Høymork and Reimers. However, the Saint-Césaire sample of calves is small and collapses all occupations and sexes. As a result of these limitations, it may be best to consider both populations as roughly comparable.

Building on the above findings, the numerous antler burrs (n=168) from Saint-Césaire were measured in order to produce probabilistic statements regarding the sex of the antlers. Combined with data about the type of antler (shed or unshed) present, these estimations can be informative in regard to the season of procurement. Measurement A is the burr circumference measured directly on the pearl ring (*cercle de pierrures*). Measurement B is the antero-posterior diameter of the beam taken 1-cm above the pearl ring (Figure 40). When the brow tine (*andouiller d'oeil*) converges with the burr, the point of lowest diameter, often the pearl ring, was measured. These measurements are then plotted in a scatter plot. The mathematical relationship between measurements A and B is important here, as they can be used to predict burr circumference of incomplete specimens. This regression is useful as it can contribute to increase sample size. Measurement B can be used to predict measurement A using the following equation:

$$B = 0.981 + 0.282 * A$$

where B is the burr circumference and A the antero-posterior diameter of the beam. The regression shown in Figure 41 explains 85.1% of the variation. The data for all the Saint-Césaire antlers indicate that no antler with a burr circumference larger than 80 mm has an

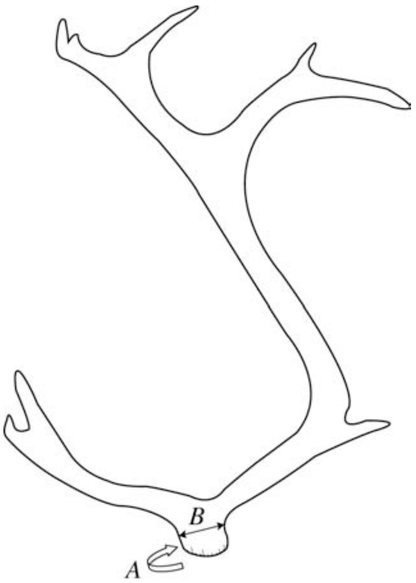

Figure 40. Measurements of the reindeer antler. Measurement *A* is the burr circumference measured directly on the pearl ring, whereas measurement B is the antero-posterior diameter of the beam taken 1 cm above the pearl ring.

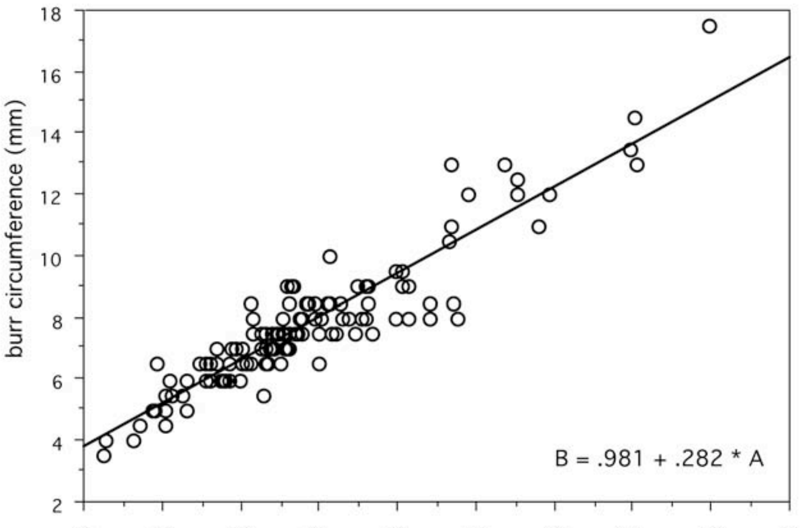

Figure 41. Regression of burr circumference versus antero-posterior diameter for the reindeer antlers of Saint-Césaire.

antero-posterior diameter smaller than 20 mm. In addition, no antler with a beam circumference larger than 120 mm has an antero-posterior diameter smaller than 42 mm. Therefore, these values can be used for predicting the sex of the incomplete burrs of Saint-Césaire. In this study, antlers with an antero-posterior diameter smaller than 20 mm are attributed to females, whereas values above 42 mm are ascribed to adult males.

Epiphyseal fusion

There is very limited information on the timing of epiphyseal fusion in reindeer. Fortunately, there are some exceptions. Hufthammer (1995) published a summary of epiphyseal fusion in reindeer. Her results suggest that the scapula head may be a useful seasonal indicator, as the *tuber scapulae* was fused by six months on all the specimens she studied but loose on a two month-old individual. Therefore, a loose *tuber scapulae* would indicate summer to late fall procurement. However, it is possible that the fusion of this part varies between populations and with nutritional condition. Epiphyseal fusion in other parts is too variable for determining season of death.

Barone (1999) supplies information on the fusion of the centers of ossification in horse and cattle, the latter being close phylogenetically to the bison. He found that many cranial parts fuse at an early age and with limited variation. However, horse and bison crania tend to be severely fragmented in archaeological sites and are, for this reason, of limited value here. More useful is the age at which the horse radius fuses with the ulna (3-5 months). This means that an unfused radio-ulna would signal death in spring to fall.

Except for the skull bones, no epiphyseal fusion appears reliable for detecting season of procurement in cattle.

Fetal bones

Growth of bones is very rapid in fetuses. In some, if not most, species, bone growth appears to follow a power function, being initially rapid before increasingly slowing down toward birth. Season of procurement can be estimated with some accuracy by measuring the diaphyseal length of fetal bones in species characterized by synchronous birthing and the production of a single young per year. The range of variation in these developmental age predictions is generally limited and may be as small as a few weeks to a few months depending on the species. However, fetal bones do not preserve well and are sometimes difficult to identify. Concerning this problem, the descriptions provided by Prummel (1987a; 1987b; 1988; 1989) were most helpful for the identification of the horse fetal specimens of Saint-Césaire. Further, in some species, reindeer for instance, fetuses are selected against in transport (Binford 1978:86).

The approximate age of reindeer fetal bones can be estimated based on the linear regression presented by Spiess (1979), although caution must be used since Spiess himself acknowledges that the equation he gives is no more than a rough approximation of developmental growth in this species and may be incorrect. The equations of Bünger-Marek (1972; as cited in Prummel 1989) for fetal cattle are probably good approximations of bison fetal growth, as both species are partially interfertile (Mitchell and Gates 2002). For horse, raw data from Habermehl (1975, as cited in Prummel 1989) and data read from the graphs of Guffy *et al.* (1970) were used to generate a number of regressions (Table 53 and Appendix A). The equations derived from these regressions use the square root of the diaphyseal length to predict age in days. A very high proportion of the variability in these data, between 98.5 and 99.4%, is explained by these regressions (Figure 42). Moreover, the fit between the two sources of data is very good, which increases the robustness of the regressions.

Part	Source of data	Regression	r^2
humerus	Habermehl 1975	y = -9.9036+25.6397*(SQRT(x))	0.994323
radius	Guffy *et al.* 1970; Habermehl 1975	y = 6.77872+21.9387*(SQRT(x))	0.990776
metacarpal	Guffy *et al.* 1970; Habermehl 1975	y = 32.0941+20.6867*(SQRT(x))	0.985071
femur	Habermehl 1975	y = -6.7754+22.5592*(SQRT(x))	0.993468
tibia	Guffy *et al.* 1970; Habermehl 1975	y = 7.91166+21.9623*(SQRT(x))	0.985217
metatarsal	Guffy *et al.* 1970; Habermehl 1975	y = 29.5154+19.4317*(SQRT(x))	0.988001

Table 53. Equations for the estimation of fetal age (in days) for horse long bones. y = is the fetal age in days after conception, x = is the diaphyseal length in mm, SQRT is square root, r^2 is the coefficient of determination. The data used to calculate the regressions are presented in Appendix A. The data of Habermehl (1975) are those cited by Prummel (1989).

Incorporating variation in birth synchrony in fetal age estimates

In general, fetal age estimates are used to predict season of procurement based on the assumption of birth synchrony. A common procedure is to select a “mean” breeding date and use it to extrapolate season of procurement. However, variation in the distribution of births in a given year is rarely taken into account in this approach, nor is the variation in the onset of the calving season from one year to the next incorporated. In this study, this variation is explored and integrated in the age estimates.

The developmental age predictions for the fetal bones from Saint-Césaire are presented along with 80% confidence intervals for horse, reindeer, and bison. More inclusive intervals (e.g., 90% or 95%) could not be calculated with the available data. Variation being very small in the growth data, these confidence intervals incorporate only variation in birth synchrony. In bison, birth synchrony is moderate, and an 80% confidence interval of 60 days is added to the developmental age calculated from the equations of Bünger-Marek. This figure was computed by rounding up the mean of the number of days (49.6) necessary to account for 80% of the births in various bison populations of North America (data in Berger and Cunningham 1995:117)[7]. Rounding up is necessary, as it is not possible to know precisely the peak date of the calving period in late Pleistocene France. August 1st is considered the peak day of conception for bison, based on data on gestation length provided by Berger and Cunningham (1995). In wild horse, the birthing period is slightly more spread than in bison, 75% of the births occurring in 60 days on average in a feral population of Nevada (Berger 1986). Taking this observation into account, the 80% confidence interval proposed for horse is 70 days. No rounding up is made here, as variation in birth synchrony is believed to have been slightly less in Pleistocene France, due to its more seasonally contrasted climate, than it is today in the feral horse populations studied by Berger that are located much closer to the

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[7] It is important to note that the interval given by Berger and Cunnigham (1994) does not correspond to the most compressed births. Rather, the interval reflects the time elapsed from the first to 80% of the births, that is, beginning with the most extreme left value of the normal distribution (the earliest birth) to the right. As a result, 40% of the births on each side of the mean may give an interval smaller than the 49.6 days time span calculated here. However, because the distribution of births in a year tends to follow a lognormal curve (Berger and Cummingham 1994), most births being compressed in the first few weeks of the calving season with increasingly fewer buriths occurring later, this problem might be minor.

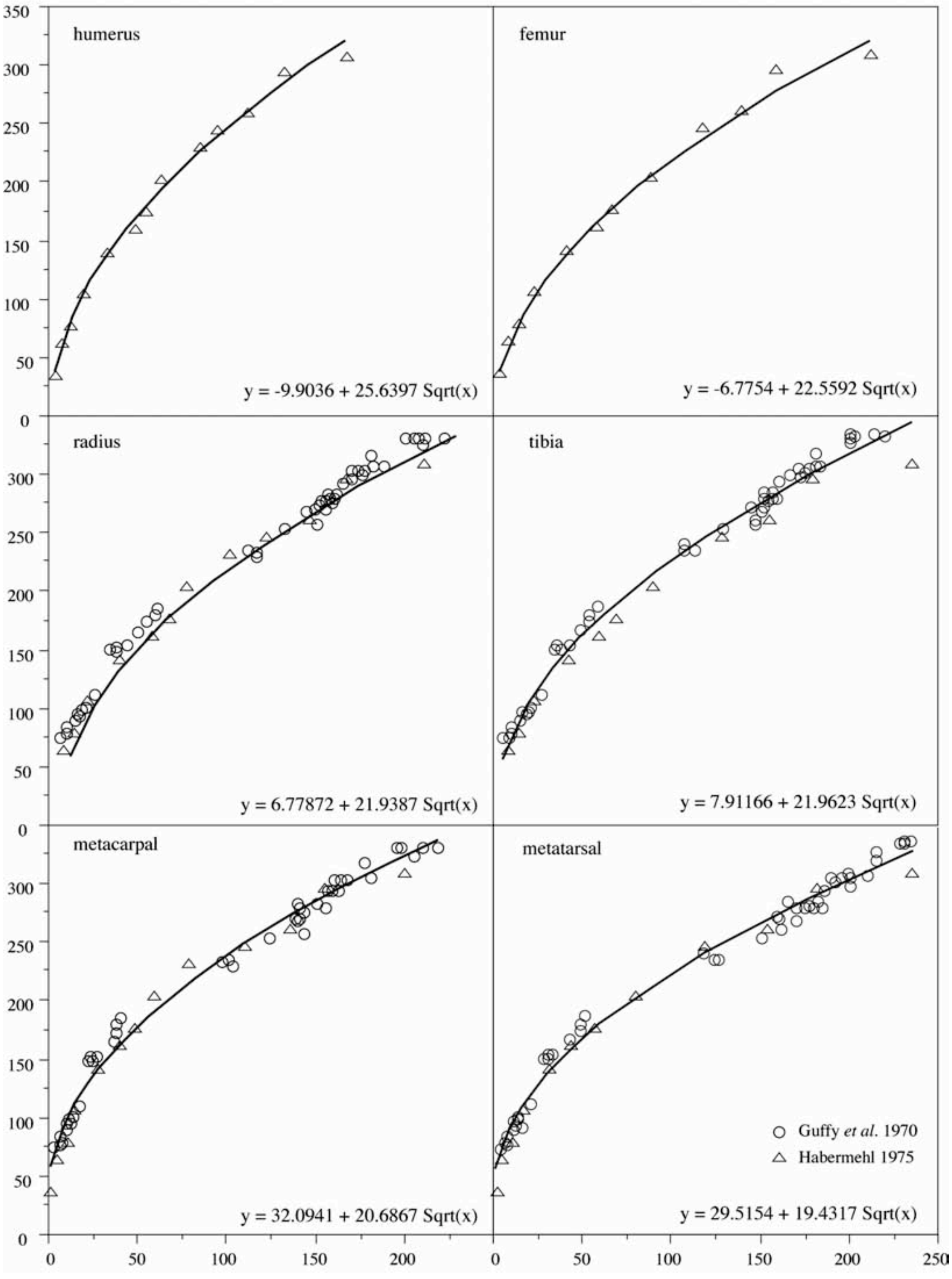

Figure 42. Regression of developmental age (in days) versus diaphyseal length (in mm) for horse fetal bones. The data are from Guffy *et al.* (1970) and Habermehl (1975, in Prummel 1989).

equator. Conception in late Pleistocene France was set as beginning on June 15th, as suggested by data supplied by Montfort *et al.* (1994) and Berger (1986).

In reindeer, births are highly synchronous and the onset of the calving season is comparable, for the same latitude, across populations. Therefore, the 80% confidence interval covers 10 days. The mean gestation length in reindeer is approximately 228 days (Miller 1982; Geist 1998) and the peak breeding date is set as being October 1st. In horse, the mean gestation length is about 345 days in horse (Montfort *et al.* 1994) and is somewhat shorter, 285 days (range 277-293 days in a four 4-year period) on average in bison (Berger and Cunningham 1994).

Seasons of procurement in the assemblages

With these methods in hand, it is now possible to look at seasons of procurement in the assemblages. Obviously, more data are generally available for the most common taxa and the largest assemblages. Starting with the Denticulate Mousterian, seasonality data is provided for each occupation, including the stratigraphically less precise EJOP and EJO samples.

The Denticulate Mousterian (EGPF) assemblage

An isolated bison d_3 has been attributed to a fetus. This suggests that this calf died in winter or spring. An unspecified lower deciduous tooth of horse presents no evidence of wear. Death in spring or early summer is most likely, as the individual is younger than a modern four month-old individual and would be no more than a month old based on data provided by Levine (1979:332). Unfortunately, no other information on seasonality is available for this assemblage. Importantly, this is the only level of Saint-Césaire without reindeer antlers. More information should become available once the study of this level is completed.

The Châtelperronian? (EJOP inf) assemblage

More information on seasonality was gathered for this level. A d_2 and a d_3 or d_4, both of horse, are characterized by the absence of wear. It is uncertain whether these teeth come from the same individual. Using the age classification of Levine, these teeth are from a fetus or a foal that was less than two weeks old. This implies death in spring or early summer. Eight reindeer antlers also belong to this occupation. All are shed antlers from juveniles or adults (Table 54). Calves are absent. Three, and possibly five, of the antlers in Figure 43 might have been from females. These antlers were probably acquired in the snow-free season. An additional unshed burr is incomplete but has a circumference larger than 115 mm and is attributed to a male. Collecting of this specimen would have occurred in the snow-free season. A fetal bone from an unidentified mammal was also found in this occupation (Table 55). Assuming that this bone is from a reindeer, horse or bison, a group that comprises 95.3% of the identified faunal remains from the site, death is attributed to fall or winter. This interpretation would also hold if the specimen is from red deer or *Megaceros*.

layers	Unshed Antlers n	Unshed Antlers %	Shed Antlers n	Shed Antlers %	Total n	Total %
Evol Aurignacian (3)	3	75.0	1	25.0	4	100.0
Evol Aurignacian (4)	9	45.0	11	55.0	20	100.0
Aurignacian I (5)	47	67.1	23	32.9	70	100.0
Aurignacian 0? (6)	1	11.1	8	88.9	9	100.0
low density (7)	2	25.0	6	75.0	8	100.0
EJO (6-7)	*2*	*28.6*	*5*	*71.4*	*7*	*100.0*
Châtelperronian (8)	3	13.0	20	87.0	23	100.0
Châtelperronian? (9)	0	0.0	8	100.0	8	100.0
EJOP (8-9)	*2*	*10.5*	*17*	*89.5*	*19*	*100.0*
Total	69	41.1	99	58.9	168	100.0

Table 54. Proportions of shed and unshed antlers by level at Saint-Césaire. The mixed EJOP and EJO samples are shown in italic.

	horse	artiodactyls	mammal	total
	n	n	n	n
Evolved Aurignacian (3)			1	1
Evolved Aurignacian (4)	2			2
Aurignacian I (5)	12	1	9	22
EJO (6-7)	*2*		*1*	*3*
Châtelperronian (8)			7	7
Châtelperronian? (9)			1	1
EJOP (8-9)			*3*	*3*
Total	16	1	22	39

Table 55. Distribution of fetal bones by species and level.

The Châtelperronian (EJOP sup)

An unworn horse d_3 or d_4 corresponds to an animal that died at a very young age, well before four months based on a modern specimen, and, possibly, is a fetus or a neonate according to Levine's classification. Death in spring or early summer is most likely.

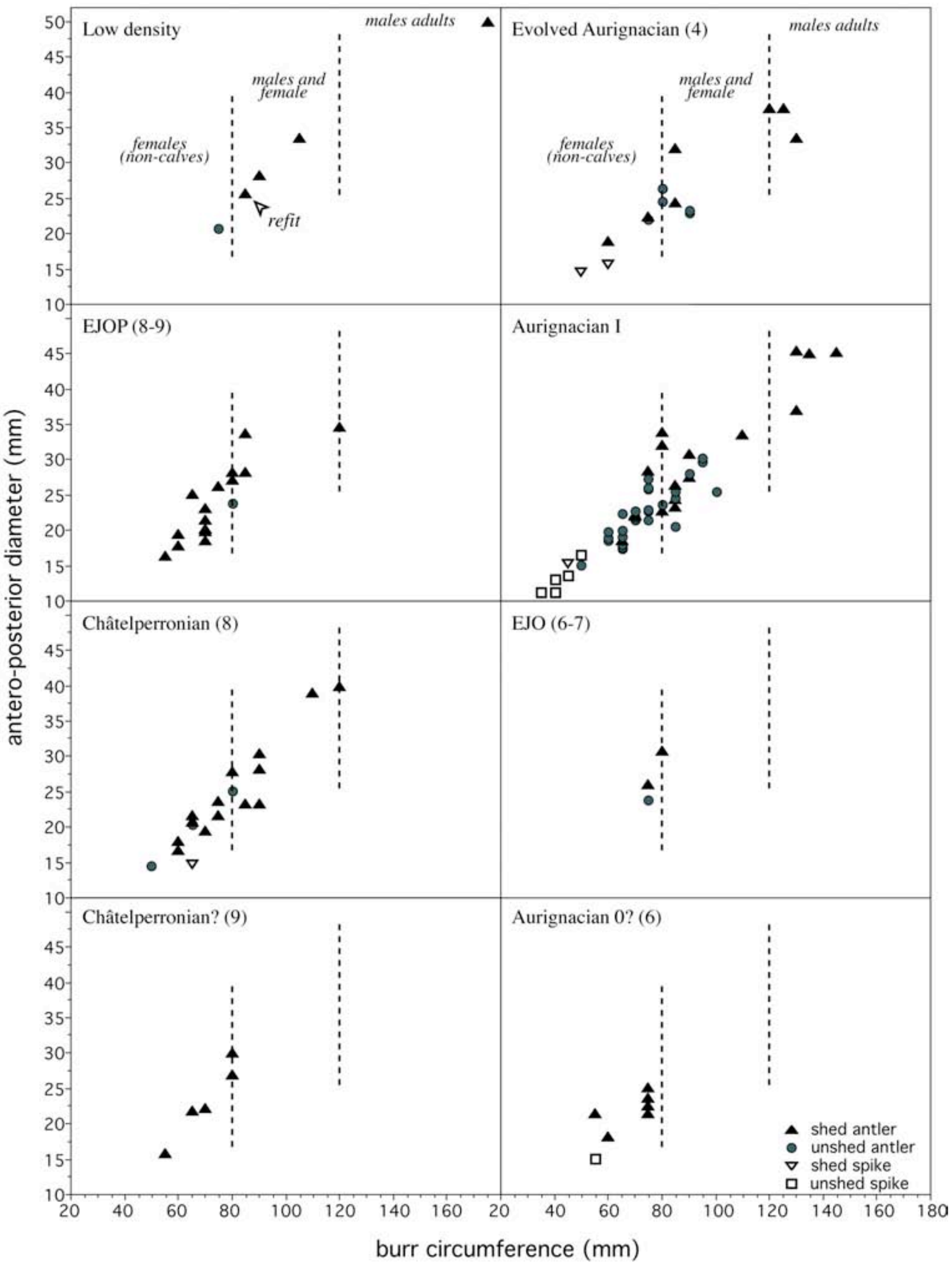

Figure 43. Distribution of antler burr circumference versus beam antero-posterior diameter for the Saint-Césaire reindeer antlers. Burr circumference <80 mm (left dashed line in the squares) are probably from females, whereas those >120 mm (right dashed line in the squares) are attributed to males (see text for details).

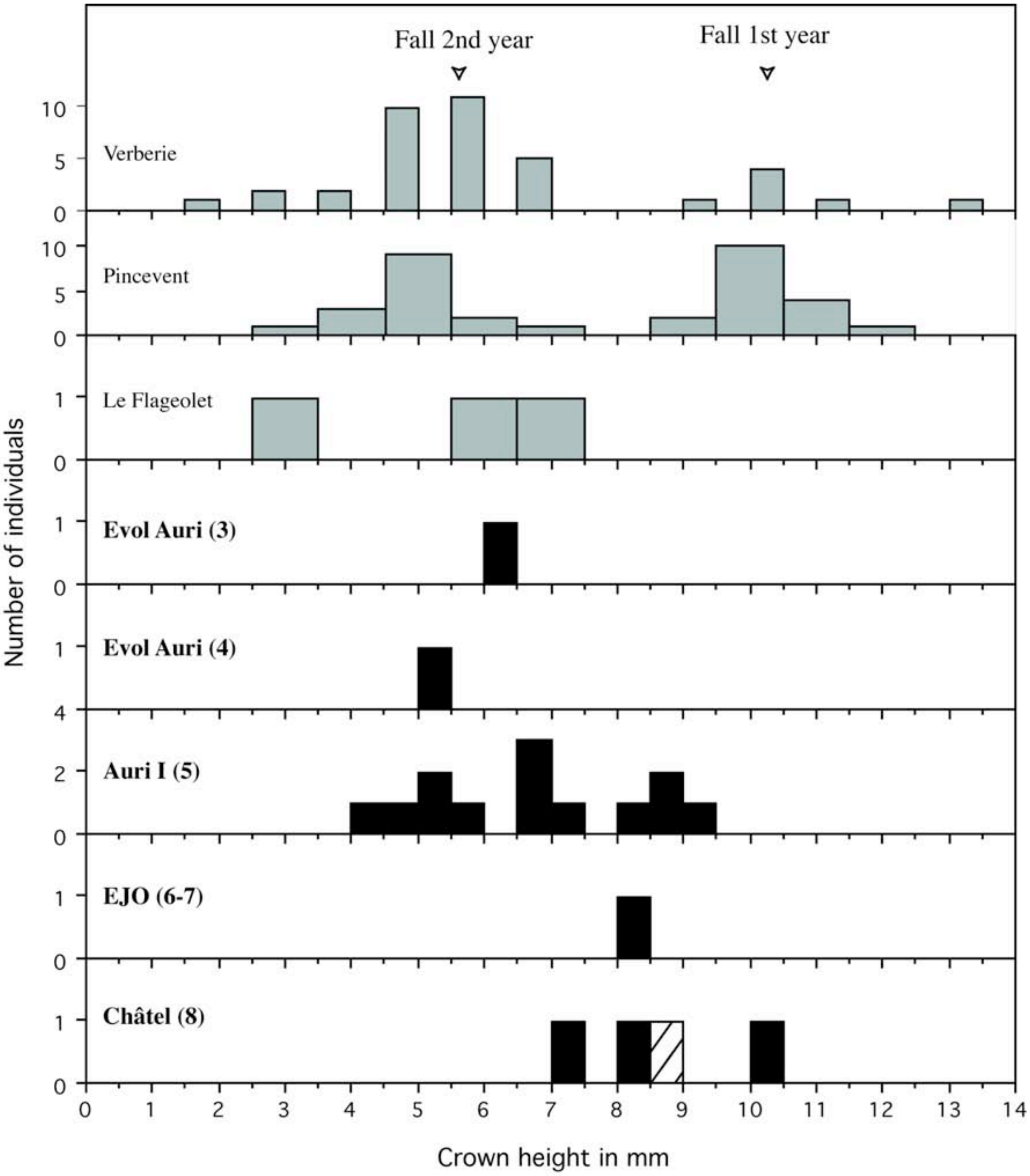

Figure 44. Crown height measurements for the reindeer d_4 of Saint-Césaire compared to Verberie and Pincevent (data from David and Enloe 1993).

Figure 45. Reindeer antlers from the Châtelperronian of Saint-Césaire.

Three reindeer teeth allow predictions of seasons of carcass acquisition. Two teeth, a d_4 and a d_3, are from individuals that were in their first and second winter or spring, respectively, when they were obtained. The third individual is represented by a d_2 and was procured in summer or fall. Comparisons with Verberie and Pincevent, two sites thought to have been occupied in fall (David and Enloe 1993), support these inferences (Figure 44). Several reindeer antlers are attributed to the Châtelperronian occupation. The majority (87%) of the specimens are shed antlers. A shed spike would have been picked up in the snow-free season. At least eight (one not shown) shed and two unshed antlers are from females, based on burr circumference. The shed antlers are interpreted to have been gathered between spring and fall, the unshed ones between fall and spring. In addition, two shed antlers (one not shown) are possibly from young males. These would have been acquired also in the snow-free season.

Two unworn d_4 can be used for determining the seasons of bison procurement. These isolated teeth may belong to the same individual. Both are small and may have been erupting. Based on the classification of Frison and Reher (1970, 1980), this calf was obtained in spring or summer. Two M_1 or M_2, visibly from two different individuals, do not show evidence of wear. According to the above age classification, these teeth are from calves or yearlings acquired in spring or summer.

Seven fetal bones are associated with this level. Unfortunately, none could be identified precisely. Assuming that these fetal bones are from bison, horse or reindeer, the size of these specimens is consistent with fall or winter procurement.

Three fish vertebrae from two different species (salmon and an unspecified cyprinid) were recovered in this level. These three vertebrae correspond to two, and perhaps, as many as three individuals, and were inspected for seasonality information. Akin to cementum deposition, fish vertebrae grow incremental structures that allow the assessment of season of capture by using the proportion of the last annulus that is present (Le Gall 2003). Because these three vertebrae have exactly the same three-dimensional coordinates, signifying that they were found together, and are the only fish remains of the whole site, a reasonable argument can be made that these represent a single event.

However, according to Le Gall (pers. comm. 2002), one vertebra is associated with an individual caught in fall, whereas a second vertebra is derived from an individual probably captured in spring. The third vertebra is broken but the last annulus is visible on the fragment. This individual died in winter. These contradictory results may be explained by a lack of preservation of the external annulus on some or all of the specimens, or they instead indicate that these vertebra were collected in different seasons. The former explanation is favored here. It is unknown whether these fish remains were brought to the site by humans or by other biological agents.

	Age Classes							
	I (foetus)	II (0-3)	III (3-5)	IV (5-12)	V (12-17)	VI (17-24)	V/VI (15-20)	total
Evol Aurignacian (3)					1		1	2
Evol Aurignacian (4)						2	1	3
Aurignacian I (5)				9		2	1	12
Aurignacian 0? (6)	1							1
EJO (6-7)				1				1
Châtelperronian (8)				1	1	1		3
EJOP (8-9)				1[1]				1
Total	1			12	2	5	3	23

[1] most probably from the Châtelperronian (EJOP sup) level based on stratigraphic information

Table 56. Distribution of reindeer teeth by age class for individuals younger than 24 months. The age classes are those defined in Table 52 and are indicated along with the age interval in months.

The EJOP sample (EJOP inf and EJOP sup)

A horse d$_2$ exhibits little wear, suggesting that specimen is from a near-term fetus or a foal that was no more than 1 or 2 months old. Procurement of this individual occurred in spring or early summer. Season of bison acquisition can be investigated using three teeth. The first two are unworn isolated d$_4$ and may have been erupting. In addition, an M$_2$ is unworn. If the age classification proposed by Frison and Reher is reliable, spring or summer are the most likely seasons of death for these individuals.

A reindeer d$_4$ is consistent with procurement in winter or spring. There is little doubt that this specimen was in fact associated with the Châtelperronian (EJOP sup) based on its stratigraphic position. Several antlers have been identified in the EJOP assemblage. Most are shed. Twelve shed (one not shown) antlers are attributed to females and would have been collected during the snow-free season. An unshed antler from a female or a young male was picked up from fall to spring. In addition, three fetal bones were recovered from this level. These could not be identified to taxon, but may reflect acquisition in fall or winter.

The low density (EJO inf) assemblage

Although this occupation is represented by a very small faunal assemblage, several reindeer antlers were found. Most are shed. A very large burr, undoubtedly from a prime male, is evidenced by the plot distribution in Figure 43. This male antler would have been collected in the snow-free season. Two unshed antlers (one not shown) would have belonged to as many females and were obtained in fall to spring. One of the shed antlers, shown by an arrow in Figure 43, was refitted with its pedicle (Figure 46). The animal apparently died shortly before shedding its antlers. The antler may have become isolated from the skull as a consequence of cultural activity, trampling or postdepositional processes. Based on the burr circumference, this individual was a female or a juvenile male. Acquisition would have taken place in late winter or spring.

The Aurignacian 0? (EJO sup) assemblage

A reindeer d_3 represents a near-term fetus or a neonate. This individual is associated with winter or spring procurement. Reindeer antlers are also relatively common in this assemblage. Those that could be measured are all shed female antlers. Collecting would have been occurred in spring, summer and fall, most likely during the snow-free period. An unshed spike antler, likely from a calf, was procured from fall to spring.

Figure 46. Saint-Césaire. A reindeer antler refitted with its pedicle from the low density (EJO inf) assemblage.

The EJO sample (EJO inf and EJO sup)

Two horse fetal bones, a humerus and a metapodial, were identified in the EJO sample. The humerus comes from an individual that is a 150-day-old and was obtained in fall (Table 57). Although incomplete, the metapodial seems to have been procured during the same season, as suggested by its small size, and may belong to the same individual. Fetal remains from an unspecified mammal were also recovered. Acquisition in the fall or winter is most likely. Shed specimens are best represented among the reindeer antlers of EJO. Only three burrs, two shed and one unshed, could be measured. Two and, perhaps, all three, were from females. Collecting of the shed antlers was most likely carried out during the snow-free season, while the unshed one could have been obtained at any time between fall and spring. Lastly, a reindeer d_3 indicates acquisition in winter or spring.

Level	Species, Side and Part	Length (mm)	Age at Death (days)	Month of Death	80% interval
Evol Auri (4)	horse left femur	19.9	94	17 September	12 Aug-22 Oct
Evol Auri (4)	horse right humerus	23.1	113	6 October	1 Sept-10 Nov
Early Auri (5)	horse right femur	60.0*	168	30 November	26 Oct-4 Jan
Early Auri (5)	horse right femur	27.8	112	5 October	31 Aug-9 Nov
Early Auri (5)	horse right tibia	21.8	110	3 October	29 Aug-7 Nov
Early Auri (5)	horse left metatarsal	255.0	336	17 May	13 April-21 June
Early Auri (5)	horse metatarsal	40.0*	152	14 November	10 Oct-19 Dec
Early Auri (5)	horse right humerus	28.0*	126	19 October	14 Sept-23 Nov
Early Auri (5)	horse left radius	39.2	144	6 November	2 Oct-11 Dec
Early Auri (5)	horse right radius	40.5	146	8 November	4 Oct-13 Dec
Early Auri (5)	horse metacarpal	15.7	114	7 October	2 Sept-11 Nov
Early Auri (5)	horse metapodial[1]	14.9	105-112	6 October	1 Sept-10 Nov
Early Auri (5)	artiodactyls right radius[2]	30.0*	133	11 December	12 Nov-10 Jan
EJO (6-7)	horse right femur	48.0*	150	12 November	8 Oct-17 Dec

[1] Calculated for the metatarsal and the metacarpal. The 80% confidence interval incorporates both age predictions.

[2] The developmental age of this specimen is calculated using the equation for bison. Unfortunately, no equation exists for the reindeer radius.

Table 57. Predictions of developmental age and 80% confidence interval for the fetal bones of Saint-Césaire. Asterisks denote extrapolated measurement.

The Aurignacian I (EJF) assemblage

Information on seasonality is rich and varied for this assemblage. A horse deciduous incisor is attributed to a near-term fetus or a newborn foal less than 2 months old who most probably died in spring or early summer. A slightly worn d_3 or d_4 is attributed to a second foal about 2-3 months old (Figure 47). In this case, death would have occurred in summer. A horse radius has no attached ulna. If the taxonomic identification is correct, a difficult task with this type of shaft fragment, it would have been procured in spring or summer.

Reindeer teeth show interesting patterns in terms of seasonality. Using Miller's (1974) plates, eleven juveniles, nine calves, and two yearlings, are interpreted to have died in winter/spring. However, two individuals lie near the "older" boundary of their respective age class and are close to overlapping with the following one. This means that these specimens are indicative of late winter to early summer acquisition. An additional reindeer would have been procured in summer or fall. Comparisons with Pincevent and Verberie give roughly similar results. It is clear from Figure 44 that the Aurignacian I occupation of Saint-Césaire deviates from the other assemblages, although some similarities are found with the Aurignacian assemblage of Le Flageolet (Enloe 1993). Interpreting crown height data for this occupation is complicated, because it is unclear whether the three modes observed are real ones. If they are, this indicates an intermittent occupation of the site throughout the annual cycle, excluding, perhaps, the summer. Otherwise, they are the product of one or two modes, with gaps resulting from small sample size. The former explanation appears more likely. An argument can be made that no summer or fall procurement of calves is recorded in this occupation. Based on tooth wear, calves would have been obtained in the snow-covered season. Yearlings were probably killed in fall, winter, and spring. Putting together the results of both age estimation methods leads to the conclusion that reindeer procurement occurred in fall, winter, and spring. However, procurement in summer does not appear to be supported by the data.

Numerous reindeer antlers were found associated in this assemblage. A notable change in the abundance of the various types of antlers is recorded here relative to the previous occupations. Whereas unshed antlers are scarce in the levels discussed so far, this type of antler is much more abundant in the Aurignacian I and subsequent occupations. This may indicate a slight shift in the season in which antlers were collected or a shift in the hunters' activities. A minimum of twenty-nine females are represented by four shed and twenty-five (four not shown) unshed antlers. The unshed antlers were obtained between fall and spring. In contrast, the shed specimens were procured anytime from spring to fall, most likely during the snow-free period. The four male antlers that are shed suggest collecting between spring and fall. In the sample, six spike antlers are from calves or yearlings. Except for one specimen, all are shed antlers probably picked up sometime in the snow-free period. The unshed spike antler would have been obtained from fall to spring.

Fetal bones are relatively common in this level. Twelve specimens, some of which are radii and humeri (Figure 48 and Figure 49), are attributed to horses, one is from an unspecified artiodactyl, most probably reindeer or bison, and nine are classified as unidentifiable. A minimum of seven individuals are present in the horse sample. Developmental age estimates indicate death in fall for all but one of the horse specimens. The exception is a left metatarsal from an individual who died in spring. A right artiodactyl radius was also recovered from this level. If this specimen is from a near-term bison fetus, death would have taken place in late fall or early winter. If, instead, this specimen is a reindeer fetus, procurement in winter is most probable. In this latter case, however, the inference is based on visual estimation, as no equation is available for predicting the developmental age of reindeer radii. Diaphyseal length of the other, unidentified, fetal remains would be consistent with procurement in fall or winter, assuming that these bones can be ascribed to one of the three most abundant taxa in the assemblages from Saint-Césaire.

Figure 47. A horse d_3 or d_4 (right) from the Aurignacian I of Saint-Césaire.

Figure 48. Fetal reindeer radii from the Saint-Césaire Aurignacian I occupation. Bar = 1cm.

The Evolved Aurignacian (EJM) assemblage

A horse mandibular series of slightly worn d_2-d_3-d_4 was identified in this occupation (Figure 50). This mandible belonged to a foal less than 4 months old and obtained in spring or summer, based on the wear pattern. The developmental age of a right humerus and a left femur, both from horse fetuses, indicate procurement in the fall. Three reindeer teeth are also indicative of fall procurement. A nearly complete mandible and a d_4 are consistent with winter/spring acquisition. An additional d_4 corresponds to death in late summer to early winter, a determination confirmed by comparison with Pincevent and Verberie. Many reindeer antlers were identified in the faunal material associated with this occupation. It is worth stressing that shed antlers are proportionately slightly more frequent in this occupation relative to the underlying Aurignacian I assemblage. Five (two not shown), and possibly six antlers can be attributed to adult

Figure 49. Saint-Césaire. Horse fetal humeri from the Aurignacian I (upper left) and the Evolved Aurignacian EJM (lower left). Provenience for the rightmost specimen is unknown. Bar = 1cm.

Figure 50. Saint-Césaire, Evolved Aurignacian (EJM). A mandibular series of horse deciduous teeth.

Figure 51. Two unshed male reindeer antlers from the Evolved Aurignacian (EJM) of Saint-Césaire.

males. Two of these are unshed, indicating that death was most likely in fall or early winter (Figure 51). These are the only two specimens of unshed male antlers identified at Saint-Césaire. The shed male antlers would have been collected in winter or anytime thereafter during the snow-free period. Three antlers are associated with females, based on their distribution in the scatter plot. Two shed specimens are evidence of possible acquisition in spring through fall, whereas the unshed one might have been procured from fall to spring. Because of their small size, two shed spikes were found in all likelihood some time during the snow-free period.

The Evolved Aurignacian (EJJ) assemblage

Reindeer antlers are not abundant in this small assemblage and include three unshed antlers and one shed antler. Only two burrs, both unshed, could be measured (not shown). One, and possibly, both antlers are from females. Procurement would have been carried out between fall and spring. A fragmented shed burr with an antero-posterior diameter of 46.3 mm is attributed to an adult male. It could have been collected in late fall, winter or in the snow-free season. A reindeer d_4 and a M_1-M_2-M_3 mandibular series are interpreted to have been acquired in late summer to early winter. An unworn d_4 from a bison comes from an animal procured in spring or summer. A single fetal bone of an unidentified mammal was observed but not discerned to species. Postulating that this bone is from one of the three major ungulates of the site, death in fall or winter is inferred.

Conclusions on seasonality at Saint-Césaire: Food procurement versus raw material collecting

Variation in birthing synchrony in the reindeer, bison, and horse was explored in the introduction to this chapter. The strengths and weaknesses of the aging methods used in this study, as well as their precision and accuracy, were reviewed and discussed and some analytical tools were developed in order to improve these methods. These tools were then used to explore seasonality in the faunal assemblages.

A first conclusion regarding Saint-Césaire is that it is characterized by multi-seasonal occupation. Clearly, body parts obtained at different periods of the annual cycle were brought back to the site. In general, evidence of food procurement in winter and spring is typical of most assemblages (Figure 52). Animal parts obtained for food in summer and fall were also transported to the site, but the data concerning these seasons are usually more ambiguous or limited to a single taxon. Collecting of raw material like shed antlers was most probably carried out during the snow-free season. Because food spoils quickly, the connection between procurement of food parts and transport to the site is probably relatively tight. However, this might not be the case for the shed antlers, which were collected for non-alimentary purposes. Therefore, it is unclear whether occupation in the snow-free season was significant at Saint-Césaire. The fact that there is little evidence of food acquisition during this period of the year suggests that it was probably not occupied extensively in the warm months of the annual cycle.

It should be noted in this discussion that the largest assemblages from Saint-Césaire tend to be more multi-seasonal than smaller ones. In many instances, this multi-seasonality appears to be an artifact of the poor precision of some of the methods used. Indeed, large assemblages are more likely to include specimens and species that can be aged than smaller ones; thereby increasing the chance of having all seasons represented. The obvious implication is that some seasons of procurement may, and probably do, go unidentified in small assemblages. To a lesser extent, this is probably true on occasion of larger assemblages as well. Another problem is that the less precise the aging method is, the more multi-seasonal the site appears to be. For instance, compared to methods based on tooth wear, crown height, shed antlers or fetal remains, precision decreases with unshed antlers, a part that may be procured at any time from fall to spring, and, less likely, in other seasons, as well. Therefore, assemblages with unshed antlers may look more multi-seasonal than they really are. The fact that excluding unshed antlers from the discussion results in only four assemblages having evidence of fall procurement, compared to nine when they are included, is a nice illustration of this problem. For these reasons, shed antlers are not included in Figure 52.

A second conclusion emerging from the analysis of the annual schedule at Saint-Césaire is that season of procurement varies with species. For instance, summer was apparently an unimportant season for reindeer procurement throughout the faunal sequence, although shed antlers were sometimes collected in that season. Rather, tooth wear and antlers show that the modal periods of procurement for this species were in winter and/or spring, and to a lesser extent, in fall as well. Evidence of fall procurement is strongest for the Aurignacian I and Evolved Aurignacian occupations. It is interesting to note that shed female antlers are frequent, sometimes numerous, in the samples.

The abundance of shed antlers in the assemblages also has an important behavioral implication: Saint-Césaire is likely to have been located relatively close to a reindeer calving ground. This might be confirmed by the scarcity of unshed male antlers in the assemblages. However, Binford (1978) has stressed that male antlers are often selected against in transport decisions, at least among modern caribou hunters. Moreover, it is not clear what were the criteria of shed antler selection with respect to size, shape, age, elasticity, etc. Therefore, understanding the causes responsible for the relative scarcity of shed male antlers in the occupations will need more work.

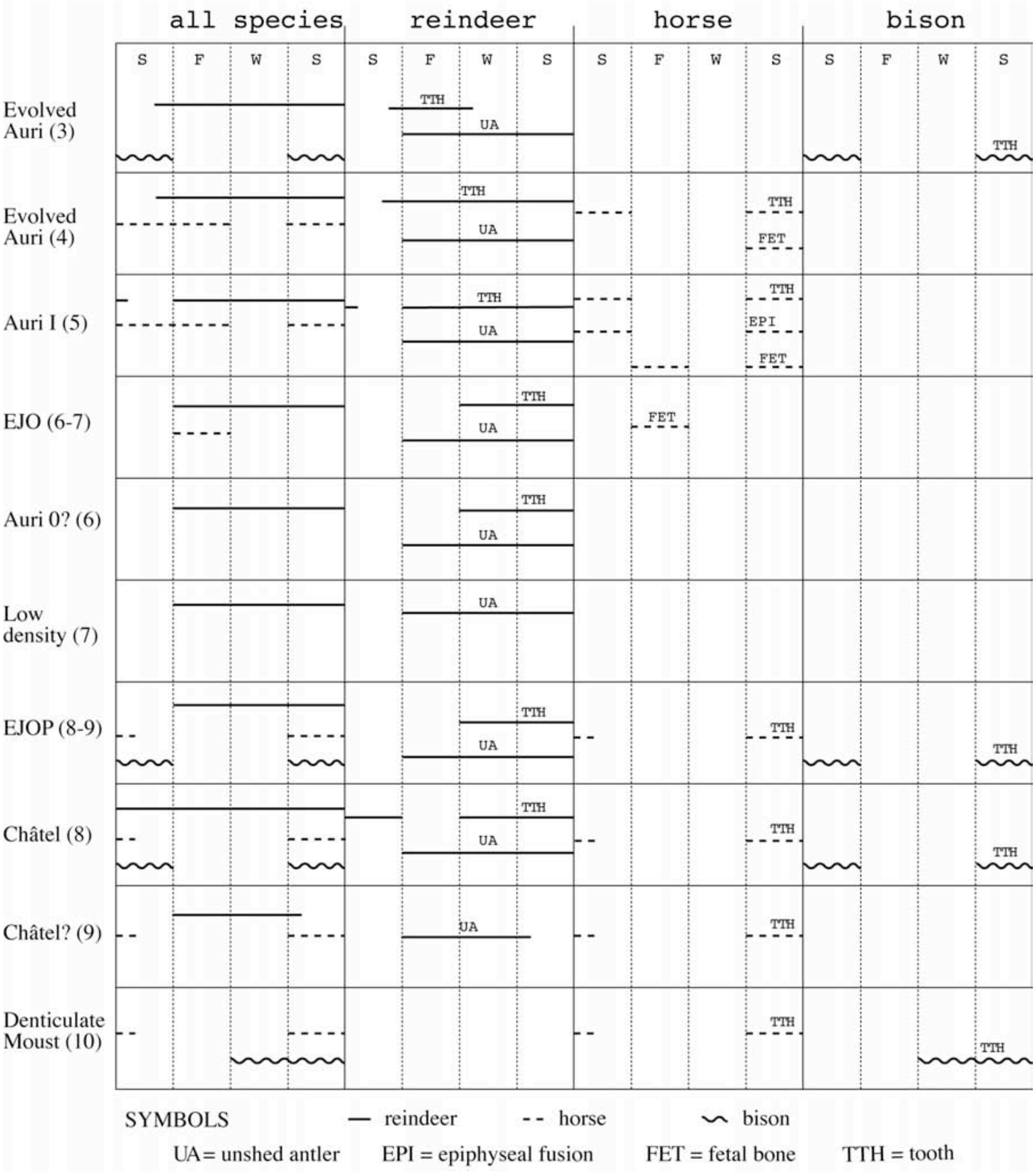

Figure 52. Summary of the seasonal evidence by species for the Saint-Césaire assemblages. The first column combines the information for all aging methods. Unidentified fetal remains and fishes are excluded from this figure.

Horses appear to be restricted to two or three modal seasons of procurement. Spring to early summer kills are documented in several occupations. In addition, all but one of the fetal remains found in the Aurignacian occupations are consistent with fall deaths. Fetal remains (from a horse?) were also found in the EJOP assemblages, including the Châtelperronian. These remains are similar in size to fetal bones identified as horse bones in the Aurignacian levels, which may indicate that they are from the same species, although this remains to be demonstrated. In contrast to reindeer, there is little evidence of winter kills in the cycle of horse procurement.

Unfortunately, data on bison are, somewhat more tenuous and more tentative. Tooth wear suggests that the seasonal schedule was comparable to the one documented for the horse. The EJOP assemblages include several calves interpreted to have been killed in spring/summer. A fetus in the Denticulate Mousterian is indicative of procurement in winter, whereas at least one calf was obtained in spring/summer in the most recent Aurignacian occupation. No support was found for fall procurement of this species in the samples.

Both stability and change are perceptible in the sequence of Saint-Césaire. The schedule of horse and, perhaps, bison procurement seems to have been remarkably consistent over the occupations. With respect to reindeer, the patterns tend also to be repeated throughout the sequence, with some exceptions. First, no antlers were associated with the Denticulate Mousterian. In this case, deviation from the other assemblages may not be meaningful if antlers were acquired for bone tool making, which seems possible, as this activity was not a normal component of the behavioral repertoire of the

Mousterians. However, antlers may have been collected for other purposes as well, for instance to be used as drying racks. Thus, the absence of antlers in the Denticulate Mousterian may signal a change in the range of activities carried out at the site. Second, the dominance of shed over unshed antlers in the EJOP and EJO assemblages is reversed inverted or nearly so in the Aurignacian I and Evolved Aurignacian levels. As argued, this may indicate a slight shift in the season of occupation or a broadening of the period in which the site was visited. Third, more convincing evidence of fall procurement exists in the most recent part of the Saint-Césaire sequence.

Procurement in winter and/or spring is documented in most, if not all, the assemblages, which fits the expectations for a valid application of the archaeological test elaborated in Chapter 3. Therefore, the assemblages from Saint-Césaire are relevant for testing the replacement model. Moreover, the relative stability of the seasonal patterns throughout the sequence may reflect some stability in site function, which also strengthens the relevance of Saint-Césaire for testing the replacement model. However, the fact that seasons of procurement other than winter and spring are also evidenced in the assemblages complicates the picture. This means that Saint-Césaire is not only a diachronic palimpsest of occupations accumulated over the years, but also consists of seasonal palimpsests, that is, an accumulation of seasonal occupations over a single annual cycle. Parts obtained in fall, for instance, are analytically superimposed over the patterns associated with winter and spring. It may be argued that this "behavioral overprinting" has been similar across levels. Importantly, the assemblages corresponding chronologically to the Middle to Upper Paleolithic transition, the Châtelperronian, the EJO occupations, and the Aurignacian I, are all characterized by similar seasonal patterns, excluding shed antlers. It is important to point out that seasons of procurement in the mixed EJOP assemblage are consistent with those observed in the Châtelperronian, from which the former is mostly derived. Again, it is reemphasized that procurement of animals may have increased during the fall season in the Aurignacian I and Evolved Aurignacian assemblages compared to previous occupations. However, this shift appears to be minor. In general, the annual cycle of procurement seems to have been relatively stable throughout the sequence at Saint-Césaire and shows no evidence of major shift in occupation. In this respect, the fact that this has been the case despite significant climatic changes is all the more interesting and will be the focus of the next chapters.

CHAPTER 7

TESTING THE RESOURCE DEPRESSION HYPOTHESIS ON THE SAINT-CÉSAIRE ASSEMBLAGES

In this Chapter, the Saint-Césaire assemblages are examined with respect to the archaeological implications derived from the replacement model (Chapter 3). Specifically, it was argued that a modern human demic expansion would result in: i) an increased transport of parts of low utility and/or high processing costs (e.g., phalanges, vertebrae), ii) marrow exploitation of low utility parts, iii) an increase in scavenging, iv) grease rendering of long bone epiphyses and other fatty parts, and the v) exploitation of low-ranked taxa. These lines of evidence will be used to determine whether the implications of the replacement model appear to be verified by the data from Saint-Césaire.

Decision-making and utility indices

As argued in the previous chapters, Saint-Césaire is unlikely to have been a kill site given its topographic setting. Rather, it was a locality to which parts were transported. However, none of the species examined so far are represented by complete skeletons. Excluding elements that are frequently burned, it is obvious that some parts were transported preferentially. What structured these transport decisions? Were parts selected for transport according to meat and fat? As a function of within-bone nutrients such as marrow and bone grease (Marshall and Pilgram 1991)? Is there evidence of fat maximization, a critical resource in nutritionally-stressed human populations? Was selection of bones for fuel carried out opportunistically at the shelter based on parts available or was it performed at the kill prior to transport?

Some of these issues on decision-making can be explored by plotting the abundance of skeletal parts versus utility indices (e.g., Binford 1978; Metcalfe and Jones 1988; Emerson 1993; Brink 1997; Outram and Rowley-Conwy 1998). Utility indices are analytical tools that estimate the food value of individual body parts in a species, generally in terms of meat, fat, marrow, bone grease, or a combination of these. These indices are most often based on weight (in g) or calories. In many cases, the values derived for each part are then scaled to the highest value obtained. When this procedure has been followed, indices are said to be *standardized* and are denoted by a capital "s."

In these models, *bone grease* generally refers to the lipids found in the bone tissue (excluding marrow). Some (e.g., Binford 1978) distinguishes yellow from white grease. In caribou, yellow grease is obtained from ribs, mandible, and vertebrae, and is low in oleic acid (a fatty acid that has a low melting point, a key factor in using and storing fat). The Nunamiut do not consider yellow grease very desirable. In contrast, white grease, found in long bone epiphyses, is high in oleic acid and is prized by the Nunamiut (Binford 1978). *Marrow* is found within the medullary cavity of some bones, especially long bone shafts, and has a high fat content. Small amounts of marrow are also found in the phalanges, talus, mandible, scapula, calcaneum, and innominates. *Meat* consists of the usable muscle mass and often includes non-skeletal fat.

Binford (1978) combined the index for meat, marrow, and white and yellow grease into a single index called the GUI or the General Utility Index. Because Binford noted that some parts of low food utility, called "riders" (e.g., patella), were transported simply because of their proximity to parts with high food value (e.g., femur), he modified his index in order to take this effect into account. This became known as the Modified General Utility Index or MGUI. However, problems were found in the calculation of these indices (Chase 1985), and a more simply derived model, the Food Utility Index or FUI, has been offered as an alternative (Metcalfe and Jones 1988). The FUI model will be used here.

Were low utility parts transported to Saint-Césaire?

The initial abundance of innominates, vertebrae, malleolus, carpals, and tarsals cannot be estimated with confidence at Saint-Césaire. As a result, these parts were excluded from the correlations. Ribs were also excluded from the analysis, as a result of the uncertainty clouding the interpretation of their abundance.

Different categories of parts might have been transported for different reasons. As a result, correlations between the utility and the abundance of skeletal parts in the Saint-Césaire assemblages are examined for all elements together and for long bones only. Importantly, abundance of long bones is assessed in this study based on shaft portions. In cases where utility values are provided for long bone halves only (e.g., Outram and Rowley-Conwy 1998), the average of the published values for the proximal and distal parts is used. Because what concerns us here is the ranking of skeletal parts with respect to utility, Spearman's rho correlations (r_s) are used instead of chi-square comparisons. This is because we are not looking for absolute similarity between the assemblages, as minor changes might have occurred as a result of slight shifts in seasonal occupation, activities carried out at the site, and a host of other factors, but rather testing for consistency in decision-making.

Element	*Wildebeest*	*Reindeer*	*Horse*	*Element*	*Wildebeest*	*Reindeer*	*Horse*
atlas (AT1)	0.55	0.47	0.51	innominate (AC1)	0.64	0.64	0.65
axis (AX2)	0.41	0.42	0.37	femur prox (FE2)	0.51	0.52	0.30
cervical vert. (CE1)	0.52	0.45	*0.50*	*femur shaft (FE4)*	*1.16*	*1.15*	*1.09*
thoracic vert. (TH1)	0.38	0.38	0.32	femur distal (FE6)	0.38	0.32	0.30
lumbar vert. (LU1)	0.58	0.49	0.48	patella (PA1)	0.44	0.57	0.40
sacrum (SC1)	0.35	0.37	0.36	tibia prox (TI1)	0.42	0.35	0.30
rib (RI3)	1.02	0.96	0.50	*tibia shaft(TI3)*	*1.12*	*1.13*	*1.07*
scapula (SP1)	*1.02*	*1.01*	1.03	tibia distal (TI5)	0.48	0.73	0.45
humerus prox (HU1)	0.32	0.26	0.23	fibula (MAL/FIB)	0.75	0.68	0.59
humerus shaft (HU3)	*1.10*	*1.12*	*1.10*	talus (AS1)	0.67	0.68	0.67
humerus distal (HU5)	0.51	0.48	0.36	calcaneum (CA2)	0.92	0.94	0.69
radio-ulna prox (RA1)	0.51	0.53	0.37	cubo-navicular (NC1)	0.59	0.56	0.71
radio-ulna shaft (RA3)	*1.07*	*1.09*	*1.08*	greater cuneiform (cun)	0.79	0.71	0.60
radio-ulna distal (RA5)	0.47	0.49	0.42	metatarsal prox (MR1)	0.83	0.90	0.59
scaphoid (SCA)	0.76	0.70	*0.62*	*metatarsal sh. (MR3)*	*1.14*	*1.08*	*1.10*
lunate (LUN)	0.70	0.67	0.57	metatarsal dist. (MR5)	0.54	0.41	0.58
magnum (CAP)	0.67	0.69	*0.62*	*phalanx 1 (P1-2)*	*1.02*	*0.92*	*1.02*
hamatum (HAM)	0.77	0.72	*0.67*	*phalanx 2 (P2-2)*	*0.56*	*0.72*	*0.59*
metacarpal prox (MC1)	0.72	0.92	0.55	*phalanx 3 (P3-1)*	*0.53*	*0.48*	*0.57*
metacarpal sh. (MC3)	*1.15*	*1.10*	*1.10*	*skull (teeth)*	.	.	.
metacarpal dist. (MC5)	0.56	0.48	*0.56*	*mandible (teeth)*	.	.	.

Table 58. Selected scan sites for wildebeest, horse, and reindeer (data from Lam *et al.* 1999). Skeletal parts used in this study are shown in italic.

In order to avoid potential problems of differential preservation, it was decided to focus here only on those elements that have similar bone "density." These elements include long bone shafts, the skull, mandible, scapula, and phalanges (Table 58). The only exception to this rule are the second and third phalanges. For reindeer and horse, density measurements given by Lam *et al.* (1999) are used. Although values for bison are available (Kreutzer 1992), data derived for another bovid (Lam *et al.* 1999), the wildebeest (*Connachaetes taurinus*), are adopted instead. This is because the density data generated by Kreutzer may not be completely accurate, as medullary cavities were not excluded from the calculations (Lam *et al.* 2003). Characteristically, the inclusion of the medullary cavity in the calculations depresses the density values for the marrow bones.

The use of elements with similar density should help to counter concerns related to differential preservation, a pervasive problem in the application of these models to archaeological materials (Lyman 1984, 1992; Grayson 1989).

In the following pages, we will consider each line of evidence presented in Chapter 4. Understanding transport decisions in relation to skeletal part utility will contribute to the investigation of resource depression at Saint-Césaire and will provide a broader framework for the interpretation of the evolution of the subsistence system during the Middle to Upper Paleolithic transition in southwestern France.

Selection of bison skeletal parts for transport

Data on body part representation has been presented in Chapter 4. These data are explored here in relation to utility models. Evidence for transport of bison, horse, and reindeer skeletal parts at Saint-Césaire are reviewed in this perspective.

Inter-assemblage correlations of the rank order of skeletal parts are presented in Table 59 for the Saint-Césaire bison samples. Except for the cell assessing the relationship between the two smallest bison samples (Châtelperronian? and

Aurignacian I), all the assemblages are significantly correlated with each other. This suggests that bison skeletal parts were given similar rank orders in transport throughout the Saint-Césaire sequence. Contrasting abundance of skeletal elements with various models may highlight which dimension of utility, for instance meat, grease, marrow, potential as fuel, or a combination of these, (was or) were favored in these decisions. However, isolating these factors is not always easy, as many of the utility models discussed below are also strongly correlated with each other.

	Inter-Assemblage Correlations: Bison			
	Auri I (5)	Châtel (8)	Châtel? (9)	Moust (10)
Aurignacian I (5)	-	**<.02**	<.11	**<.03**
Châtelperronian (8)	.858	-	**<.05**	**<.02**
Châtelperronian? (9)	.575	.725	-	**<.02**
Denticulate Mousterian (10)	.817	.904	.883	-

Table 59. Spearman's rho correlations (cells below the dashes) between bison assemblages at Saint-Césaire. *p* values (cells above the dashes) ≤ 0.05 are shown in bold.

Decisions regarding the transport of bison skeletal parts can be evaluated by looking at the association between their respective abundance and the (S)AVGFUI model for whole bones developed by Emerson (1993) for North American bison. This model is an average (AVG in the acronym) of four bisons of various age and sex classes and it measures the total amount of tissue minus their associated dry bone weight. "S" means that the values have been standardized. This model is based on calories and was generated following the FUI model protocol (Metcalfe and Jones 1988). Abbreviations for the skeletal elements displayed in the utility diagrams are provided in Table 60.

Element	*Abbreviation*	*Element*	*Abbreviation*
skull	sk	femur	fem
mandible	man	tibia	tib
scapula	scp	metatarsal	mt
humerus	hum	phalanx 1	pha1
radio-ulna	rul	phalanx 2	pha2
metacarpal	mc	phalanx 3	pha3

Table 60. Abbreviations for the skeletal elements displayed in the utility diagrams.

At Saint-Césaire, the abundance of skeletal parts in the four largest bison assemblages correlates positively with the (S)AVGFUI model save for the femur (Table 61 and Figure 53). We have already seen that refit data indicate that the femur is possibly under-identified relative to other parts and that this bias is probably magnified in large ungulates. Therefore, the anomalous position of the femur with respect to other elements may be analytical rather than real. However, differential identification alone may not explain fully the very low proportion of femurs in the assemblages. Nevertheless, in order to evaluate the effect of this potential source of bias, correlation coefficients were recalculated excluding the femur.

Abundance of Bison Skeletal Parts Versus the (S)AVGFUI and Total Fat Models												
	(S)AVGFUI						Total Fat Model					
	all elements		all minus femur		long bones only		all elements		all minus femur		long bones only	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Aurignacian I (5)	.754	**<.04**	.768	**<.05**	.771	<.09	.863	**<.03**	.830	**<.05**	.771	<.09
Châtelperronian (8)	.754	**<.04**	.827	**<.03**	.829	<.07	.851	**<.03**	.902	**<.03**	.829	<.07
Châtelperronian? (9)	.367	<.30	.655	<.09	.043	<.93	.345	<.37	.625	<.13	.043	<.93
Dent Mousterian (10)	.562	<.12	.738	<.06	.514	<.26	.685	<.08	.875	**<.04**	.514	<.26

Table 61. Abundance of bison skeletal parts in various assemblages from Saint-Césaire versus the (S)AVGFUI and Total Fat models (Emerson 1993:142, Figure 8.2b and p. 143, Figure 8.3b, respectively). Ribs and elements that are frequently burned in the Saint-Césaire sequence are excluded (see text for explications). $p \leq 0.05$ are shown in bold.

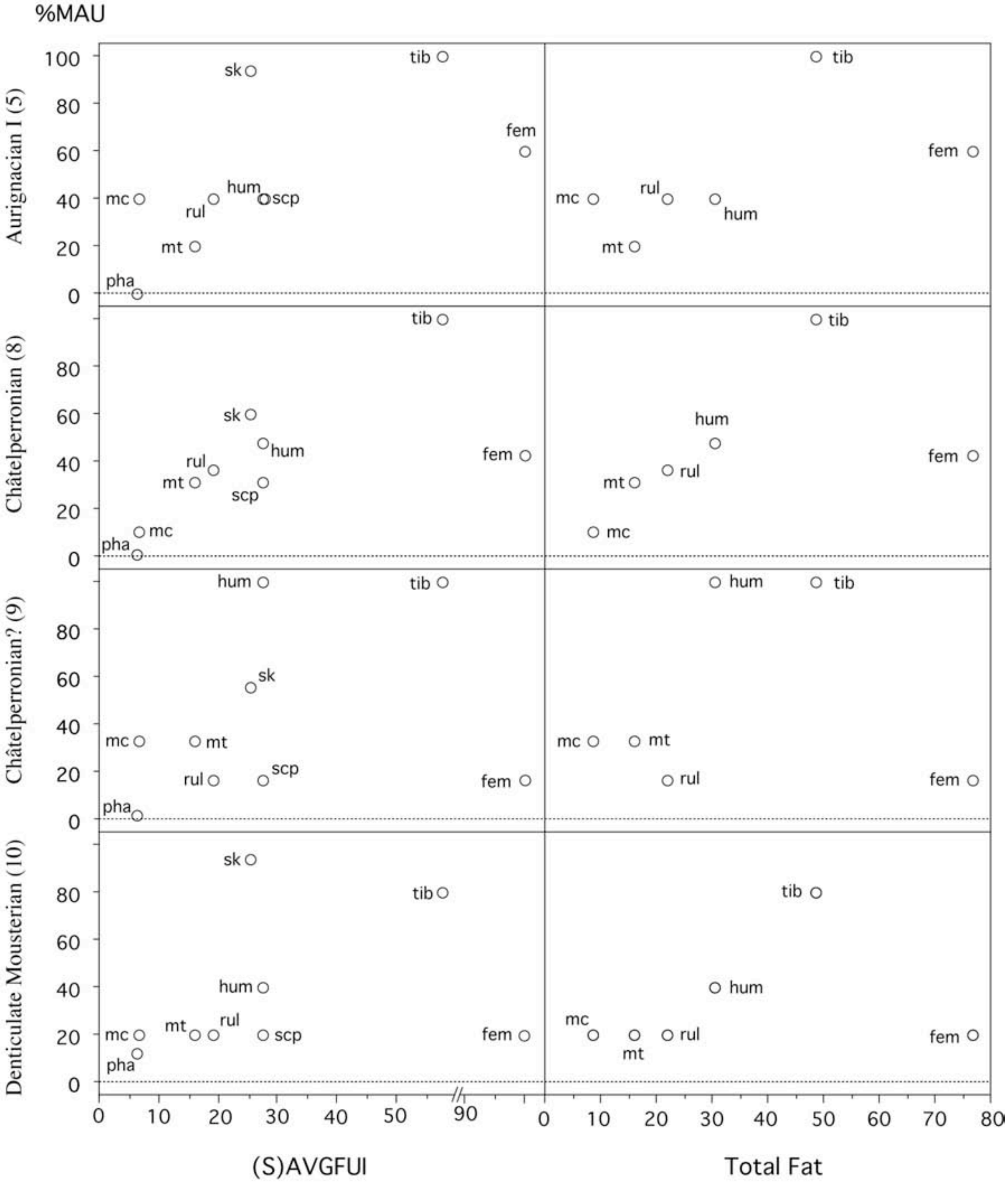

Figure 53. Relationship between the abundance of bison skeletal parts in four assemblages from Saint-Césaire and the (S)AVGFUI and Total Fat models (Emerson 1993:142, Figure 8.2b and p. 143, Figure 8.3b, respectively).

Removing the femur from the samples increases the correlation in all four assemblages. On the other hand, when the sample is limited just to long bones (including the femur), the correlation coefficients decrease in the Denticulate Mousterian and Châtelperronian? samples, but remain high in the Châtelperronian and Aurignacian I samples. None of these correlations are significant, although those for the Denticulate Mousterian and Châtelperronian? samples are close to reaching significance. The decreased statistical significance of the long bone-only sample compared to the correlations obtained for all the elements is possibly explained by the under-identification of the femur and the small number of elements included.

Relationships between abundance of bison skeletal parts and fat utility are displayed in Figure 53. The utility model used is the standardized Total Fat Model ([S]MAVGTF) for whole bones developed by Emerson (1993) for North American bison. In this model, "M" means that values are modified to account for the effect of riders. The Total Fat model is more narrowly defined than the FUI model and focuses only on skeletal, intramuscular, and dissectible fat utility (excluding stomach and intestinal deposits), and is modified to account for the effects of riders (Emerson 1993:140). This model is important as it measures a dimension said to be critical in populations under stress (Speth and Spielmann 1983; Speth 1990).

In general, skeletal elements appear to correlate with fat utility in the Saint-Césaire assemblages (Table 61). Correlations are high, positive, and significant in the Châtelperronian and Aurignacian I assemblages, and close to reaching statistical significance in the Denticulate Mousterian. However, abundance of skeletal parts in the Châtelperronian? assemblage is not significantly correlated with fat. Excluding the femur increases the correlation in three of the four assemblages but decreases it slightly in the Aurignacian I sample. Results for the long bone-only sample replicate exactly those obtained with the (S)AVGFUI model, which shows that both indices rank long bones identically.

In addition to the previous indices, Emerson (1993) produced a (S)MAVGMAR index focusing on the caloric yield of bison marrow. This marrow index is standardized and modified to account for the effect of riders.

Abundance of Bison Skeletal Parts Versus the Marrow and Skeletal Fat Models

	Marrow						Skeletal Fat					
	all elements		all minus femur		long bones only		all elements		all minus femur		long bones only	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Aurignacian I (5)	.821	**<.03**	.732	<.08	.829	<.07	.857	**<.03**	.821	**<.05**	.771	<.09
Châtelperronian (8)	.970	**<.02**	.991	**<.02**	.943	**<.04**	.923	**<.02**	.991	**<.02**	.829	<.07
Châtelperronian? (9)	.560	<.14	.759	<.07	.271	<.55	.393	<.30	.688	<.10	.043	<.93
Dent Mousterian (10)	.810	**<.04**	.911	**<.03**	.714	<.12	.714	<.06	.911	**<.03**	.514	<.26

Table 62. Correlations between the abundance of bison skeletal parts in various assemblages from Saint-Césaire and the (S)MAVGMAR (marrow) and (S)MAVGSKF (skeletal fat) models (Emerson 1993:144, Figure 8.5a and p. 143, Figure 8.4a, respectively). $p \leq 0.05$ are shown in bold.

At Saint-Césaire, all of the bison assemblages correlate with the marrow index, except that from the Châtelperronian? occupation (Figure 54). Correlation coefficients are very high in three of the four assemblages (Table 62). *All* the assemblages are significantly correlated with marrow or close to attaining statistical significance when the femur is excluded from the correlations. Correlations remain strong in the samples limited to long bones save for the Châtelperronian? occupation. In general, correlation coefficients are improved with the (S)MAVGMAR model in comparison with the previous two indices. This suggests that marrow was more highly ranked

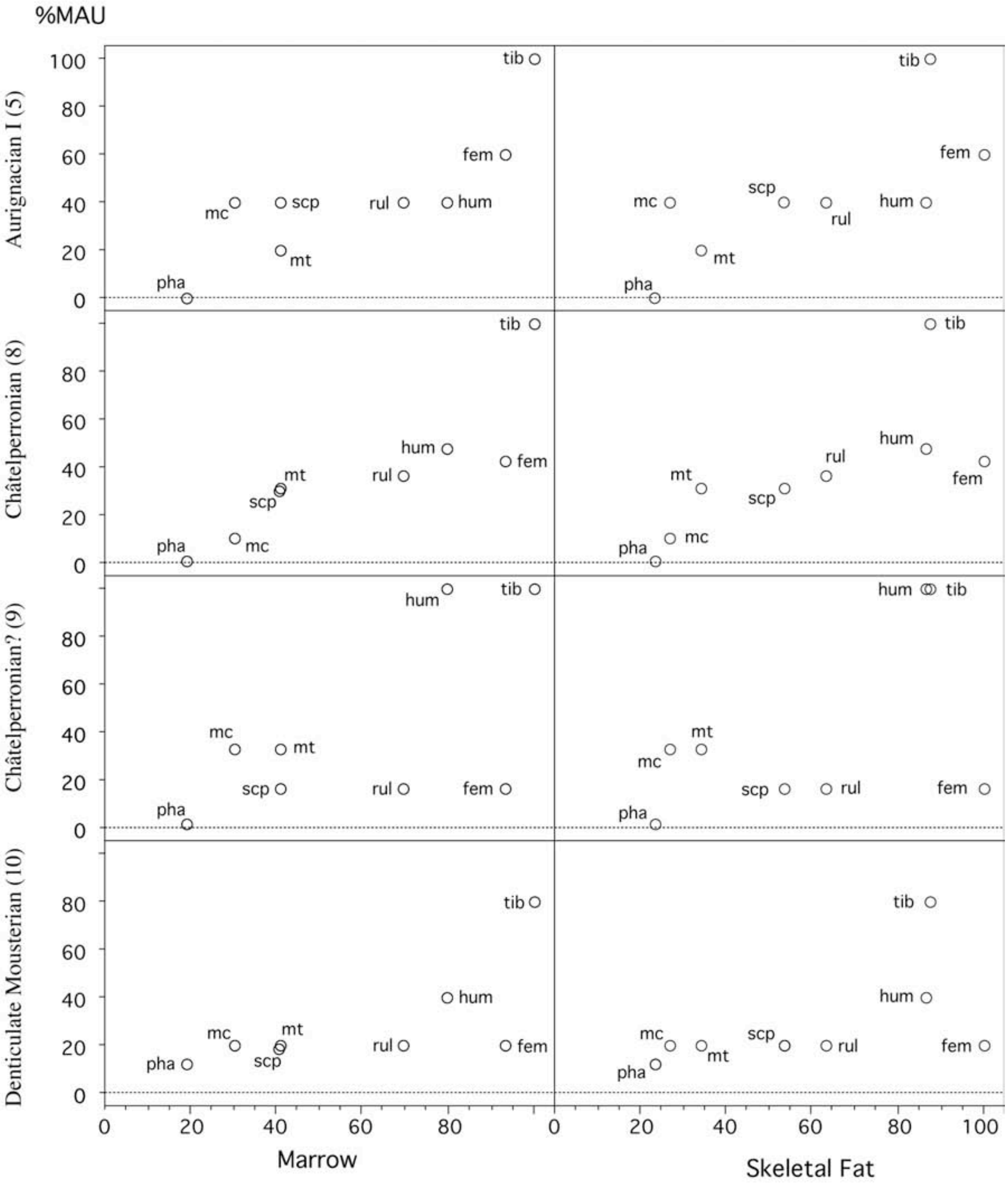

Figure 54. Relationship between abundance of bison skeletal parts in four assemblages from Saint-Césaire and the (S)MAVGMAR (Marrow) and (S)MAVGSKF (skeletal fat) models (Emerson 1993:144, Figure 8.5a and p. 143, Figure 8.4a, respectively).

in transport decision-making than were either fat alone or the total quantity of tissue and fat-related products.

A fourth model focusing on skeletal fat, the (S)MAVGSKF index, has been presented by Emerson (1993). This index partly replicates the previous model, as it includes marrow along with the lipids found in the bone spongy parts (e.g., epiphyses). Nonetheless, the skeletal fat model may help evaluating whether parts were selected for transport based on within-bone nutrients.

Correlations between skeletal fat values and the bison assemblages from Saint-Césaire give results comparable to those obtained with the marrow model. However, the correlation coefficients are slightly lower in general, especially with respect to long bones (Table 62 and Figure 54), than with the marrow model, which suggests that including skeletal fat may result in a fit with the archaeological assemblages that is not as strong than that obtained for marrow alone. This might be taken to indicate that skeletal fat is not the most parsimonious factor for describing abundance of skeletal parts in the assemblages.

However, is the skeletal fat model an appropriate scale for measuring grease utility? Ethnoarchaeological data might help answering this question.

Binford (1978) collected information on bone grease rendering on two occasions during his study of the Nunamiut. First, a woman was asked: “to save bones exactly as she would if planning the manufacture of white bone grease” (Binford 1978:35). This episode occurred in summer. Two women were asked to do the same in spring 1971. Although there were notable differences in the pool of parts available in each of the two episodes, Binford (1978:36-37) found a very strong linear relationship[8] in the types and proportions of skeletal parts selected by these women.

This result implies that ranking of skeletal elements relative to grease rendering might be relatively consistent across behavioral contexts. This may also include, perhaps, periods when animals are nutritionally stressed, given that bone grease is suspected to be rarely depleted, even in this type of situation (Brink 1997). The Nunamiut data may help determine whether the bison assemblages from Saint-Césaire are correlated with bone grease. Similarity in skeletal morphology, marrow weight (Brink 1997), and bone density (Lam *et al.* 2003) suggest that the caribou data on grease rendering can be reasonably extended to bison.

For Binford (1978), high percentage of oleic acid (used as a proxy of grease quality), low processing time, and part volume are what the Nunamiut try to maximize when selecting bones for grease rendering. It is important to note in this discussion that whereas bone grease weight is usually highest in the proximal limbs, oleic acid tends to increase distally (Binford 1978). Therefore, these two factors are likely to produce very different rank orders of parts.

In his study of bison leg fat, Brink (1997) suggested that bone grease weight alone is a more useful gauge of grease utility than Binford's measure of percentage of oleic acid. However, this last factor should not be dismissed too quickly. When percentages of parts selected by the Nunamiut for bone grease manufacture are plotted against the mean grease weight in bison legs (Brink 1997), two linear relationships, not one, can be distinguished (Figure 55). This means that proportions of parts selected by the Nunamiut

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[8] The correlation is not provided by Binford, but was calculated to be $r_s = .922$, $p \leq 0.001$ after exclusion of the metacarpal not initially present in both episodes.

cannot be described accurately by bone grease weight alone, although this dimension appears to be the most important factor of selection, as stressed by Brink. Equally important in Figure 55 is the finding that skeletal parts are ranked similarly in both selection episodes. In agreement with Binford's intuition, parts that are selected more often than expected based on total fat content are the metapodials and distal tibia, exactly those elements with the highest percentage of oleic acid. This suggests that oleic acid is possibly also a significant factor in the Nunamiut selection of bones for grease rendering.

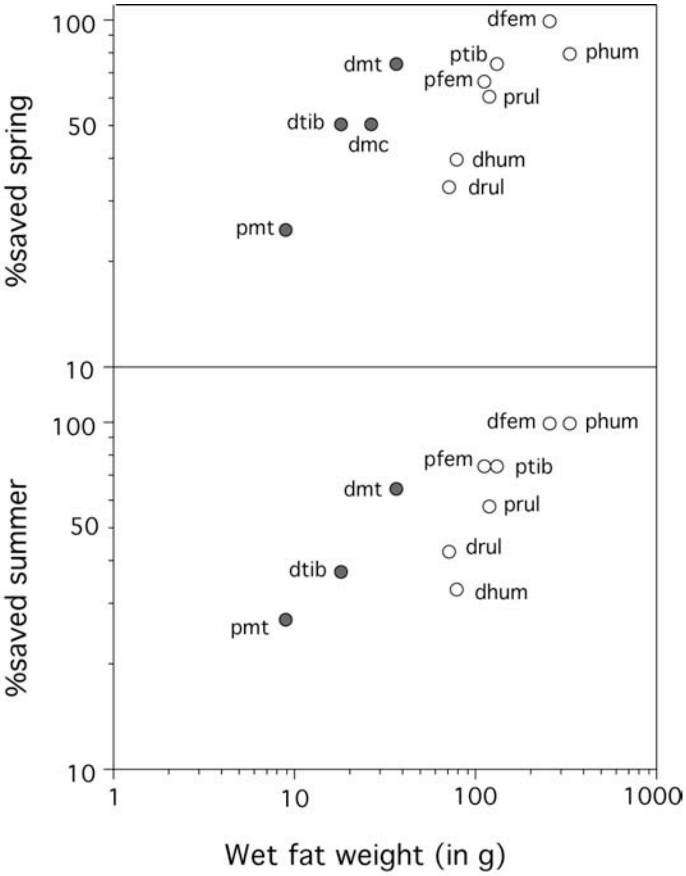

Figure 55. Relationship between proportions of parts selected by the Nunamiut for bone grease manufacture in two episodes (Binford 1978:36, Table 1.13, columns 3 and 6) and mean fat weight in bison long bones (Brink 1997:263, Table 3). Both axes are in $\log_{10}$. Shaded circles represent elements that do not fall on the same line as the others. The "p" in front of the element name denotes proximal, whereas the "d" stands for distal.

It might be useful to contrast the Nunamiut summer and spring episodes of part selection for grease rendering with the abundance of bison skeletal parts in the Saint-Césaire assemblages. Both episodes are used here due to a lack of precise information on the season of bison procurement in the assemblages. However, this has little impact on the discussion, as both episodes are highly correlated, as emphasized above. The Nunamiut values correspond to the proportion, by element, of specimens selected for grease rendering. As usual, ribs and elements that are commonly burned at Saint-Césaire were excluded, as well as the metacarpal not present in the ethnoarchaeological sample.

It is important to note that the Nunamiut models of part selection can also be conceived as approximating a *fuel index*. This is because skeletal parts can be expected to be selected for fuel as a function of their grease utility. The Nunamiut models can therefore help to determine if bones were transported to Saint-Césaire based on their potential as fuel.

Abundance of Bison Skeletal Parts Versus the Spring and Summer Episodes of Grease Rendering

	Spring						Summer					
	all elements		all minus femur		long bones only		all elements		all minus femur		long bones only	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Aurignacian I (5)	.821	**<.03**	.768	≤.06	.886	**<.05**	.705	<.09	.643	<.16	.625	<.22
Châtelperronian (8)	.827	**<.03**	.848	**<.04**	.771	<.09	.830	**<.05**	.900	**<.05**	.600	<.24
Châtelperronian? (9)	.494	<.20	.812	**<.05**	.043	<.93	.536	<.19	.857	<.06	.050	<.93
Dent Mousterian (10)	.685	<.08	.875	**<.04**	.514	<.26	.625	<.13	.843	<.06	.300	<.55

Table 63. Correlations between proportions of parts selected in spring and summer by the Nunamiut for grease rendering (Binford 1978:36, Table 1.13, columns 3 and 6) and the abundance of bison skeletal parts in various assemblages from Saint-Césaire. $p \leq 0.05$ are shown in bold.

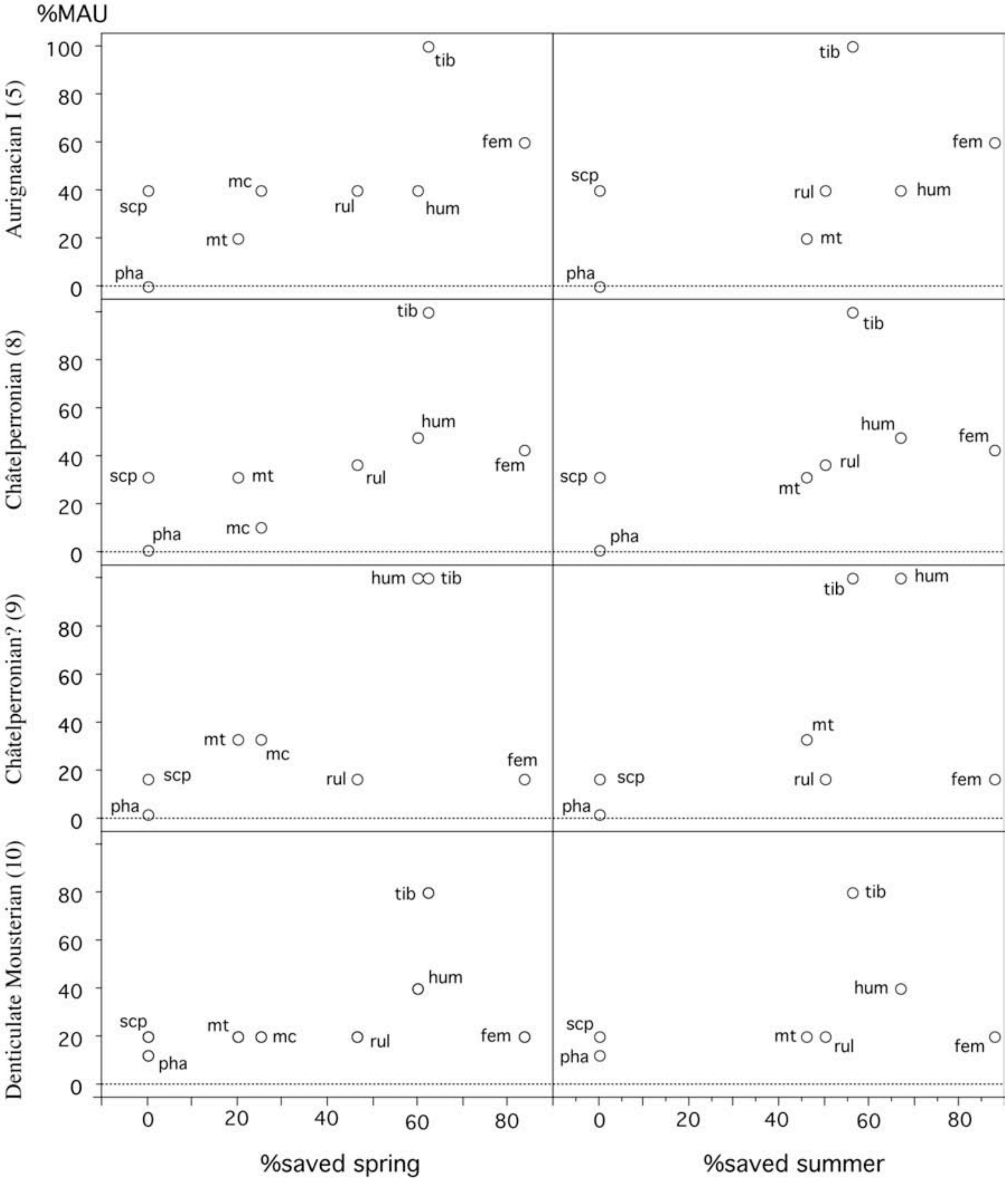

Figure 56. Relationships between the abundance of bison skeletal parts in four assemblages from Saint-Césaire and the proportions of reindeer parts selected in spring and summer by the Nunamiut for grease rendering. Nunamiut data from Binford 1978:36, Table 1.13, columns 3 and 6.

Among the four bison assemblages, two, the Châtelperronian and Aurignacian I, are positively and significantly correlated with the spring episodes of part selection (Table 63 and Figure 56). However, the Denticulate Mousterian occupation is close to being significantly correlated. With respect to the summer episode, only the correlation for the Châtelperronian reaches statistical significance. Exclusion of the femur increases the correlation coefficients in all cases, except for the Aurignacian I assemblage. In contrast, correlations are rarely significant when the samples exclude parts other than long bones. The Aurignacian I is an exception to this trend as the long bone-only sample is statistically correlated with the Nunamiut spring episode of part selection.

Correlations between the Nunamiut episodes of part selection and the bison assemblages from Saint-Césaire give results comparable to those obtained with the marrow model. However, the correlation coefficients tend to be lower in general, especially in the long bone-only sample, which suggests that including bone grease seems to decrease the fit with the archaeological assemblages from those obtained for marrow alone. This might be taken to indicate that grease or fuel utility is not the most parsimonious factor for describing abundance of bison skeletal parts in the assemblages.

Of all the models with which the bison assemblages have been compared, the marrow and skeletal fat utility models appear to give slightly higher correlation values than the other models. Therefore, marrow and skeletal fat might be the best indices for predicting bison skeletal part abundance in the occupations. The slightly higher correlations obtained with the marrow model suggest that marrow might have been the primary dimension along which decisions were made with respect to skeletal part transport. Fuel utility may not have been as important in transport decision-making. It should be noted that the differences in correlation coefficients between these two models are small, however.

Compared to the other samples, the Châtelperronian? bison assemblage is not as strongly correlated with the utility models examined. This lack of correlation seems to be explained by the under-representation of the radio-ulna in this occupation, in addition to the femur. Small sample size might also be responsible for this pattern. Nonetheless, even in this assemblage, skeletal part abundance tends to correlate with marrow utility.

Selection of horse parts for transport

Horse assemblages are small at Saint-Césaire and are smallest in the Denticulate Mousterian and Châtelperronian occupations. Table 64 shows inter-assemblage correlations relative to the rank order of body parts in the five largest horse samples from Saint-Césaire. Most assemblages are significantly correlated, or almost significantly correlated, with each other. Some of these correlations are highly significant. However, no significant correlation was found between the Denticulate Mousterian and the Aurignacian I assemblages. These results suggest that, as for bison, the ranking of horse skeletal parts was structured similarly relative to transport across the occupations.

Two utility models, the first focusing on FUI, the second on marrow, have been published recently for horse (Outram and Rowley-Conwy 1998). Unfortunately, no model is available for bone grease. Thus, our discussion concentrates on the former two indices. However, before proceeding to the analysis of the assemblages, it is necessary to emphasize some points about the Marrow Index (Outram and Rowley-Conwy 1998:842, Table 3).

	Inter-Assemblage Correlations: Horse				
	Evol Auri (4)	Auri I (5)	Châtel (8)	Châtel? (9)	Moust (10)
Evolved Aurignacian (4)	-	**<.05**	**<.04**	***<.01***	***<.01***
Aurignacian I (5)	.607	-	**<.02**	**<.05**	<.23
Châtelperronian (8)	.640	.752	-	**<.05**	<.07
Châtelperronian? (9)	.888	.603	.608	-	**<.02**
Denticulate Mousterian (10)	.876	.369	.559	.741	-

Table 64. Spearman's rho correlations (cells below the dashes) between horse assemblages at Saint-Césaire. *p* (cells above the dashes) ≤ 0.05 are shown in bold. *p* ≤ 0.01 are shown in bold italic.

Outram and Rowley-Conwy noted considerable inter-individual fluctuation in marrow weight (Emerson's marrow index was based on calories) within their sample. As emphasized rightly by them, the amount of trabecular bone in long bone shafts, which varies significantly between individuals in equids, including adults, may be responsible for these fluctuations (see also Blumenschine and Madrigal 1993).

Another problem is that the mean marrow values published by Outram and Rowley-Conwy are much higher than those presented by Blumenschine and Madrigal (1993) for zebra, a closely related taxon. These differences might result from the fact that the sample on which the marrow index is based consists of three old riding animals (all >15 years), one described as "particularly fat" (Outram and Rowley-Conwy 1998:839). Conversely, Blumenschine and Madrigal focused on young, probably much leaner, wild animals procured in East Africa. Because the source of these discrepancies is unclear, age, sex, activity levels, health, and nutritional condition being likely contributing factors, it might be complicated to apply this model to archaeological samples. For all these reasons, the horse Marrow Index should be used with caution. In contrast, meat distribution in body parts is said by Outram and Rowley-Conwy to be less variable across individuals.

The abundance of horse skeletal parts in five assemblages from Saint-Césaire is plotted against (S)FUI (Outram and Rowley-Conwy 1998) in Figure 57. The FUI model conflates all types of tissues and fat-related products by element minus their associated dry bone weight. However, it should be kept in mind that because the horse assemblages are fairly small, sampling is more likely to affect the results here compared to bison or reindeer.

Skeletal part abundance tends to correlate positively with FUI in the horse assemblages. However, the pattern is not as clear as with bison, and there is much variation in some assemblages. Correlations are significant or close to attaining significance in the Denticulate Mousterian, Châtelperronian, and Aurignacian I assemblages (Table 65). The Châtelperronian? and Evolved Aurignacian EJM samples are not significantly correlated with FUI. As noted previously in the discussion on bison, the femur also tends to be under-represented in the horse samples. Correlation coefficients increase and become significant or almost significant in all of the assemblages when this element is excluded. In contrast, correlations are weak or vanish in the long bone-only samples.

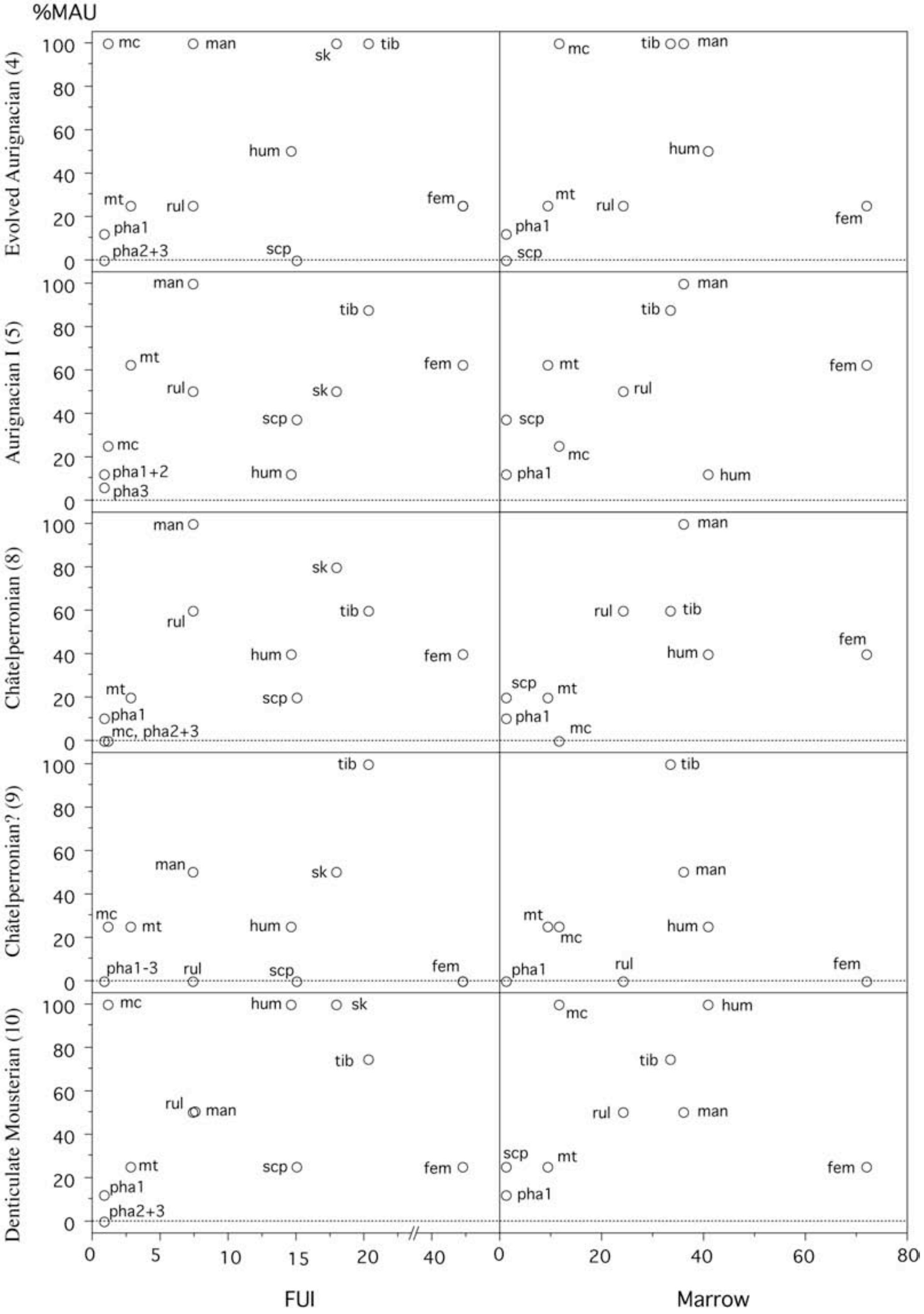

Figure 57. Relationship between abundance of horse skeletal parts in five assemblages from Saint-Césaire and the (S)FUI and Marrow models (Outram and Rowley-Conwy 1998, p. 845, Table 6 and p. 842, Table 3, respectively).

Abundance of Horse Skeletal Parts Versus the FUI and Marrow Models

	FUI						Marrow					
	all elements		all minus femur		long bones only		all elements		all minus femur		long bones only	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Evol Aurignacian (4)	.493	<.11	.575	<.07	-.071	<.88	.562	<.11	.738	<.05	.043	<.92
Aurignacian I (5)	.657	**<.03**	.639	**<.05**	.443	<.33	.367	<.30	.280	<.46	.014	<.97
Châtelperronian (8)	.715	**<.02**	.773	**<.02**	.629	<.16	.629	<.08	.690	<.07	.457	<.31
Châtelperronian? (9)	.462	<.13	.689	**<.03**	-.043	<.93	.354	<.32	.673	<.08	-.157	<.73
Dent Mousterian (10)	.538	<.08	.675	**<.04**	-.257	<.57	.479	<.18	.756	**<.05**	.057	<.90

Table 65. Correlations between the abundance of horse skeletal parts in various assemblages from Saint-Césaire and the FUI and Marrow models (Outram and Rowley-Conwy 1998:845, Table 6 and p. 842, Table 3, respectively). ***p*** **≤ 0.05 are shown in bold.**

Keeping in mind the above cautionary notes, the horse samples from Saint-Césaire are compared with marrow wet weight (Outram and Rowley-Conwy 1998:842). A minor modification was made to this model. Outram and Rowley-Conwy provide no value for the scapula, although they acknowledge that a small amount of marrow is usually found in this element. A value of 1 g (equal to the marrow weight for the first phalanx) was attributed arbitrarily to this part. This is because it might be interesting to examine whether marrow content can explain the lack of scapula at Saint-Césaire.

Marrow weight tends to correlate positively with abundance of parts in the horse samples from Saint-Césaire (Figure 57). As shown in Table 65, however, none of the correlations is statistically significant, although the Châtelperronian sample is close to reaching significance. Removing the femur increases the correlation coefficients in most assemblages. Conversely, there is little correlation between abundance of parts and marrow utility in the long bone-only sample. In this respect, it is interesting to note that four of the six complete ungulate long bones identified at Saint-Césaire are from horse. All four bones are metapodials. This might indicate that horse metapodials were not marrow-cracked systematically, perhaps due to the limited amount of marrow present in these bones (Blumenschine and Madrigal 1993).

In summary, the horse assemblages tend to correlate positively with the FUI model and, to a lesser extent, the marrow model, even though the relationships are not in general as strong as in bison. However, these trends become weak or vanish when the samples are limited to long bones, even when the possible under-identification of the femur is taken into account. The most likely explanation for these weaker correlations is the inherent variation in the sample from which the utility indices were derived and the small sample size of the archaeological assemblages.

Selection of reindeer parts for transport

Reindeer assemblages are moderately to fairly large in the Aurignacian occupations from Saint-Césaire, but are much smaller in the Denticulate Mousterian and the Châtelperronian. Did the same transport decisions operated in all assemblages? The answer appears to be yes. Correlations between the six largest reindeer assemblages from Saint-Césaire are all very strong, positive, and statistically significant. The three cells that do not reach significance all involve the Châtelperronian. Does this mean that the Châtelperronian sample differs from the others?

Because the reindeer sample is small for the Châtelperronian occupation, this difference might result from sampling error. When the assemblages are compared with the EJOP reindeer sample, all three cells become statistically significant (Denticulate Mousterian: $r_s = .701$, $p < .03$; Aurignacian 0?: $r_s = .788$, $p < .01$; Aurignacian I: $r_s = .729$,

$p < .02$). This suggests that the Châtelperronian is in line with the other assemblages. These strong inter-assemblage correlations indicate that very similar decisions were embraced relative to the transport of reindeer skeletal parts throughout the occupation of Saint-Césaire.

	Inter-Assemblage Correlations: Reindeer					
	Evol Auri (3)	Evol Auri (4)	Auri I (5)	Auri 0? (6)	Châtel (8)	Moust (10)
Evol Auri (3)	-	***<.01***	**<.03**	***<.01***	**<.02**	**<.03**
Evol Auri (4)	.837	-	***<.01***	***<.01***	**<.02**	***<.01***
Auri I (5)	.685	.853	-	***<.01***	<.08	***<.01***
Auri 0? (6)	.792	.795	.937	-	<.06	***<.01***
Châtelperronian (8)	.773	.741	.544	.580	-	<.11
Mousterian (10)	.685	.888	.953	.876	.495	-

Table 66. Spearman's rho correlations (cells below the dashes) between reindeer assemblages at Saint-Césaire. *p* (cells above the dashes) ≤ 0.05 are shown in bold. *p* ≤ 0.01 are shown in bold italic.

The abundance of reindeer skeletal parts in the assemblages from Saint-Césaire is first compared with the FUI model (Metcalfe and Jones 1988). These assemblages tend to correlate positively with FUI (Figure 58). Correlations are significant or close to reaching significance in four of the six samples, the exceptions being the Aurignacian 0? and the Evolved Aurignacian EJM assemblages. Excluding the femur does not change the correlation coefficients substantially. When the samples are limited to long bones, correlations become much weaker in three assemblages, and somewhat stronger in the other three. Thus, the FUI model is a reasonably good predictor of the abundance of reindeer skeletal parts at Saint-Césaire, although is does not optimally explain the frequencies of long bones in the samples.

Abundance of Reindeer Skeletal Parts Versus the FUI Model and Parts Selected for Grease Rendering

	FUI						Grease Rendering					
	all elements		all minus femur		long bones only		all elements		all minus femur		long bones only	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Evol Aurignacian (3)	.336	<.27	.352	<.27	.457	<.31	.815	**<.02**	.858	**<.02**	.257	<.57
Evol Aurignacian (4)	.743	**<.02**	.675	**<.04**	.771	<.09	.885	***<.01***	.858	**<.02**	.600	<.18
Aurignacian I (5)	.675	**<.03**	.741	**<.02**	-.043	<.93	.715	**<.04**	.858	**<.02**	-.214	<.64
Aurignacian 0? (6)	.493	<.11	.659	**<.04**	-.086	<.85	.706	**<.04**	.846	**<.02**	-.257	<.57
Châtelperronian (8)	.568	<.06	.559	<.08	.800	<.08	.867	***<.01***	.854	**<.02**	.800	<.08
Dent Mousterian (10)	.701	**<.03**	.677	**<.04**	.171	<.71	.739	**<.03**	.762	**<.04**	-.086	<.85

Table 67. Correlations between the abundance of reindeer skeletal parts in various assemblages from Saint-Césaire and two utility models: i) the FUI (Metcalfe and Jones 1988:492, Table 2) model, and ii) proportions of parts selected in spring by two Nunamiut women for grease rendering (Binford 1978:36, Table 1.13, column 6). $p \leq 0.05$ are shown in bold. $p \leq 0.01$ are shown in bold italic.

Binford (1978) made a detailed study of skeletal fat utility in caribou and sheep. Based on the classification used by his informants and chemical analyses, he distinguished white from yellow bone grease and generated indices to account for these differences. However, these indices suffer from the same problems highlighted by Chase (1985) and Metcalfe and Jones (1988) concerning the MGUI model; the derivations are complex and it is not easy to understand what exactly is being measured. Additionally, values for one of the variables incorporated in the formulae, bone density, are probably incorrect (Lyman 1984; Lam *et al.* 1998, 2003).

An alternative is to compare the Nunamiut data provided by Binford (1978) on skeletal parts selected for the manufacture of white bone grease with the Saint-Césaire assemblages, as performed in the discussion on bison. Values from the spring episode (Binford 1978:36, Table 1.13, column 6) are used here, as these are congruent with the seasons of reindeer procurement at the site.

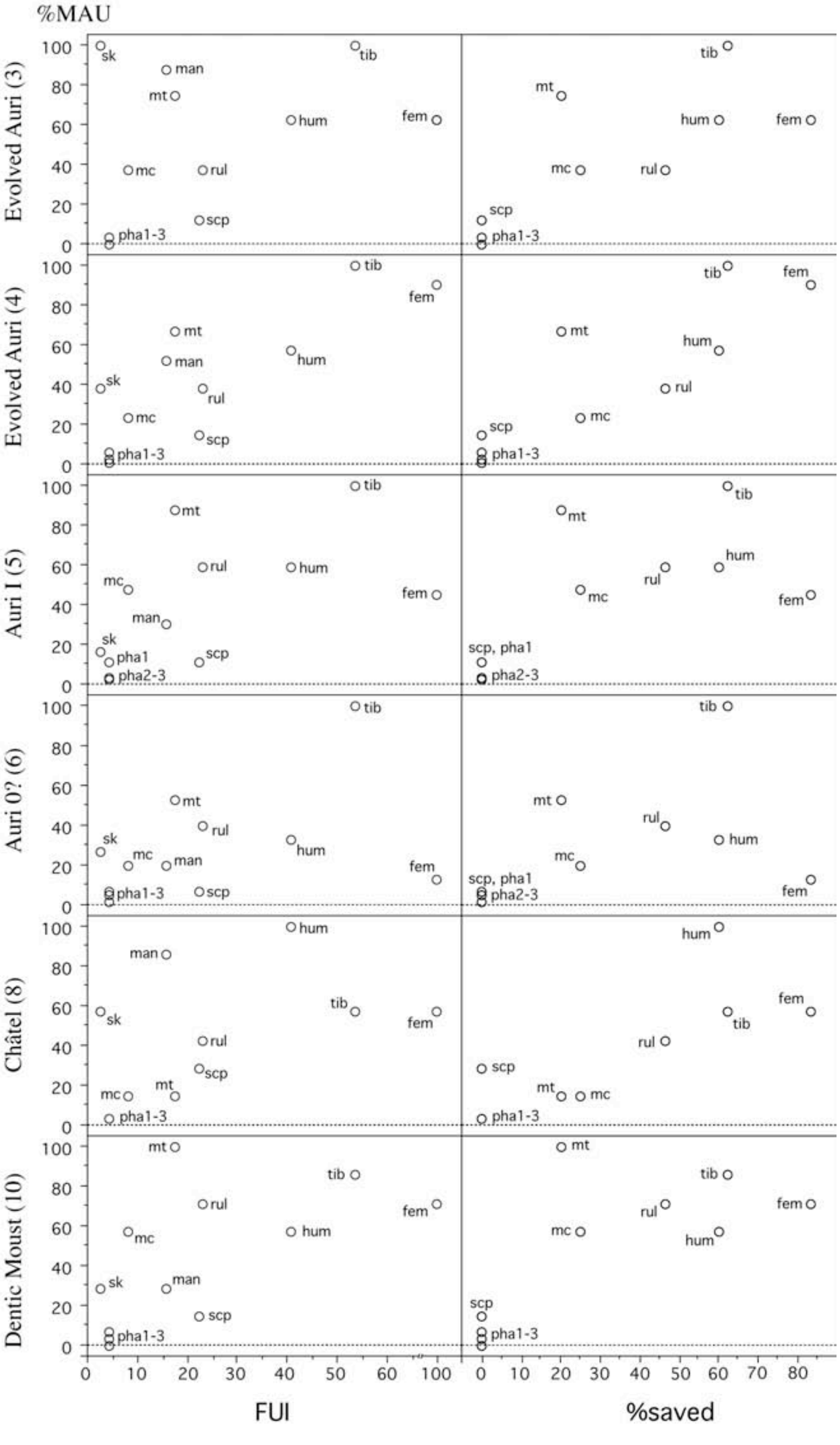

Figure 58. Relationship between the abundance of reindeer skeletal parts in six assemblages from Saint-Césaire and two models: i) (S)FUI (Metcalfe and Jones 1988:4392, Table 2), and ii) proportions of parts selected in spring for grease rendering by two Nunamiut women (Binford 1978:36, Table 1.13, column 6).

All the reindeer assemblages from Saint-Césaire are significantly correlated with the spring episode of part selection (Table 67 and Figure 58). Excluding the femur increases the correlation coefficients in most assemblages. However, long bones alone do not correlate well with the Nunamiut bone grease model save for the Châtelperronian assemblage. To assess whether this last result is a byproduct of small sample size, the same correlation was calculated with the EJOP assemblage. The results obtained (r_s = -357, $p < 0.43$) suggest that this difference is probably due to sampling error.

In general, the Nunamiut model of grease rendering is better at predicting reindeer element representation at Saint-Césaire than the FUI model. However, long bones are very poorly correlated with the Nunamiut model. Two outliers, the femur and the metatarsal, appear to be responsible for this lack of correlation. This might indicate that long bones were not primarily selected for transport as a function of bone grease or fuel utility.

Building on Binford's data, Jones and Metcalfe (1988) showed that the volume of the marrow cavity is a very good predictor of parts selected by the Nunamiut for making *Akutuk*, a marrow-based dish (Binford 1978:29).

Marrow cavity volume is positively and significantly correlated with abundance of parts in the reindeer assemblages from Saint-Césaire (Figure 59 and Table 68). Removing the femur results in correlation coefficients that are very high: between 68.7 and 98.4% of the variation is explained by this factor alone, excluding the Châtelperronian assemblage. The long bone-only samples are also positively correlated with marrow cavity volume, but the relationship is significant or close to being significant in only two assemblages (the Evolved Aurignacian EJM and EJJ samples).

Interestingly, the marrow model predicts perfectly the ranking of long bones in the Evolved Aurignacian EJM assemblage. Removing the femur from the long bone sample increase the correlations in the other occupations, resulting in three of the five assemblages being significantly or almost significantly correlated with marrow cavity volume. However, the correlations are not significant in the Denticulate Mousterian and Châtelperronian samples.

As was true for bison, marrow cavity volume best explains skeletal part abundance at Saint-Césaire, including long bones. This is the single case in which the Châtelperronian might depart from the general trend. However, the reindeer sample being small for this occupation, this difference is only weakly supported. Using the EJOP sample rather than the Châtelperronian sample increases the correlation coefficient slightly ($r_s = .500$, $p = .32$), but the relationship is still not significant.

Abundance of Reindeer Skeletal Parts Versus Marrow Cavity Volume

	all parts		all minus femur		long bones only		long bones minus femur	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Evolved Aurignacian (3)	.794	**<.02**	.829	**<.02**	.886	**<.05**	.975	<.06
Evolved Aurignacian (4)	.964	***<.01***	.950	***<.01***	1.000	**<.03**	1.000	**<.05**
Aurignacian I (5)	.873	***<.01***	.992	***<.01***	.414	<.36	.975	<.06
Aurignacian 0? (6)	.800	**<.02**	.975	***<.01***	.371	<.41	.900	<.08
Châtelperronian (8)	.579	<.09	.575	<.11	.457	<.31	.375	<.46
Dent Mousterian (10)	.927	***<.01***	.954	***<.01***	.657	<.15	.725	<.15

Table 68. Correlations between the abundance of skeletal parts in six reindeer assemblages from Saint-Césaire and marrow cavity volume (data from Binford 1978:26, Table 1.7). $p \leq 0.05$ are shown in bold. $p \leq 0.01$ are shown in bold italic.

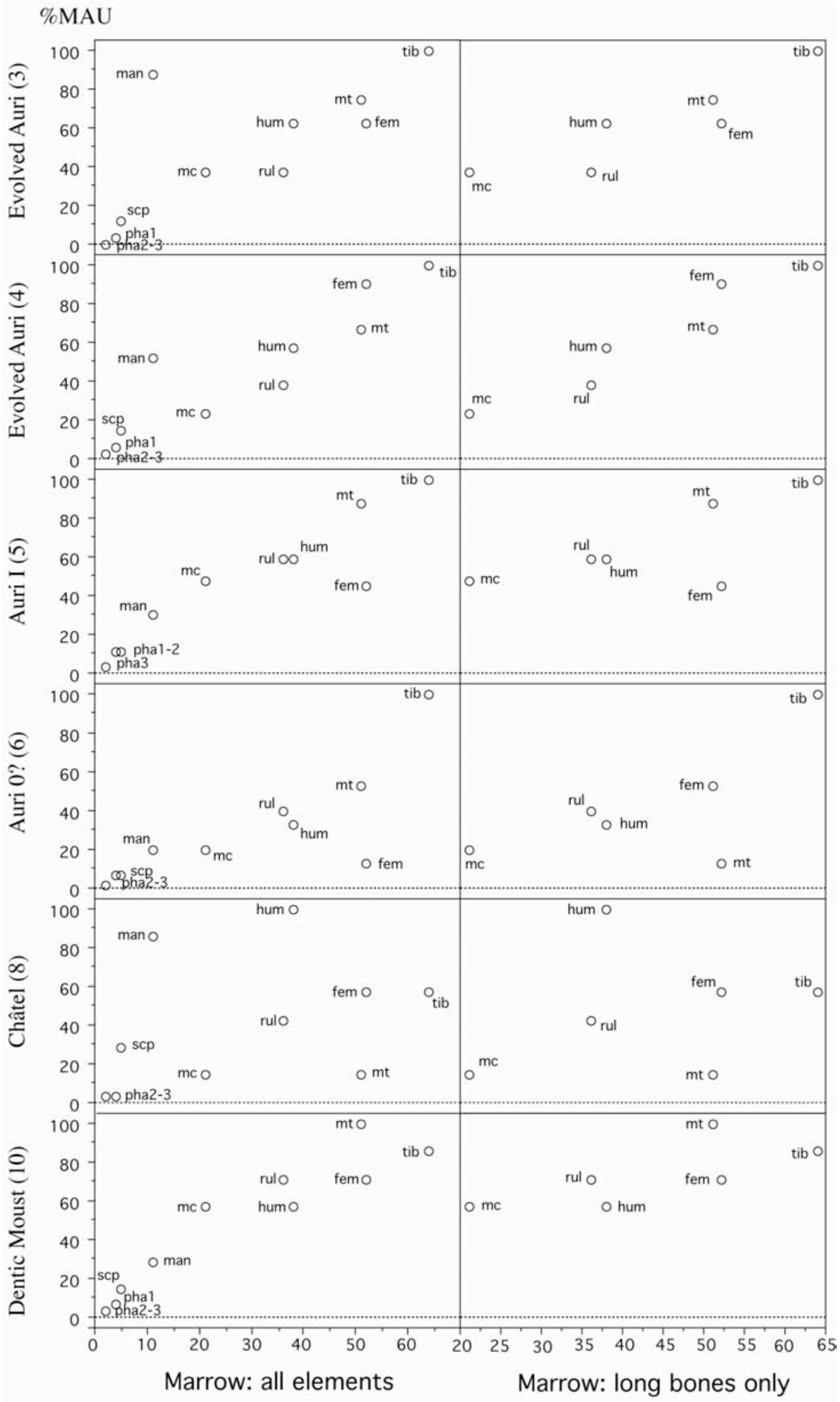

Figure 59. Relationship between abundance of skeletal parts in six reindeer assemblages from Saint-Césaire and marrow cavity volume (Binford 1978:26, Table 1.7). Right diagrams show the same relationships but for long bones only.

An alternative to the utility index approach is to compare Saint-Césaire with known kill assemblages. Kill sites are interesting because fewer dimensions of behavior structure them compared to residential sites. As a rule, low utility parts are abandoned at the former locations, whereas high utility parts are transported back to the shelter. Nutritional condition and sex are two other major factors structuring transport decisions. It might not be unreasonable to expect shelters and kill sites to be negatively correlated in terms of skeletal part abundance.

However, the ethnographic reality is more complex. Shelters and kill sites are not closed behavioral systems and, sometimes, change functions (Binford 1980). Furthermore, body parts may follow complex trajectories. Skeletal parts are likely to be introduced into residential sites because they contain nutrients (Marshall and Pilgram 1991), and as a result of the "rider" effect (Binford 1978). Conversely, food might be moved out of residential locations and transported to other sites, as a result of visits paid to friends, hunting and gathering expeditions, "snacking," residential and logistical moves, offerings, exchange, etc. (Birket Smith 1959; Balikci 1970; Lee 1976; Wiessner 1982; Kelly 1995). Therefore, these and other factors might blur the simple complementary nature of kill and residential sites with respect to skeletal part composition.

For many reasons, however, *skeletal elements*, in contrast to food, are not as likely to be moved out of residential sites. This is because skeletal parts are expected to be processed and discarded at residential camps, where time and other factors may be less constraining (O'Connell *et al.* 1988). Furthermore, foragers are concerned with reducing weight and bulk in moves (Kelly 1995). Hence, it is common to observe strategies aimed at minimizing bone weight in transported loads, as, for instance, through the manufacture of biltong or pemmican (Bartram 1993). Reduction of bulk and weight may have been especially critical during the snow-covered season in Paleolithic France. Of course, this is not to deny that bones are moved out regularly from residential sites. However, it is reasonable to argue that this last type of transfer is limited and does not change assemblage composition extensively.

Anavik and Anaktiqtauk are hunting locations described by Binford (1978:75-87). In both cases, occupation occurred during the spring migration, in agreement with one of the major seasons of reindeer procurement at Saint-Césaire. The Nunamiut intercepted fifty-three and fifty-eight caribou, respectively, at these sites. Importantly for this discussion, the group who created these assemblages was portrayed as enjoying greater subsistence security than was true in former times (Binford 1978:36). Skeletal part abundance in these kill sites is expected to correlate negatively with the Saint-Césaire occupations. A lack of correlation might provide information on level of nutritional stress reflected by the assemblages, for instance, by showing that more low-utility parts were transported to shelters than expected, based on the Nunamiut model. However, such results should be interpreted carefully, as they may also indicate differences in transport constraints, destination of skeletal parts, and dismemberment strategies. Despite this, comparisons with the Nunamiut kill assemblages may be productive.

The abundance of skeletal parts in the reindeer assemblages from Saint-Césaire is compared to Anavik in Figure 60. It is fairly clear that the occupations correlate negatively with the Nunamiut kill assemblage. Two additional patterns are apparent in

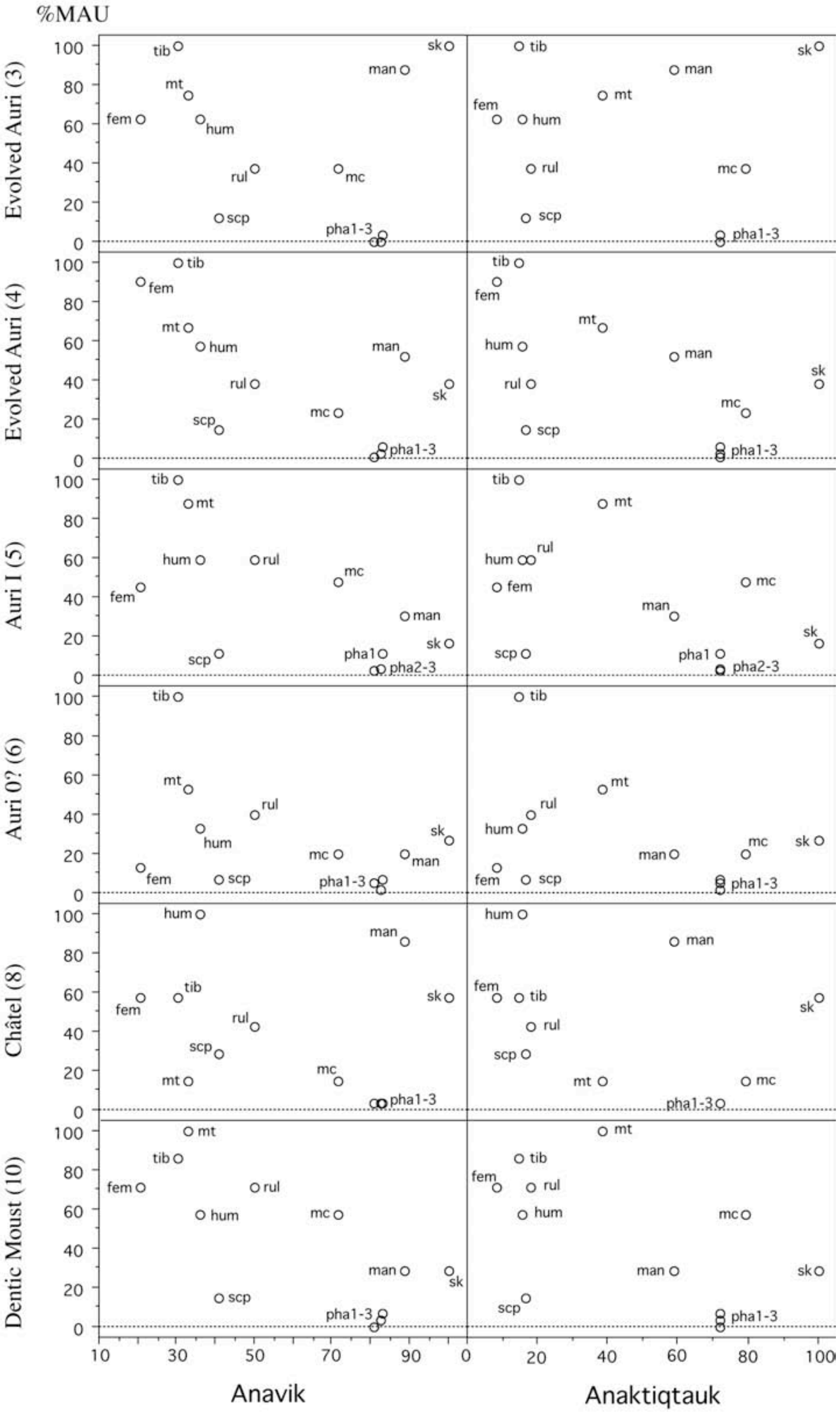

Figure 60. Relationship between the abundance of skeletal parts in the reindeer assemblages from Saint-Césaire and two reindeer kill assemblages produced by the Nunamiut. Data from Binford 1978:78, Table 2.9.

Abundance of Reindeer Skeletal Elements at Saint-Césaire Versus Anavik and Anaktiqtauk

	Anavik		Anavik minus head		Anaktiqtauk		Anaktiqtauk minus head	
	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Evolved Aurignacian (3)	-.164	<.59	-.852	<**.02**	-224	<.46	-.609	<.07
Evolved Aurignacian (4)	-.628	<**.04**	-.903	<***.01***	-.645	<**.04**	-.721	<**.04**
Aurignacian I (5)	-.608	<**.05**	-.661	<**.05**	-.490	<.11	-.436	<.20
Aurignacian 0? (6)	-.406	<.18	-.664	<**.05**	-.336	<.27	-.427	<.20
Châtelperronian (8)	.-208	<.50	-.782	<**.02**	-.463	<.13	-.794	<**.02**
Dent Mousterian (10)	-.677	<**.03**	-.788	<**.02**	-.523	<.09	-.515	<.13

Table 69. Correlations between the abundance of reindeer skeletal parts in six assemblages from Saint-Césaire and the Anavik and Anaktiqtauk kill site assemblages (Binford 1978:78, Table 2.9). $p \le 0.05$ are shown in bold. $p \le 0.01$ are shown in bold italic.

these diagrams. Head parts tend to be over-represented at Saint-Césaire relative to other skeletal elements, especially in the small samples. On the contrary, the scapula is not as common as one would predict, based on the kill assemblage. The femur tends also to be under-represented, possibly due to differential identification.

Rank order correlations between the reindeer assemblages and Anavik are all negative (Table 69). However, only three assemblages, the Denticulate Mousterian, Aurignacian I, and the Evolved Aurignacian EJM samples, are significantly correlated with Anavik. Correlations reach significance in all six assemblages when the head is excluded (the reason for excluding this part is discussed below).

Assemblages tend also to correlate inversely with Anaktiqtauk (Figure 60). However, only two correlations, involving the Denticulate Mousterian and the Evolved Aurignacian EJM samples, are statistically significant or almost significant (Table 69). Elements of the forelimb (especially the scapula, humerus, and radio-ulna) are generally under-represented compared to the modern kill sample. In contrast, the skull and, to a lesser extent, the mandible, are often over-represented.

Correlation coefficients increase in four assemblages when the head is excluded, although only three of these relationships (Châtelperronian and the Evolved Aurignacian EJM and EJJ samples) are statistically significant or close to reaching significance. These results corroborate earlier findings and show that high utility parts were transported to Saint-Césaire, whereas most low utility parts are presumed to have been abandoned at kill sites. However, how can the under-representation of the forelimb, particularly the scapula, and the over-representation of the head be explained? Why are the correlations with Anavik stronger than with Anaktiqtauk?

Fat is mobilized late in the mandible in undernourished animals, whereas most of the lipids in the brain remain stable regardless of animal condition (Davis *et al.* 1987; Speth 1983; Stiner 1994; Levine 1998). This might explain why the head content is relished by many foragers, depending on the sex, body size, nutritional condition, and age of the animal (Yellen 1977; Binford 1978). Therefore, the fact that heads are abundant in the assemblages from Saint-Césaire might have a nutritional explanation. However, at least two other alternatives must be examined before accepting this proposition.

As argued above, the practice of using antlers for making tools might have increased the utility of the head. Abundance of antlers in the assemblages and the presence of some tools made of this material appear to support this hypothesis. Yet, heads are also well represented in the Denticulate Mousterian, despite the fact that antlers and bone tools, excluding retouchers, are lacking in this occupation. This suggests that even if antlers contributed to increase the utility of the head, this factor alone might not explain fully the over-representation of skulls and mandibles in the assemblages.

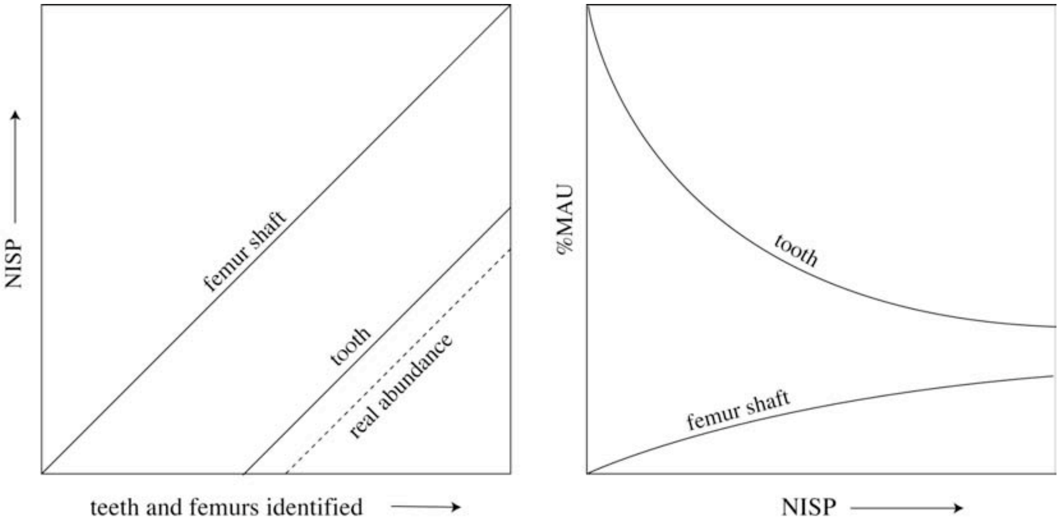

Figure 61. Hypothetical model of the relationship between identification of parts and sample size expressed in a) NISP, and b) %MAU. The real abundance of femurs and teeth is identical in this model.

Identification bias is another possible explanation for the over-representation of heads at Saint-Césaire. It was emphasized in Chapter 5 that the ease with which most teeth can be identified might inflate head abundance. The *slope of identification*, that is the relation between the number of specimens deposited in a site and the number of these specimens identified taxonomically, is probably closer to 1 for teeth compared to other parts[9] in fragmented assemblages. Due to the fact that MNE does not increase linearly but

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[9] Taxonomic identification is inferred to increase quasi-linearly with sample size. We have seen that identification differs also between long bones (e.g., the femur shaft tends to be under-identified relative to the metatarsal shaft for instance). Concerning the Nunamiut kill assemblages, the slope of identification should be relatively comparable between elements, as these assemblages were recorded immediately after the event (Binford 1978:83) and were not affected by episodes of postdepositional breakage and other taphonomic processes, as is the case at Saint-Césaire.

instead follows a power function (Grayson 1984), head over-representation should be magnified in small MNE samples (Figure 61). For the same reason, with increasing sample size, proportionately fewer heads are expected to contribute to MNE relative to other parts. This identification bias affects NISP as well. In this case, however, head over-representation should remain unaffected by sample size.

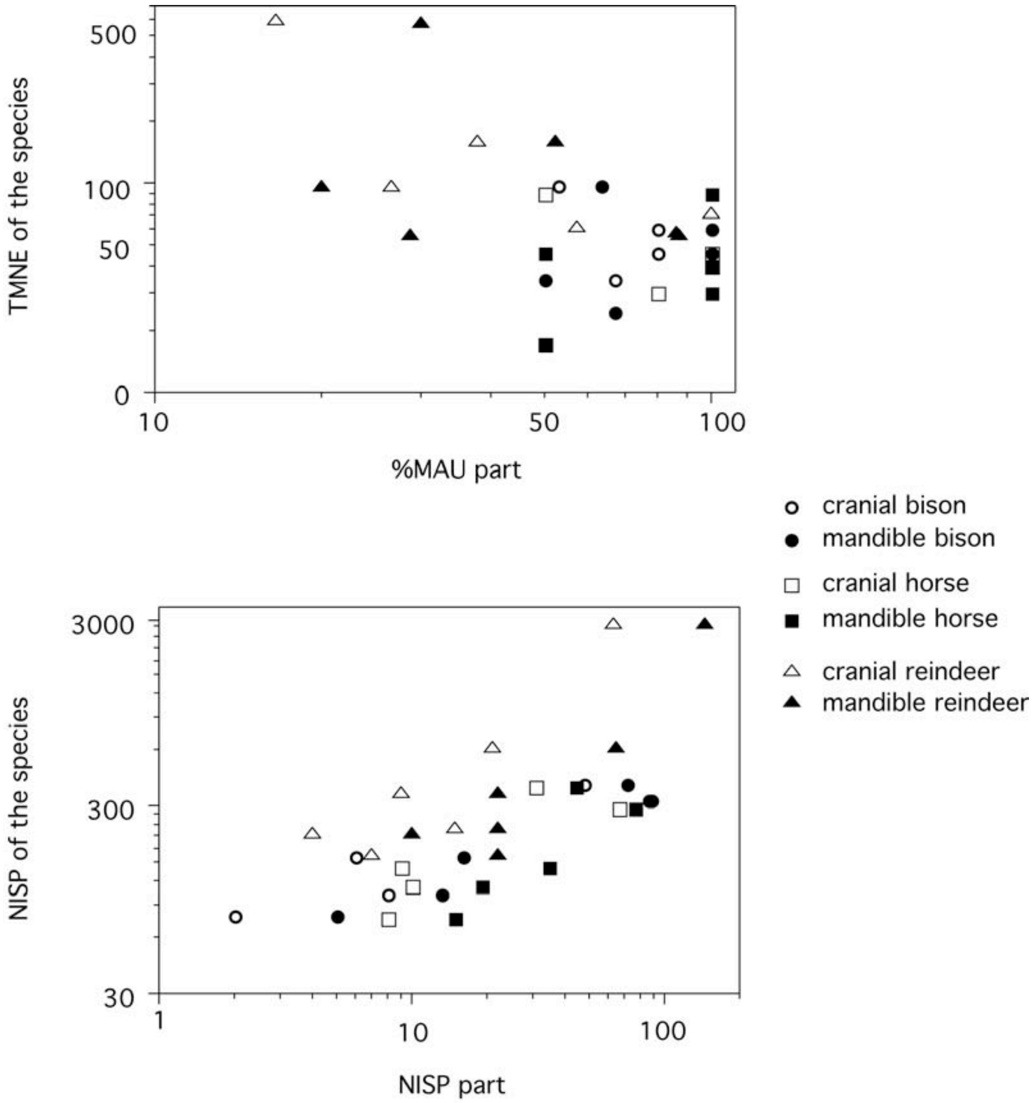

Figure 62. Saint-Césaire. Distribution by species and assemblage of %MAU values for the cranium and mandible in reindeer, bison, and horse versus the species total MNE (TMNE, above) and the species total NISP (below). Only the reindeer, bison, and horse samples discussed in this chapter are included. Both axes are in log$_{10}$.

Figure 62 shows %MAU values for the skull and mandible versus the total MNE (TMNE) by species and assemblage. What is being examined here is whether head representation increase with decreasing sample size. It is clear from this diagram that the relationship between these variables is roughly linear and negative: the smaller the assemblage, the higher the proportion of heads relative to other parts. This set of data seems to support the hypothesis of an increased over-representation of heads in small MNE samples and might explain the weaker correlations obtained between the smallest reindeer assemblages from Saint-Césaire and the Nunamiut kill sites.

However, these patterns might also be interpreted as indicating that heads were transported more often in small assemblages than in larger ones. It is possible to test this proposition using NISP, as this unit increases linearly with sample size (Grayson 1984). If the hypothesis of differential transport is true, proportionately more head fragments should be found in small than in large NISP samples.

Figure 63 plots the abundance of skull and mandible fragments in the reindeer assemblages from Saint-Césaire versus sample size. This is the same graph as the one shown in the bottom of Figure 62 but for reindeer only. The distribution does not indicate an over-representation of head parts in the smaller reindeer samples, as both skeletal parts[10] increase roughly linearly with sample size. Therefore, an analytical bias favoring head representation in small MNE samples is the most likely explanation for variation in the abundance of this part at Saint-Césaire. This result implies that sample size may explain much of the variation in the abundance of skulls and mandibles in the Saint-Césaire samples.

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[10] Differential fragmentation might explain why the skull and the mandible do not fall on the same line. For instance, maxillary teeth are more often found isolated at Saint-Césaire than mandibular teeth.

The scapula is under-represented in the Saint-Césaire assemblages compared to what we would expect based on the Nunamiut kill sites. As argued in Chapter 4, bias identifiability is not likely to explain the under-representation of the scapula at Saint-Césaire (excluding the fragile portions of the blade). Further, this part is under-represented in both small and large assemblages, which suggests that sample size is not causing this pattern.

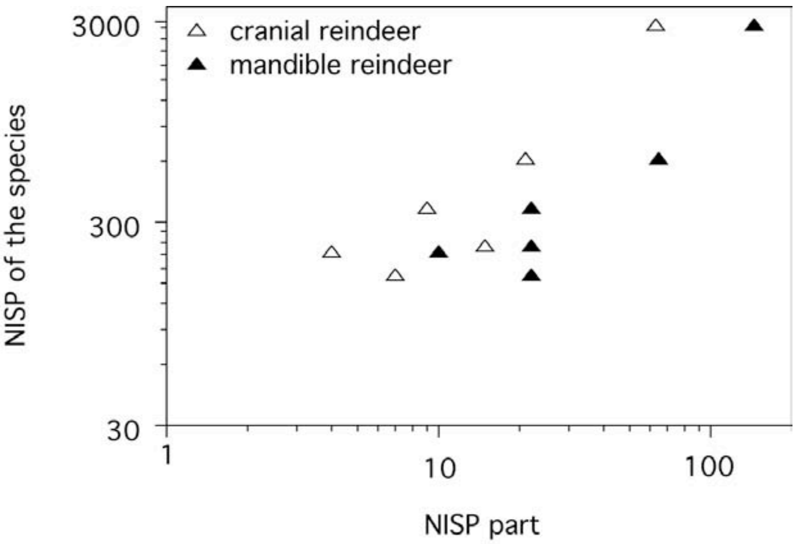

Figure 63. Saint-Césaire. Distribution by assemblage of NISP values for reindeer cranial and mandible fragments versus the total NISP for the same species. Both axes are in log$_{10}$.

Three alternative explanations can be offered for the low proportion of scapulae in the assemblages. The first possibility is that its abundance has been reduced through burning. However, the fact that only a single scapula fragment is burned in the sequence undermines this proposition. A second possibility is that carnivore ravaging reduced its abundance. The relatively low frequency of carnivore marks (2/40) on the reindeer scapula at Saint-Césaire does not support this hypothesis. A third possibility is that this element was frequently abandoned at the kill in order to decrease transport costs. This is not unreasonable, as the scapula is a low-utility bone. This proposition might find support in the Nunamiut data.

According to Binford (1978:82), time constraints resulted in the culling of more forelimbs at Anavik than at Anaktiqtauk. However, Anavik predicts well the transport of forelimbs at Saint-Césaire, with the exception of the scapula. This suggests that these three sites vary in the way the forelimb has been dismembered and transported. Differences in transport constraints might explain some of this variation. The use by the Nunamiut of means of transportation (dog sleighs, pack dogs, snowmobiles) presumed absent from the Middle and early Upper Paleolithic repertoire certainly decreases costs of carrying riders. Therefore, it can be hypothesized that the under-representation of the scapula in the occupations of Saint-Césaire signal dismemberment strategies aimed at reducing transport costs of the forelimb. An alternative is that the underrepresentation of the scapula may also signal differences in drying and meat preservation strategies.

Another possibility is that the scapula might have been frequently abandoned at the kill location because the forelimb was too lean. Indeed, Binford (1978) observed that this part was seldom transported in the spring. For males, this part is likely to have been lean in mid winter, whereas in females, this would correspond to the end of spring and early summer. However, the fact that the humerus and radio-ulna are generally well represented at Saint-Césaire seems to argue against this hypothesis.

The fact that the abundance of the first, second, and third phalanges decreases distally to the metapodials in the assemblages may provide support to the hypothesis that the under-representation of scapulae at Saint-Césaire reflects concerns for load weight reduction. Phalanges also decrease distally in several other Paleolithic assemblages in southwestern France for which large samples are available, for instance at Combe-Grenal, layer 23 (Guadelli 1987:446), Grotte du Renne at Arcy-sur-Cure (David and Poulain 2002: 57 and 68), Abri Pataud, levels 14 and 11 (Sekhr 1998:305 and 310), Cuzoul du Vers, layer 23 (Castel 1999a:95), and Combe-Saunière, layer IV (Castel 1999a:232). Although this explanation seems convincing, bone density also decreases distally in the phalanges (Lam *et al.* 1999). Therefore, one should also consider the hypothesis of differential preservation to account for the decreasing abundance of phalanx remains with distance from the metapodials in these assemblages.

In conclusion, comparisons with various utility indices and ethnoarchaeological data indicate that low utility parts were apparently infrequently transported to Saint-Césaire, contrary to the expectation derived from the replacement model. The elements that were transported are generally those with the highest utility. Marrow was possibly the most important factor in these decisions, at least with respect to reindeer and bison parts. Lastly, there is very little evidence of change in transport decisions between the occupations. Instead, consistency in decision-making seems to be documented.

Was grease rendering practiced at Saint-Césaire?

Burning of long bone extremities is fairly clear at Saint-Césaire when one considers the under-representation of epiphyses relative to shafts and the high proportion of those that survived that are burned. Conversely, we have seen that long bone shafts are extremely abundant and rarely burned, including those from the NSUTS and the debris samples. These patterns are most probably explained by the high grease content of long bone epiphyses (Brink 1997), and the fact that these portions burn well (Costamagno *et al.* 1999).

Innominates, tarsals, carpals, and vertebrae, which are all characterized by high fat content and/or amount of connective tissue, are frequently burned also. Other short bones like the patella and lateral malleolus might have been burned still articulated to the long bone epiphyses. These patterns are not limited to Saint-Césaire and have been observed in other Paleolithic sites of southwestern France, for instance at Saint-Germain-la-Rivière (with the exception of the scapula often burned at this site), Grotte du Placard (Costamagno *et al.* 1999), Cuzoul du Vers, and Combe-Saunière (Castel 1999a).

If long bone epiphyses, innominates, vertebrae, carpals, and tarsals were burned almost systematically at Saint-Césaire because they contain fat, connective tissue, and marrow in some cases, an implication might be that grease rendering is unlikely to have been practiced in the assemblages. Indeed, fat-depleted parts can be expected to burn poorly and be ignored as fuel, as suggested indirectly by recent burning experiments of shaft fragments and dry bones (Costamagno *et al.* 1999). The absence of boiling stones and fire-cracked rocks in the occupations may provide support for these propositions (Vehik 1977). However, one should be careful with this line of evidence, as there might have been other means to extract grease than using boiling stones (e.g., bones put next to coal).

Were low-utility parts processed at Saint-Césaire?

At Saint-Césaire, no significant shift in the rank order of skeletal parts can be detected between the occupations. We have also seen that transport focused on high-utility parts and that some specific parts were generally burned. With the possible exception of horse metapodials, long bones were marrow-cracked systematically, as shown by the very low proportion of complete specimens and the relatively high frequency of percussion notches in the assemblages. However, do the low-utility parts show signs of marrow exploitation? If yes, are there changes associated with this activity over the course of the occupations at Saint-Césaire?

These questions can be answered by studying six elements with marginal amounts of marrow: the mandible, scapula, phalanges, innominates, calcaneum, and talus. It is worth reiterating that older Nunamiut informants reported to Binford (1978:31 and 36) that, in former times, marrow is known to have been extracted from some of these parts in periods of food scarcity.

Unfortunately, it is sometimes difficult to diagnose dynamic loading at Saint-Césaire, especially on fragile elements like the scapula and mandibles, because many specimens have been affected by postdepositional breakage. Burning, as well as small sample size, also limit interpretation. Thus, the discussion here is more cursory and qualitative in nature than for other aspects of the assemblages. Lastly, it should be noted that taxa other than ungulates are excluded from this analysis, as it is currently unclear which agent has been responsible for their accumulation.

Information concerning the Denticulate Mousterian is very limited, as the study of this level is not completed yet. Only three specimens can be used to document marrow extraction in this level. The molar region of a bison mandible and two first phalanges (bison and reindeer) do not appear to have been marrow-cracked. However, it seems that other mandibles in the sample were deliberately broken in order to get access to the marrow cavity.

In the Châtelperronian, marrow seems to have been exploited from two bison mandibles. One bison and one reindeer first phalanx from this occupation show what appears to be evidence of marrow extraction. Additionally, three innominates from as many species (reindeer, bison, and horse) were not marrow-cracked. The same can be said of one reindeer scapula and two complete calcanei. One scapula from the low-density EJO inf occupation was not exploited for its marrow content. Three reindeer first phalanges belonging to the Aurignacian 0? were probably marrow-cracked. In contrast, one talus from this level is relatively intact.

More data are available for the Aurignacian I occupation. At least one, and possibly as many as three, reindeer mandibles, out of six partially complete specimens, were fractured in order to obtain marrow. The other three specimens appear to have been broken postdepositionally. Most first and second reindeer phalanges from this level are broken and were probably marrow-cracked (Figure 64). Conversely, some of the horse phalanges seem to have been ignored. None of the partially complete scapula (0/2) from this level shows evidence of dynamic loading. Two reindeer calcanei are relatively complete. Other fragments are very small and might derive from burned specimens. In addition, one, and perhaps, both unburned reindeer tali found in this occupation were probably complete when they were deposited (see Figure 43).

One reindeer mandible in the Evolved Aurignacian EJM assemblage was probably marrow-cracked. Most first and second phalanges in this occupation are broken, possibly as a result of the same activity. No evidence of marrow extraction is apparent, however, on two calcanei, out of three unburned specimens recovered from this level. One reindeer mandible from the Evolved Aurignacian EJJ has been fractured for its marrow. In addition, one horse phalanx found in this occupation is split axially, a feature that has been associated with dynamic loading (Bouvier 1979; Cabrol 1993). In contrast, the marrow from one innominate and two complete calcanei was ignored.

Figure 64. Reindeer first phalanges recovered in the Aurignacian I assemblage from Saint-Césaire. Only three specimens are complete.

Although the information is limited, some general tends can be noted regarding the exploitation of low-utility parts at Saint-Césaire. Mandibles and first and second phalanges were often fractured in order to get access to their marrow content. This strongly suggests that nutritional stress was not uncommon during the Middle to Upper Paleolithic transition. This is in agreement with evidence of marrow exploitation of mandibles and phalanges in other Middle (Binford 1978:149; Guadelli 1987:440; Stiner 1994; Rendu 2002), and Upper Paleolithic assemblages (Castel 1999a; Costamagno 1999) in Western Europe. In contrast, marrow from the scapula, calcaneum, talus, and innominates was generally overlooked at Saint-Césaire.

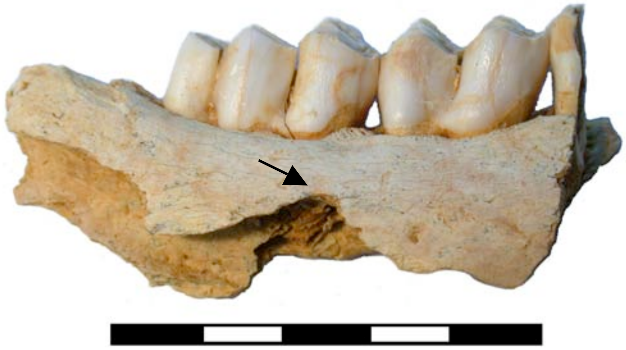

Figure 65. A marrow-cracked reindeer mandible recovered in the Evolved Aurignacian EJJ occupation from Saint-Césaire. The arrow indicates the point of impact.

Although the data are limited, the study of low-utility parts does not suggest major shifts in marrow exploitation during the occupation of Saint-Césaire. The same types of elements appear to have been used and ignored throughout the sequence. Because low utility elements were rarely transported, marrow-cracking is believed to have been a *post hoc* activity carried out at the shelter based on the available pool of skeletal parts. Low utility parts ignored in marrow exploitation were generally used as fuel, with the exception of the scapula. This is not surprising given that skeletal fat has been argued to increase bone inflammability (Costamagno *et al*. 1999).

Decline in foraging efficiency and carnivore taphonomy

In this section, the discussion shifts from body part exploitation to taxa selection. Framed in the perspective of optimality models (Stephens and Krebs 1986), the taxonomic composition of the Saint-Césaire assemblages is explored here in relation to foraging efficiency.

Significant climatic changes are recorded during the late Pleistocene in France (Guyot 1990; Guyot *et al.* 1993). There is little doubt that these climatic fluctuations introduced periodic changes in the abundance and types of species present in the environment (Delpech 1983; Grayson and Delpech 2001). Yet, low-ranked taxa (carnivores, lagomorphs, birds, and fishes) were largely ignored prior to the Magdalenian (see some exceptions in Cochard 2004). This lack of change in the breadth of species exploited suggests that human groups set a threshold in energy returns that was not reevaluated substantially prior to the last glacial maximum. The stability of this strategy also suggest that even if mass capturing techniques were in use or developed during the late Pleistocene, caloric returns were not high enough to increase the relative rank of the low-ranked taxa.

Low-ranked taxa are present at Saint-Césaire, but are usually rare. Do these taxa show evidence of a decline in foraging efficiency during the Middle to Upper Paleolithic transition? Before this issue can be addressed, it is necessary to determine whether humans are responsible for the accumulation of low-ranked taxa in the assemblages.

Lagomorphs are scant at Saint-Césaire. Only ten fragments were found, two of which show evidence of carnivore damage. No cutmarks, traces of burning, or evidence of dynamic loading was observed on the specimens. However, a hare radius found in the Aurignacian I level was modified into a tool. This specimen was not included in this study.

Three fish remains discussed in Chapter 6 were recovered in the Châtelperronian and probably correspond to a single deposition event. It is unknown whether these remains have a natural, as opposed to a cultural, origin.

The agent responsible for the accumulation of carnivores at Saint-Césaire is also unclear. No cutmarks, traces of burning, or percussion notches were recorded on these remains (n=114). In contrast, two specimens are gnawed. It should be noted, however, that a hyena tooth in the Denticulate Mousterian sample studied by Ferrié (2001) is cutmarked. In the sample included in the present study, metapodials and phalanges are relatively abundant compared to other parts (n=22). Skinning might explain this abundance (Leroi-Gourhan 1965; Poplin 1972, 1976). However, the lack of cutmarks on the carnivore feet appears to argue against this possibility.

Birds (n=49) are also poorly represented at Saint-Césaire (see the study by V. Laroulandie, Appendix 2). No evidence of human, raptor, or carnivore activity was recorded on the specimens analyzed by Laroulandie. Taxa that are common in bird assemblages accumulated by Magdalenians, for instance the grouse (*Lagopus albus*), snowy owl (*Nyctea scandiaca*), and alpine chough (*Pyrrhocorax graculus*) (Laroulandie 2000, 2003), are very rare or absent at Saint-Césaire. Although birds probably reflect background accumulation, human intervention cannot be entirely ruled out, based on these criteria.

The lack of evidence of cultural modification does not necessarily mean that humans were not involved in the procurement of low-ranked taxa at Saint-Césaire. Other lines of evidence suggest, however, that humans played little role in their accumulation.

The bulk of the low-ranked taxa at Saint-Césaire consists of carnivores (114/176), especially foxes. Carnivores are not randomly distributed in the assemblages. An increase in relative abundance is noted in the Châtelperronian, low-density, and Aurignacian 0? assemblages (Figure 66). However, variations in the relative abundance of carnivore remains seem to be accompanied by parallel changes in the proportions of specimens modified by carnivores. A plausible implication is that carnivore remains are unrelated to cultural accumulations and correspond to animals that were killed by humans when scavenging faunal debris in the site or were preyed upon by other carnivores.

Alternatively, these results might mean that when humans increased carnivore consumption, they increased procurement of scavenged animals as well. If true, this pattern should be unrelated to frequencies of burning in the assemblages. This is not the case. Proportions of specimens modified by carnivores and the abundance of carnivore remains correlate negatively with proportions of burned specimens in the Saint-Césaire occupations (Figure 67). A likely explanation is that heavily burned assemblages were less attractive to carnivores. If burning can be correlated with intensity of occupation, another possibility would be that an increase in human occupation decreased the probability of carnivore ravaging.

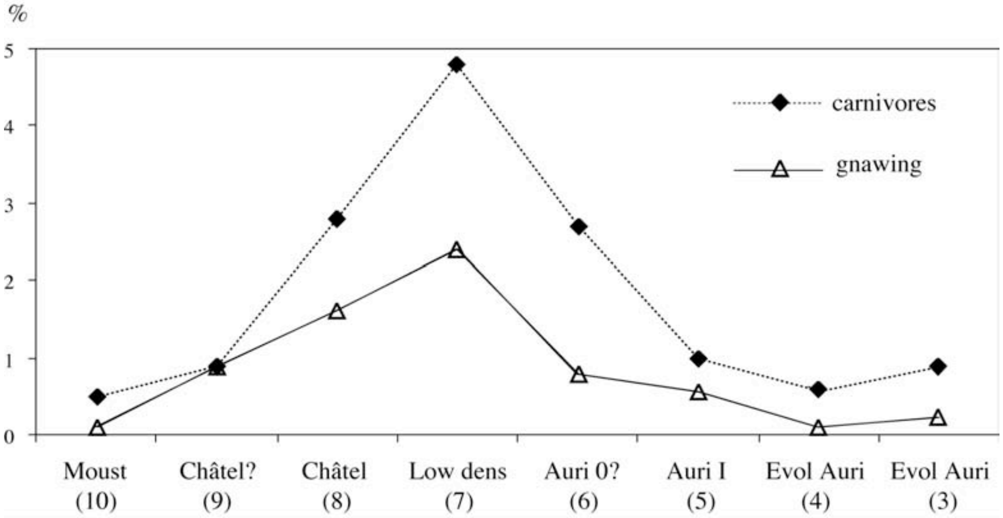

Figure 66. Relation between the relative abundance of carnivore remains and proportions of specimens modified by carnivores in the assemblages from Saint-Césaire.

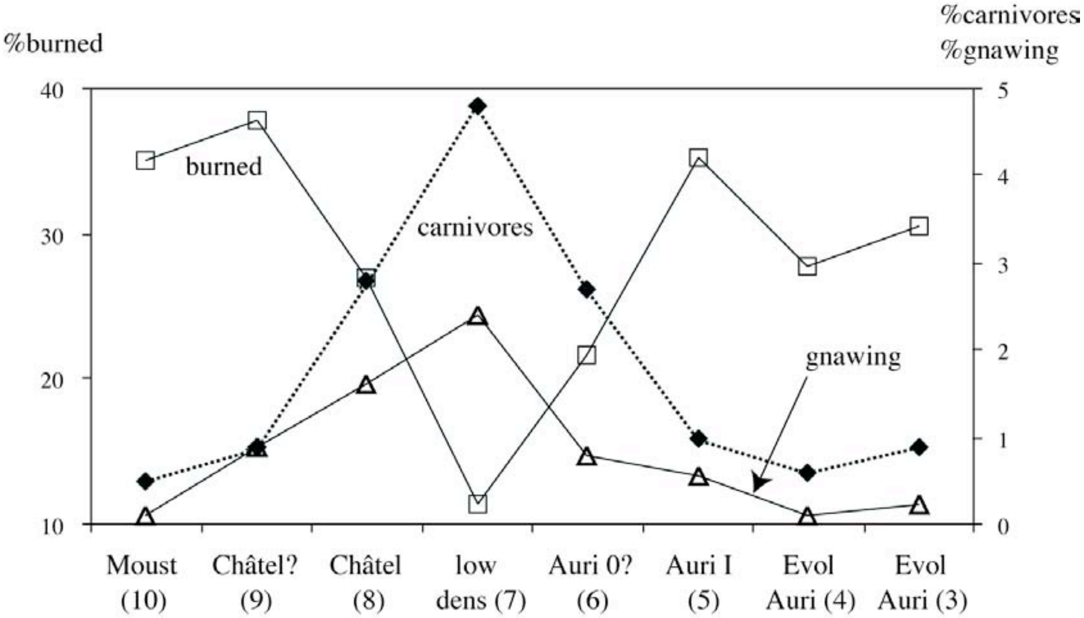

Figure 67. Relation between the relative abundance of carnivore remains, specimens modified by carnivores, and burned specimens in the assemblages from Saint-Césaire.

These results suggest that carnivore abundance and human activity are inversely correlated at Saint-Césaire and do not signal shifts in prey selection. Therefore, it can be concluded that low-ranked taxa are likely to have been accumulated by nonhuman foragers.

Summary of the findings

As discussed in Chapter 5, the few long bone epiphyses that could be identified in the Saint-Césaire assemblages are often burned. Innominates, vertebrae, carpals, and tarsals also show high percentages of burning. Because burning is not random but affects some specific categories of bones, these elements were probably burned as fuel. This conclusion is corroborated by the observation that burned specimens are thoroughly carbonized in the occupations rather than slightly charred, as one would expect from roasting and cooking. Few burned specimens were identified taxonomically in the Denticulate Mousterian and Châtelperronian, most likely due to biases inhibiting the identification of burned specimens from large ungulates. In spite of this, the under-representation of long bone epiphyses, the abundance of burned indeterminate fragments, in addition to patterns in skeletal part representation indicate that bones were used for fuel in these occupations as well.

It was also emphasized that burning is most common on elements with significant grease content and/or amount of connective tissue (e.g., long bone epiphyses). Because fat-depleted specimens like shafts burn very poorly (Costamagno *et al.* 1999), it is reasonable to infer that elements that show evidence of burning in the assemblages were used as fuel while they were still greasy. If correct, this implies that grease rendering was probably not a common practice at Saint-Césaire.

Comparisons with several utility models show that low-utility parts are significantly under-represented at Saint-Césaire. A possible explanation is that limited transport capacity had for effect of increasing the need for body part processing at kill locations. In general, marrow and bone grease utility best predict the abundance of elements in reindeer and bison assemblages at Saint-Césaire. In horse, abundance of parts might be more closely correlated with FUI, although the trends are less clear in this case. An important finding from the study of skeletal representation is the stability in decision-making observed thoroughout the sequence of Saint-Césaire with respect to the transport of reindeer, horse, and bison skeletal elements. This consistency in decision-making is one of the most robust patterns at Saint-Césaire.

Long bones were marrow-cracked systematically in the assemblages. Very few bones were left complete. Extraction of marrow from low-utility parts was also observed. Marrow was often obtained from first and second phalanges. Mandibles were also frequently exploited for their marrow content. Conversely, marrow from the scapula, innominates, and calcanei seems to have been ignored.

Change in species exploitation is another line of evidence used for testing the replacement model. One possible implication of this model is that low-ranked taxa like carnivores, lagomorphs, birds, and fishes increased in abundance during the Middle to Upper Paleolithic transition. An increase in the proportion of carnivore remains is recorded in the Châtelperronian and Aurignacian 0? occupations from Saint-Césaire. Yet, it was shown that this shift in carnivore abundance is matched by a parallel increase in the proportions of specimens modified by carnivores. Because both phenomena correlate negatively with proportions of burning, a factor that is likely to decrease bone attractiveness, it was concluded that carnivores are most probably unrelated to the human occupations at Saint-Césaire. This seems to be true of the other small taxa as well.

Clearly, these results do not support the implications derived from the replacement model. Comparisons with other assemblages will show that these results are not specific to Saint-Césaire.

CHAPTER 8

REGIONAL COMPARISONS

The patterns highlighted in the study of Saint-Césaire might be specific to this site. Therefore, it is important to compare the patterns found in the assemblages from this site with other occupations documenting the Middle to Upper Paleolithic transition. This will allow us to evaluate if the patterns uncovered at Saint-Césaire are representative of this period.

The number of faunal assemblages documenting the Middle to Upper Paleolithic transition is very small in southwestern France. Moreover, the analysis of some important sites is still in progress. To further complicate the picture, faunal samples are often small and distorted by the recovery methods that were used. Two exceptions, the Grotte du Renne at Arcy-sur-Cure and the Abri Pataud, are discussed here. These sites are important because they are characterized by large samples, full recovery of the specimens, and unambiguous evidence of extensive occupation by humans.

Grotte du Renne (Arcy-sur-Cure)

The Grotte du Renne at Arcy-sur-Cure belongs to a complex of caves located near the Cure River south of the Paris Basin. This site was excavated by André Leroi-Gourhan and his team between 1949 and 1963 (David *et al.* 2001). The cultural sequence of Grotte du Renne comprises fourteen levels consisting of several Mousterian, Châtelperronian, Aurignacian, and Gravettian occupations (Leroi-Gourhan and Leroi-Gourhan 1964). Five of these levels document the transition from the Middle to the Upper Paleolithic. These are levels XI (Denticulate Mousterian), X, IX, VIII (Châtelperronian), and VII (Proto- or Early Aurignacian). The fauna associated with three of these occupations has been published (David and Poulain 1990, 2002; David 2002) and is described below.

Based on NISP, the Denticulate Mousterian of Grotte du Renne is dominated by reindeer (59.7%), followed by horse (24.6%). Other ungulates are scantly represented. Cutmarks and percussion notches indicate the anthropic nature of the accumulation. Carnivores represent 6.3% of the sample (David and Poulain 1990). However, carnivore ravaging appears to be extremely limited in this assemblage. Most of the carnivore specimens (53/91 or 58.2%) are from bear. Because cubs and neonates are predominant in the bear sample, David and Poulain (1990:320) concluded that these animals accumulated naturally. One hyena phalanx, however, shows evidence of cultural modification (David and Poulain 1990).

David and Poulain (1990; David *et al.* 2001; David 2002) have presented preliminary results for levels X (subdivision Xc) and VIII, respectively, the earliest and latest Châtelperronian occupations from Grotte du Renne. The study of the other Châtelperronian assemblage (level IX) is still in progress.

Taxonomic composition in the relatively large faunal sample from level Xc is comparable to the one described for the Denticulate Mousterian, with some changes in the relative abundance of the two major species. Reindeer increases in frequency and represents 70.0% of the assemblage, whereas horse (13.7%) declines in abundance (David 2002). Other ungulates are rare. Carnivores (10.7%) are relatively abundant in the assemblage (David and Poulain 1990). Bear (5.2%) and hyena (3.9%) are the most common carnivores. Traces of nonhuman intervention are scarce in this level.

As in the Denticulate Mousterian assemblage, some of the bear remains from level Xc suggest denning activities unrelated to the human occupation (David 2002). In contrast to the Denticulate Mousterian sample, however, the carnivore remains from level Xc show extensive evidence of cultural modification (David 2002). Most of the cutmarks identified on these specimens result from skinning (Leroi-Gourhan 1965; David and Poulain 1990). A hyena radius, however, has a disarticulation cutmark (David and Poulain 1990). Lastly, many carnivore teeth have been worked into pendants (Leroi-Gourhan and Leroi-Gourhan 1964).

The assemblage from the Châtelperronian level VIII, the most recent Châtelperronian occupation shows, however, a very different picture, given that it is dominated (54.9%) by bear remains (David 2002). Reindeer (32.1%) and horse (7.7%) elements are also present. Slightly less than two thirds of the bear remains are deciduous teeth representing at least 77 individuals. In contrast, only twelve adults are recorded. Cutmarks are absent in this assemblage. However, some burned bones and a relatively large lithic assemblage (171 tools and 118 cores) attest to human activities. Based on this information, this occupation has been interpreted as a palimpsest of episodes of bear denning and human occupations (David 2002). As a result of this ambiguity, this assemblage is not compared with the Saint-Césaire occupations.

Most of the large ungulate remains in the Denticulate Mousterian (level XI) and Châtelperronian (level Xc) occupations are from adults (David and Poulain 1990). As at Saint-Césaire, very few epiphyses of ungulates were identified in these assemblages, a phenomenon attributed to burning (David 2002). In the Denticulate Mousterian level XI, 39.7% of the fragments smaller than 3cm are burned compared to 45% of the fragments smaller[11] than 2cm in the Châtelperronian level Xc (David and Poulain 1990). In general, these proportions are comparable to those observed at Saint-Césaire.

In the reindeer sample from the Châtelperronian level Xc, innominates, vertebrae, carpals, tarsals, ribs, antlers, and phalanges tend to be underrepresented relative to heads, tibias, humeri, radio-ulnae, and metatarsals (David 2002). Phalanges are slightly more abundant in this occupation than at Saint-Césaire and are often fractured (David and Poulain 1990:321), possibly as a result of marrow-cracking. As in the Saint-Césaire occupations, the abundance of phalanx remains decreases distally to the metapodials. Importantly, skeletal representation is said to be similar in the Denticulate Mousterian occupation (David and Poulain 1990:321).

The Early Aurignacian occupation (level VII) of Grotte du Renne has recently been published in detail (Schmider 2002). The data presented here summarizes the findings of David and Poulain (2002) concerning the faunal remains. Horse (47.6%) and reindeer (34.4%) remains are most frequent in this assemblage. Other ungulates are poorly represented. In contrast, carnivore (15.1%) remains are fairly abundant. Again, the bear is the most common carnivore (61.2%). The fox is next in abundance. Rare specimens of hyena, wolf, and cave lion were recovered in this occupation. Birds (n=23),

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[11] No value is available for fragments smaller than 3cm.

dominated by the crow (*Corvus corax*), lagomophs (n=39), and marmots (n=3) are also scant in the assemblage (Mourer-Chauviré 2002; David and Poulain 2002). No evidence of cultural modification was recorded on these last taxa. However, an ulna from a lagomorph was tooth-marked, possibly by a fox (David and Poulain 2002).

Horse exploitation in the Aurignacian level VII

Based on teeth and fetal bones, horse procurement would have occurred in fall and winter in level VII. The horse elements that are most abundant in this occupation are associated with long bones and heads. Carpals, tarsals, scapulae, innominates, phalanges, and vertebrae are uncommon. As in the Denticulate Mousterian level XI and the Châtelperronian level Xc, long bone epiphyses are largely absent due to burning. David and Poulain (2002:51) have based this proposition on the observation that nearly half of the unidentified epiphyses (47%) are burned. Abundance of vertebrae, innominates, carpals, and tarsals is also affected by burning. Conversely, only two phalanges and none of the ribs are burned.

Cutmarks are present in the horse sample but are relatively rare (2.2%, excluding teeth). Mandibles were marrow-cracked almost systematically (David and Poulain 2002:53). Some of the phalanges were probably exploited for their marrow. These results are in line with those reported for Saint-Césaire.

Reindeer exploitation in the Aurignacian level VII

Reindeer was also procured during the snow-covered season in the Aurignacian level VII of Grotte du Renne, based on teeth. As at Saint-Césaire, the long bones are best represented in the reindeer sample. However, antlers are relatively rare in the Aurignacian of Grotte du Renne and heads are better represented in this occupation than is generally the case at Saint-Césaire. Ribs and vertebrae are also poorly represented, as are scapulae, phalanges, carpals, and tarsals. Long bone epiphyses are generally burned. Slightly less than haft of the first (7/20) and second phalanges (6/16) were fractured (David and Poulain 2002:69). In contrast, marrow-cracking was performed systematically on long bones.

Comparisons between Grotte du Renne and Saint-Césaire

Comparisons of the faunal assemblages from Grotte du Renne with those from Saint-Césaire are likely to yield meaningful results, given that the taxonomic composition, categories of parts affected by burning, and seasons of procurement are similar at these sites.

Correlations between the rank order of reindeer skeletal parts at Grotte du Renne, levels Xc and VII, and those for the Saint-Césaire occupations are generally high and statistically significant (Table 70). These results suggest that similar decisions were made with respect to skeletal element transport at these locations. As observed at Saint-Césaire, high utility parts were transported to Grotte du Renne, whereas low-utility parts were probably abandoned at kill locations.

	Grotte du Renne											
	Châtelperronian				Aurignacian level VII							
	reindeer				reindeer				horse			
	all minus burned		all parts		all minus burned		all parts		all minus burned		all parts	
Saint-Césaire	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*	rho	*p*
Evolved Auri (3)	.911	<***.01***	.848	≤***.0001***	.764	<**.02**	.769	<***.001***	-	**-**	-	**-**
Evolved Auri (4)	.829	***<.01***	.930	<***.0001***	.622	<**.04**	.856	≤***.0001***	.720	<**.02**	.576	<**.02**
Aurignacian I (5)	.794	***<.01***	.875	<***.0001***	.673	<**.03**	.915	<***.0001***	.607	<**.05**	.645	<***.01***
Châtelperronian (8)	.858	***<.01***	.908	<***.0001***	.760	<**.02**	.893	<***.0001***	.937	<***.01***	.706	<***.01***
Châtelperronian? (9)	.802	***<.01***	.829	≤***.0002***	.790	<***.01***	.794	<***.001***	.647	<**.04**	.470	<**.05**
Dent Mousterian (10)	.696	<**.03**	.886	<***.0001***	.580	<.06	.784	<***.001***	.668	<**.03**	.723	<***.01***

Table 70. Spearman's rho correlations between the abundance of reindeer skeletal parts in Grotte du Renne levels Xc and VII and in six faunal assemblages from Saint-Césaire. $p \leq 0.05$ are shown in bold. $p \leq 0.01$ are shown in bold italic. Data for the Châtelperronian level Xc are derived from Figure 5 in David (2002:189). Data for the Aurignacian level VII are from David and Poulain (2002:57, Table IV and p. 68, Table V).

However, this is not to imply that the two sets of assemblages are identical. For instance, front legs and skulls appear to be slightly more abundant in the Aurignacian assemblage from Arcy-sur-Cure than in the Saint-Césaire occupations[12]. In spite of these small differences, the two sites are broadly comparable in terms of skeletal part abundance. Including ribs and classes of parts that are frequently burned in the computations result in remarkably high correlation coefficients, which confirms that the two sites are very similarly structured in terms of body part representation.

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[12] This difference may be exaggerated if David and Poulain included age, wear, and morphology in their calculation of the MNE values for teeth. This would increase head representtion relative to other parts in shaft-dominated assemblages (see Chapter 5).

These comparisons can be extended to horse. It should be kept in mind, however, that summer procurement of horse is not documented at Grotte du Renne. Comparisons are limited to the Aurignacian level VII assemblage, as horse is poorly represented in the Châtelperronian level Xc. Again, Table 70 shows very strong correlations with the Saint-Césaire assemblages.

Overall, the Grotte du Renne sequence shares many features with Saint-Césaire. Burning seems to affect the same range of elements. Despite some minor variation, skeletal part representation is also very similar at these sites. The limited information available suggests that phalanges and mandibles were marrow-cracked at Grotte du Renne, in agreement with the results presented in this study. As at Saint-Césaire, birds and lagomorphs are rare at Grotte du Renne and might represent natural accumulation.

A difference with Saint-Césaire, however, is the abundance of carnivore specimens with evidence of cultural modification at Grotte du Renne. Although it has been stressed that this behavior is related to skin procurement and the collecting of teeth for the manufacture of pendants (Leroi-Gourhan 1965), the possibility that some carnivores were consumed at Grotte du Renne cannot be ruled out.

Abri Pataud

The Abri Pataud is a rockshelter located in the village of Les Eyzies (Dordogne) in southwestern France. A long sequence of Aurignacian, Gravettian, and Magdalenian occupations has been uncovered at this site by H. L. Movius (Bricker 1995). Our discussion will focus on two large Early Aurignacian assemblages: levels 14 and 11.

The faunal assemblage from level 14 (NISP=2159, Sekhr 1998:35), the basal occupation of the Abri Pataud sequence, has been studied by Bouchud (1975), Spiess (1979), and Sekhr (1998). Reindeer represents between 98 and 99% of the taxa in this assemblage, depending on the counting method. Carnivores are extremely rare, with only six remains, all from fox (Sekhr 1998). A single lagomorph specimen was found in level 14 (Bouchud 1975). Bird remains were not recovered in this level.

According to Spiess (1979), two reindeer teeth suggest that level 14 would have been occupied in winter. Some data on skeletal representation and marrow exploitation are also available. In reindeer, skeletal parts that are uncommon are antlers, vertebrae, tarsals, carpals, and scapulae. This is in marked contrast to the abundance of metatarsals, mandibles, radio-ulnas, metacarpals, humeri, tibias, and heads in the same sample. Based on the data presented by Sekhr (1998:177 and 186), 6.6% of the reindeer long bones in this occupation would be cutmarked. A few retouchers were also identified. Long bone epiphyses are rare, possibly due to burning. This is not an unreasonable proposition, as burning is fairly common in the assemblages from Abri Pataud, as noted by Théry-Parizot (2002). Unfortunately, it is not possible to know which parts are affected by this phenomenon. In level 14, most long bones appear to have been marrow-cracked. In addition, marrow exploitation of horse mandibles is also reported (Sekhr 1998).

On top of level 14 are found four small assemblages, levels 13/14, 13, 12/13, and 12, and a much larger one (NISP=2701, Sekhr 1998:38), level 11. This last occupation comprises more or less equal proportions of reindeer (49.6%) and horse (47%). Carnivores are few and consist essentially (62/69) of fox remains (Bouchud 1975). One cutmarked humerus from a fox may indicate disarticulation (Sekhr 1998). Lagomorphs and birds (total of 4 specimens) are very rare (Bouchud 1975).

In terms of seasonality, one reindeer fetal humerus and one sectioned horse tooth suggest procurement in winter (Spiess 1979:195). Reindeer parts that are most abundant are metatarsals, mandibles, metacarpals, and tibias, whereas vertebrae, carpals, tarsals, innominates, phalanges, and scapulae are poorly represented. In horse, parts that are best represented are the head, tibia, humerus, and femur. The least common elements are vertebrae, tarsals, carpals, tarsals, scapulae, innominates, and phalanges. Approximately 5.0% of the reindeer long bones from this level are cutmarked, a proportion statistically similar to level 14 ($t_s = 1.45$, $p < 0.15$). Lastly, Sekhr (1998) also noted that reindeer first and second phalanges are often fractured in levels 14 and 11, which might be interpreted as evidence of marrow-cracking.

Differences in methodology prevent the comparison of these assemblages with Saint-Césaire and Grotte du Renne. Nevertheless, the available data suggest that skeletal patterns in levels 14 and 11 are in broad agreement with those identified at these sites. It can be hypothesized that the low abundance of carpals, tarsals, innominates, and long bone epiphyses in the Abri Pataud assemblages is the result of burning. These interpretations should be considered tentative, however, due to the limited information available.

Is there evidence of resource depression during the Middle to Upper Paleolithic transition?

Comparisons with three assemblages from Grotte du Renne (Arcy-sur-Cure) and two Early Aurignacian occupations of the Abri Pataud highlight strong similarities with Saint-Césaire. The Châtelperronian and Aurignacian assemblages from Grotte du Renne are strongly and positively correlated with those of Saint-Césaire with respect to skeletal representation, which reflect that similar transport decisions were made at these locations. The Abri Pataud assemblages seem to conform to these patterns.

Although the data concerning these issues are limited, burning and marrow-cracking appear to be recorded on the same categories of bones at Grotte du Renne and Saint-Césaire. For the same reasons put forward in the discussion on Saint-Césaire, data on burning suggest that bones were burned while they were still greasy at Grotte du Renne, which indirectly implies that grease rendering is unlikely to have been a significant activity at this site. The more limited information available for the Abri Pataud suggests that the assemblages from this site are not inconsistent with these results.

However, an increase in the procurement of carnivores is documented in the early Upper Paleolithic of Grotte du Renne. Unfortunately, it is currently unclear whether these taxa were consumed or exploited only for their skins and teeth, as suggested originally by Leroi-Gourhan (1965). No increase in low-ranked taxa is apparent at Abri Pataud.

In sum, the analysis of taxonomic composition, skeletal part transport, grease rendering, and marrow exploitation suggest that resource depression occurred periodically during the Middle to Upper Paleolithic transition, but was limited in extent. This corroborates the proposition made earlier that human population densities were generally kept close to carrying capacity during the late Pleistocene. Although food stress is evidenced at Saint-Césaire, Grotte du Renne, and Abri Pataud by the marrow-cracking of low utility parts, the amplitude of these stresses do not appear to have promoted changes in adaptation. This is not to mean that the human groups who occupied these sites were invariant. Rather, it seems that fluctuations associated with resource exploitation were of similar amplitude throughout the sequences or, at least, that these fluctuations were not important enough to alter the equilibrium of the adaptive system and bring about changes in subsistence strategies.

These results are not consistent with the implications derived from the replacement model. As a result, the hypothesis of a modern human demic expansion causing the extinction of Neandertal populations appears to be refuted. An alternative to this model is offered in the final section of this study.

CHAPTER 9

AN ALTERNATIVE TO REPLACEMENT MODELS: *IN SITU* EVOLUTION

We have seen in Chapters 1 and 2 that some core assumptions of the replacement model are controversial. One of the main problems with the replacement model is the argument that modern humans had a selective advantage over "archaic" populations. The fact that the Neandertals[13] are said to have competed successfully with modern humans for resources during a considerable amount of time in the Levant (Lieberman and Shea 1994; Shea 1998) is in contradiction with this assertion. To the contrary, a growing body of studies of tool production, art, and subsistence finds no support for cognitive or adaptive differences between late Neandertals and early modern humans (e.g., Chase 1987; Pelegrin 1995; D'Errico *et al.* 1998; Speth and Tchernov 2001; Grayson and Delpech 2003). The analysis of Saint-Césaire provides strong support to these conclusions.

Equally perplexing is the lack of evidence for geographical or reproductive isolation that would have prevented gene flow between archaic and modern human populations in the "hybrid zone" that the Levant would have represented in this model.

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[13] Keeping in mind that this taxonomic attribution is debated in the Levant (e.g., Arensburg and Belfer-Cohen 1998; Wolpoff 1999).

Although some cases are known of parapatric and sympatric speciation[14] in biology, these instances are very rare and usually imply some form of ecological specialization and/or sexual isolation (Futuyma 1998).

Information flow seems to have taken place between archaic and modern humans, as seen in similar changes in tool production during the Middle to Upper Paleolithic transition in Africa and Europe. In this context, it is difficult to imagine how gene flow would have been inhibited between these populations. It was also emphasized that on ecological grounds, modern human foragers would have faced adaptive problems in Eurasia due to a dearth of information on resource availability and distribution in the new local habitats. In addition, selective advantage being a relative term, it was argued that what might have been selectively advantageous in Africa or the Levant, for instance tropical body proportions, might have been disadvantageous in Western Europe or Australasia.

It is because the data are at odds with replacement models that post-hoc scenarios like the "enculturation model" have been proposed. Unfortunately, the last years have not been particularly stimulating, as ever more scenarios have been put forward for describing the purported route followed by early modern humans and for exploring possible mechanisms of demographic expansion. These scenarios fail because no solutions are provided to the above problems with the replacement model.

The lack of evidence for resource depression during the transition at Saint-Césaire, Grotte du Renne, and Abri Pataud refutes the hypothesis of a migration or demic

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[14] Parapatric speciation refers to the evolution of reproductive isolation between populations that are continuously distributed in space and in which gene flow is substantial, whereas sympatric speciation is the evolution of reproductive isolation within a randomly mating population (Futuyma 1998:498).

expansion of modern humans out of Africa, a core assumption of the replacement model. Therefore, the replacement model is unlikely to explain the Middle to Upper Paleolithic transition in southwestern France. An alternative is to consider the possibility of an *in situ* evolution of a single population over time. We will see that this hypothesis explains the data better than replacement hypotheses and is much more parsimonious.

Cycles of reindeer abundance and the Middle to Upper Paleolithic transition

At Saint-Césaire, no significant change in subsistence strategies has been detected in the assemblages. Yet, this relative stability is documented in a period of significant climatic changes (Guyot 1990; Guyot *et al.* 1993; Marquet 1993; Grayson *et al.* 2001). Because they represent a key dimension in human adaptation, it might be productive to look at the effects of climatic fluctuations on resource distribution and availability in the period under consideration. Specifically, understanding how these changes affected human demography may shed some light on factors that caused the Middle to Upper Paleolithic transition.

The discussion will focus mostly on ungulates that were regular prey during the time span under consideration, procurement shifts in taxa rarely represented in cave sequences (e.g., mammoth, wooly rhinoceros, wild ass) being relatively difficult to track. In addition, with three exceptions (Saint-Césaire, Châtelperronian?; Roc de Combe, layer 8; Abri Pataud, layer 12), only moderate to large assemblages (NISP > 400) are incorporated in the discussion, as these are generally less affected by sampling problems.

Small assemblages like those of La Ferrassie (Delpech 1983) are therefore excluded from the discussion. Moreover, large assemblages are more likely to document multiple seasons of procurement, therefore providing a fuller picture of the diversity of prey exploited in the course of an average annual cycle. Occupations with evidence of stratigraphic mixing are avoided, but may be included when disturbance has been shown to be limited in extent. In order to minimize temporal and spatial averaging, assemblages are studied according to relatively short time slices (late Mousterian, Châtelperronian, Aurignacian 0/I) and geographical regions. Late Mousterian sites are those that date to the very end of the Middle Paleolithic (*ca* 40 ky). Sites from Gironde, Périgord, and Charente are examined as a group distinct from those of the Paris Basin (Arcy-sur-Cure).

Compared to temperate and tropical climates, subarctic and arctic habitats are characterized by low species diversity, low biological productivity, and the weak development of successional processes in vegetation (Bliss *et al.* 1973; Smith 1991). As a result, forager populations living in this type of environment, for example the Cree and the Nunamiut, adjust to this narrow spectrum by “specializing” on a single or a very small number of taxa, generally reindeer and aquatic resources (Burch 1972).

This low diversity of resources and the wide seasonal and inter-annual fluctuations in resource procurement associated with these narrow spectrum economies probably explain the low human population densities in these areas (Keeley 1988). When caribou or reindeer fail in a given year, human populations face serious subsistence problems, as there is little room for falling back on other comparably nutritious resources (Burch 1972). In these situations, problems may extend to other domains of life as well, for instance clothing, as skins are often very important in this type of adaptation (Gramly

1977). Despite certain ecological differences, especially with respect to the importance of herbaceous plants, some of these problems may have characterized the cold phases of the possibly more diverse and more steppic habitats of late Pleistocene France.

Caribou and reindeer tend to cycle widely in abundance over time (Kelsall 1968; Burch 1972; Syroechkovskii 1995; Morneau and Payette 2000). This is important for our discussion, reindeer being a very common resource in Upper Paleolithic assemblages from southwestern France. Some caribou herds known to have numbered in the tens or hundreds of thousands in the past have declined to a few thousands over a few decades as a result of changes in forage conditions (Kelsall 1968; Burch 1972; Minc 1986). Importantly, such changes would have occurred, in some cases, independently of native hunting pressure using traditional weapons (Burch 1972; Nakashima and Roué 1995).

These cycles of abundance may prompt human foragers to adapt by moving into contiguous territories (small-scale migrations) or ask assistance from neighboring groups (Minc 1986). Not uncommonly, however, these high-amplitude cycles in animal populations result in death and decline in human population densities (Burch 1972). In the next paragraphs, it is suggested that a climatically-induced narrowing of species diversity during the Middle to Upper Paleolithic transition initiated similar demographic responses in human populations in southwestern France.

Diachronic trends in taxonomic composition

As we have seen, late Pleistocene human foragers preyed almost exclusively upon medium- and large-sized ungulate resources in southwestern France prior to the

Magdalenian. In this region, ungulate taxa that are considered characteristic of temperate climates like red deer and bison are often well represented in late Mousterian and Châtelperronian assemblages, including assemblages accumulated by carnivores (Delpech 1983; Chase 1986; Guadelli 1987; Guadelli *et al.* 1988; this study). However, harsher conditions appear to have prevailed in the Aurignacian (Bouchud 1966; Delpech 1983; Delpech *et al.* 2000; Grayson *et al.* 2001). This is inferred from remarkably high proportions of reindeer remains, often higher than 85%, in many Early Aurignacian assemblages from southwestern France (Bouchud 1966, Delpech 1983; Mellars 1989a, 2004). Horse is usually the second most, and as a rule the only other, abundant taxon in these reindeer-dominated assemblages.

Increase in reindeer abundance is fairly clear in the sequence of Saint-Césaire (Figure 68). While this taxon represents only 19.7 and 33.3%, respectively, of the faunal remains (in NISP counts) from the Châtelperronian and low-density occupations, its representation rises to 83.7 and 81.6% in the overlying Aurignacian 0? and Aurignacian I occupations. These differences are statistically significant save for the comparison between the two Aurignacian occupations (Châtelperronian/low-density: $t_s = 2.32$, $p < 0.03$; low-density/Aurignacian 0?: $t_s = 7.82$, $p < 0.0001$; Aurignacian 0?/Aurignacian I: $t_s = 1.07$, $p < 0.29$).

The fact that this high proportion of reindeer in the upper part of the Saint-Césaire sequence is observed in other large Early Aurignacian samples like Abri Pataud, layer 14 (1928/1960 or 98.4%, Sekhr 1998:64), Roc de Combe[15] (873/975 or 89.5%, Delpech

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[15] Based on the total of layer 7a, 7b, and 7c, including carnivores. These are studied as a single occupation because many specimens could not be attributed to one of the three stratigraphic subdivisions identified in this layer. These subdivisions are all attributed to the Aurignacian I (Bordes and Labrot 1967). This

1983:343 and 344), and Castanet[16] (1316/1552 or 84.8% Castel in Villa *et al.* in press, Table 6) suggests that this pattern is not specific to Saint-Césaire nor the result of sample size effects (Grayson 1984). Results for Roc de Combe should be considered with caution, however, as stratigraphic mixing occurred in some parts of the site (Bordes 2003).

It is possible to explore how general this shift to reindeer-dominated assemblages is in Early Aurignacian occupations by looking at Figure 68. This figure summarizes taxonomic composition for a number of faunal assemblages from southwestern France and the Paris Basin (Table 71). The assemblage distribution confirms that late Mousterian and Châtelperronian assemblages are quite different in taxonomic composition from those of the Early Aurignacian. In general, assemblages attributed to the Early Aurignacian indicate the quasi-absence of red deer and bison and the predominance of reindeer. However, the picture is not perfectly unambiguous, as horse remains are also abundant in some Early Aurignacian occupations.

For instance, horse remains are more abundant in the large Early Aurignacian occupation (layer VII) of Grotte du Renne at Arcy-sur-Cure than reindeer. Yet, the fact that these two taxa represent in combination 97.2% of the ungulates in this assemblage, or 82.0% including the carnivores (David and Poulain 2002:51), suggests that this deviation might result from variation in the local availability of the two species, this site being relatively far (300 km) from the other ones with which it is compared. An

---

decision is reasonable as no statistical difference is found between the small samples available for subdivisions 7a and 7b ($t_s = 1.38$, $p < 0.17$). Statistical tests were not run with assemblage 7c, this sample being too small (n=12).

[16] Counts for major taxa only.

alternative is that this occupation is not perfectly contemporaneous with the other Early Aurignacian assemblages (see below). Nevertheless, the very poor representation of bison and red deer in layer VII of Grotte du Renne (0.2%) and layer 11 of Abri Pataud (0.8%) is in agreement with the proposition made above that these taxa became very rare during the Early Aurignacian.

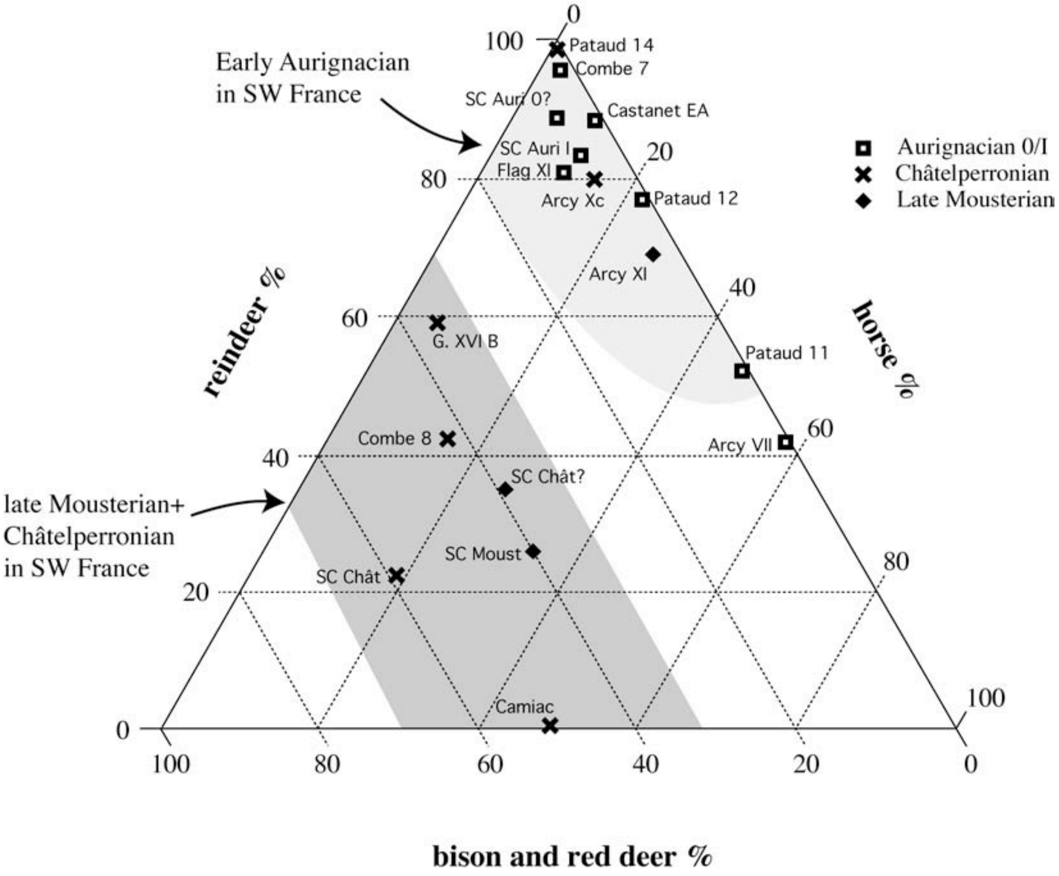

Figure 68. Relative abundance of reindeer, bison, red deer, and horse in late Mousterian, Châtelperronian, and Early Aurignacian (0/I) assemblages from southwestern France and the Paris Basin. Shaded areas do not take into accounts sites from the Paris Basin (Arcy-sur-Cure). See Table 71 for data and references. Bison and red deer are combined. Data for Saint-Césaire (SC) are from Tables 13 and 14. Legend: Grotte du Renne at Arcy-sur-Cure (Arcy); Le Flageolet I, layer XI (Flag XI); Grotte XVI, layer B (G. XVI B) Abri Pataud, layers 14, 12, and 11 (Pataud); Roc de Combe, layers 7 and 8 (Combe).

Assemblage	*Time Period*	*NISP*	*Reference*
Grotte du Renne, layer VII	Early Aurignacian	4481	David and Poulain 2002:51
Grotte du Renne, layer Xc	Châtelperronian	1726	David 2002:188
Grotte du Renne, layer XI	Mousterian	1436	David and Poulain 1990:320
Le Flageolet I, layer XI	Early Aurignacian	656	Grayson *et al.* 2001:1121
Castanet	Early Aurignacian	1552[1]	Castel (in Villa *et al.* in press: Table 6)
Grotte XVI, layer B	Châtelperronian	589[2]	Grayson and Delpech 2003:1636
Abri Pataud, layer 11	Early Aurignacian	2646	Sekhr 1998:64
Abri Pataud, layer 12	Early Aurignacian	267	Sekhr 1998:64
Abri Pataud, layer 14	Early Aurignacian	1960	Sekhr 1998:64
Roc de Combe, layer 7	Early Aurignacian	975	Delpech 1983:343-344
Roc de Combe, layer 8	Châtelperronian	183	Delpech 1983:343-344
Camiac	Châtelperronian	1035	Guadelli *et al.* 1988:62

[1] major taxa only

[2] Carnivores excluded. These are dominated by the bear, a taxon presumed to be unrelated to the human occupation (Grayson and Delpech 2003).

Table 71. NISP counts and references for the faunal assemblages that are compared with Saint-Césaire in Figure 68. Except for Grotte XVI, carnivores are included.

Horse is also well represented in the Aurignacian I of Abri Pataud, level 11. Few species other than reindeer and horse have been identified in this occupation, these two taxa representing the vast majority (97.8%) of the specimens in this sample. The high proportion of horse remains in level 11 seems to document a chronological pattern at Abri Pataud, as this taxon increases steadily in the Early Aurignacian sequence of this site. Although horse remains are absent from levels 14 and 13, this species increases to proportions of 21.7% and 46.4%, respectively, in the overlying levels 12 and 11. This increase is statistically significant for the comparisons including levels 13, 12, and 11, but not with level 14 (level 14 versus level 13: $t_s = 0.00$, $p < 1.00$; level 13 versus level 12: $t_s = 10.72$, $p < 0.0001$, level 12 versus level 11: $t_s = 8.25$, $p < 0.0001$).

Interestingly, a similar increase in horse representation is noted between the Aurignacian 0? and the Aurignacian I occupations ($t_s = 4.14$, $p < 0.0001$) and between the Aurignacian I and the Evolved Aurignacian EJM occupations from Saint-Césaire

($t_s = 1.97$, $p < 0.05$). This chronological trend indicates that reindeer was largely dominant in the earliest Aurignacian I, whereas horse increased in frequency in more recent Aurignacian occupations in southwestern France.

A cultural or climatic pattern?

Because reindeer is tightly associated with cold climatic conditions (Syroechkovskii 1995) and habitat of low taxonomic diversity, associations that probably prevailed in the late Pleistocene as well, the increase in reindeer abundance observed at Saint-Césaire may signal the onset of a climatic deterioration during the early Upper Paleolithic. Yet, are these shifts in taxonomic composition directly linked to climatic change, as proposed by Grayson *et al.* (2001), or were they mostly mediated by cultural factors, as argued by Mellars (2004)?

The hypothesis of a climatic deterioration during the Middle to Upper Paleolithic transition in southwestern France can be explored further using an independent line of evidence: the Saint-Césaire microfauna. These very small taxa are of much help here, as they most probably represent background deposition in late Pleistocene assemblages. Moreover, many rodent taxa are characterized by a relatively narrow niche and can thus be used as ecological markers (Marquet 1993).

Proportions of rodents adapted to cold latitudes are compared below with proportions of reindeer in the Saint-Césaire occupations to investigate whether similar abundance patterns are observed throughout the sequence in these two datasets. In these comparisons, MNI are used for rodents because in very small taxa a new identified *specimen* can often be identified as an additional individual as well (Grayson 1984). Therefore, MNI is more likely to increase linearly with sample size in microfaunal samples. In much larger taxa, this is rarely true and MNI will tend to increase following a power function. For these reasons, NISP is preferred here to MNI for estimating reindeer abundance.

The narrow-skulled vole (*Microtus gregalis*) and the common vole (*Microtus arvalis*) are the best represented taxa in the Saint-Césaire microfauna (Marquet 1988, 1993). Today, the narrow-skulled vole is restricted to Palearctic tundra and wooded steppe habitats and is found in Eurasia from the White Sea to the Bering Strait, with known occurrences in southern Siberia, Mongolia, and northwest China (Wilson and Reeder 1993). In contrast, the common vole is typical of more temperate environments. Its actual geographical distribution covers most of Europe, excluding southern Spain and the Mediterranean region (Wilson and Reeder 1993; Marquet 1993).

When we look at the stratigraphic distribution of macrofaunal and microfaunal taxa at Saint-Césaire, a relatively good fit is found between the respective abundance of the narrow-skulled vole and reindeer (Figure 69). This is observed in all of the occupations, with the exception of the Châtelperronian and the low-density assemblage. It should be noted, however, that the Denticulate Mousterian (n=2) and Châtelperronian? (n=9) microfaunal samples have very small sample size. However, the fact that the narrow-skulled vole represents only 55.9% of the EJOP microfaunal sample (n=68, Marquet 1993:139), a sample in which remains from both the Châtelperronian? and Châtelperronian occupations are mixed together, confirms the relatively low abundance of this taxon in the bottom of the Saint-Césaire sequence. Therefore, the data suggest that there has been a climatic deterioration during the occupation of the site, possibly between the end of the Châtelperronian and the beginning of the Aurignacian I.

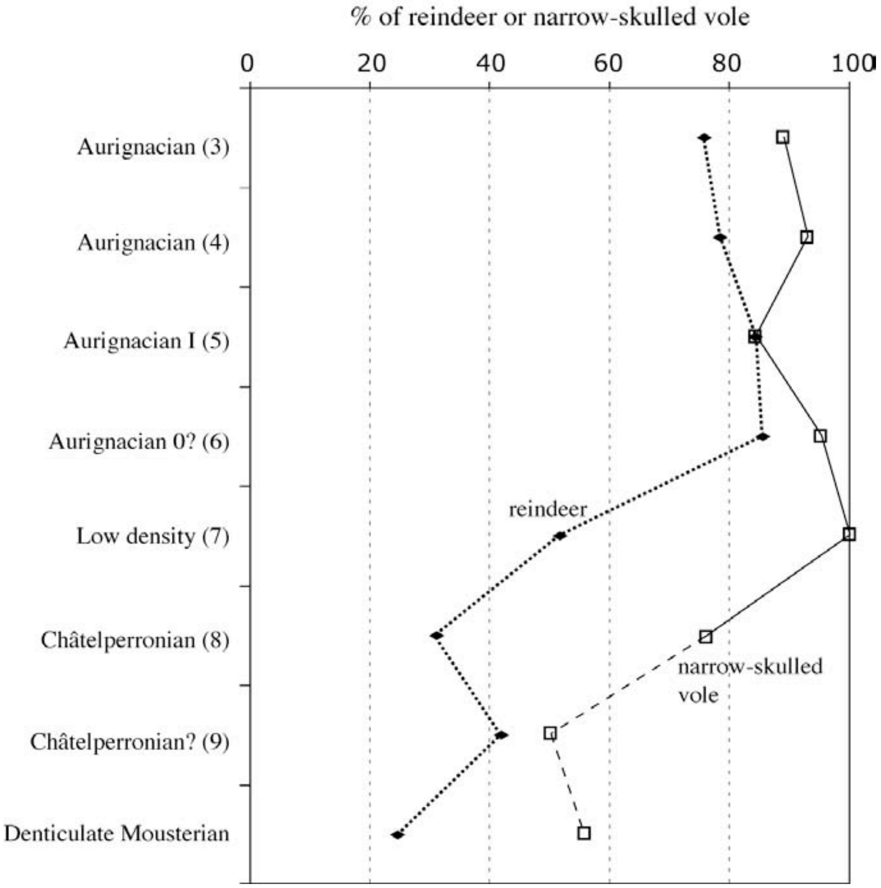

Figure 69. Proportions of reindeer (in NISP) in the macrofaunal samples from Saint-Césaire compared to proportions of narrow-skulled voles (in MNI) in the microfaunal samples from the same site. The wide dashed lines in the narrow-skulled vole line indicate small sample size. Reindeer data from Tables 13 and 14 and microfaunal data from Table 18.

Taking into account the above cautionary notes about the stratigraphic integrity of this site, data for Roc de Combe also indicate an increase in abundance of the narrow-skulled vole, which rises from 12.9% (n=31) in the Châtelperronian to 29.2% (n=294) in the Early Aurignacian occupations (Marquet 1993:73). The difference between the two occupations is statistically significant (t_s=2.16, $p \leq 0.04$). The fact that an increase in narrow-skulled vole abundance is observed in both sites confirms the hypothesis of a climatic deterioration. Unfortunately, little comparable data are available for other sites documenting the transition, generally as a result of small sample size or lack of microfaunal analysis.

Based on the present data, it can be concluded that the increase in the relative abundance of reindeer in the early Upper Paleolithic was driven by climatic change. The fact that pollen data indicate that mean July temperature decreased in France during the same period (Guyot 1990) provides strong support to these arguments. In conclusion, these results confirm the interpretations of Grayson *et al.* (2001), but appear to disprove the cultural argument put forward by Mellars (2004).

Ungulate diversity and narrow spectrum economies

It is commonly argued that human population densities were higher in general during the Upper Paleolithic in southwestern France than during the Middle Paleolithic (e.g., Mellars 1996). These inferences are generally based on site counts. However, site counts is probably a poor indicator of population density in the Paleolithic, as it is modulated by a number of variables that might not have been constant. For instance, the greater archaeological visibility of certain highly diagnostic artifacts (e.g., split-based sagaies) may inflate the representation of their associated technocomplexes. The greater depth at which Mousterian assemblages are usually found possibly results in lower probabilities of being sampled than more recent cultural periods (e.g., Magdalenian). In addition, differences in time span, changes in sedimentation rates, shifts in settlement patterns, mobility, etc. may all skew comparability of cultural periods.

A more fruitful approach is to examine ethnographic situations in which the dynamic relationship between human population densities and types and densities of resources exploited has been studied. These studies can provide insights on past forager population densities.

In that perspective, the evidence reviewed in this study suggests that it is only at the beginning of the Magdalenian that forager groups occupying southwestern France designed new strategies for coping with fluctuations in food procurement by including low-ranked resources in the diet. In this case, carrying capacity was raised in absolute terms, holding resources and climatic conditions constant. However, before the Magdalenian, *human population densities were most probably tracking climatically-induced fluctuations in ungulate diversity and abundance relatively closely, expanding and declining in response to these changes*.

The climatic deterioration identified at Saint-Césaire, and, possibly, Roc de Combe, appears to have decreased ungulate diversity during the Middle to Upper Paleolithic transition. Specifically, this would have occurred through a decline in red deer and bison populations, taxa that are both very poorly represented in the Early Aurignacian compared to most late Mousterian and Châtelperronian assemblages. This is not unexpected given the above observation that cold habitats are generally characterized by narrower taxonomic breadth. In fact, none of the large Early Aurignacian assemblages available (Aurignacian 0? and Aurignacian I occupations of Saint-Césaire, Aurignacian I of Castanet and Roc de Combe, Proto-Aurignacian/Aurignacian I of Grotte du Renne) show combined proportions of red deer and bison that are higher than 5%. This proportion decreases to only 1.6% when the comparisons are limited to Aurignacian I assemblages, that is, when we exclude the Aurignacian 0? assemblage of Saint-Césaire.

Undoubtedly, what is being monitored here is a severe contraction of red deer and bison populations in southwestern France. This contraction of red deer and bison populations suggests that the list of ungulate species regularly included in the diet was reduced from four (reindeer, red deer, horse, and bison) at the beginning of the Châtelperronian to two (reindeer and horse) at the end of this episode. It is assumed here that taxa rarely represented in early Upper Paleolithic assemblages (e.g., wooly rhinoceros, mammoth, wild boar, roe deer) did not increase, and possibly also decreased, in abundance during this episode. The available data seems to support this proposition, but this remains to be fully demonstrated.

Reduction in red deer and bison population densities was probably partially countered by an increase in reindeer abundance in southwestern France. Nevertheless, a narrowing of the ungulate spectrum would have increased human dependence on fewer, cyclically abundant, resources. Burch has convincingly shown that caribou-dependent economies are affected by high-amplitude fluctuations in food procurement:

> “The more restricted the temporal scope and geographic scope under consideration, the greater the likelihood that fluctuations will occur, the more often they are likely to occur, and the more extreme the fluctuations are likely to be. It is at the level of the individual herd that the dependability of caribou as a human resource is most questionable. Major fluctuations at this level inevitably impose severe limitations on human numbers and distributions in every locality in which caribou are a major basis of human subsistence. Since the range of a given herd can cover anywhere from tens to hundreds of thousands of square kilometers, fluctuations in a single herd might well affect a number of human populations. Given the current state of knowledge, it is not

> unreasonable to assume that *human populations largely dependent upon caribou will be faced with a major resource crisis once at least every 2 or 3 generations* (Burch 1972:356, original emphasis)"

Minc (1986) and Nakashima and Roué (1995) also discussed the vulnerability of narrow spectrum economies strongly dependent on caribou.

But how do fluctuations in reindeer abundance affect human population density? According to Burch's (1972:365, original emphasis): "among historic tarandus-hunting populations in general, and the Eskimo groups described in this paper in particular, population density consistently has been an *inverse* function of the dependence of that population on tarandus." In Paleolithic research, demographic implications ensuing from changes in ungulate taxonomic diversity have been examined with respect to cultural changes recorded during the Upper Paleolithic, for instance with respect to mobility, exchange, and labor investment in portable art (Jochim 1987).

These observations suggest that an increased dependence on reindeer during the Middle to Upper Paleolithic transition amplified seasonal and temporal fluctuations in ungulate procurement. Because the subsistence system did not seem to have been modified to cope with the deteriorating climatic conditions observed in the Early Aurignacian of southwestern France, *amplified fluctuations in prey procurement, accompanied, perhaps, by a decrease in ungulate biomass, would have resulted in declines in human population densities, rather than a demographic expansion, as generally argued.* Furthermore, because human groups are inferred to have been small and weakly interconnected, these high-amplitude fluctuations in ungulate procurement might have triggered small-scale bottlenecks in human populations. In this scenario, the lack of human occupation in the northern part of Europe during the last Glacial

Maximum (Jochim 1987; Conard and Bolus 2003) would reflect the peak of this process. These conclusions may extend to adjacent regions with broadly similar ecological conditions, for instance Germany, Switzerland, and Belgium. In fact, it may characterize Northern and Central Europe in general. Clearly, some minor regional variation is expected, but this model would remain true in its general lines.

An important point needs to be stressed concerning the scale of these fluctuations in ungulate diversity. Competition with modern humans for resources would have had nearly immediate economic effects on subsistence. In contrast, significant climatic changes are somewhat unpredictable and may transcend a single human generation. In a forager group, only elders might have experienced or be vaguely aware of such changes (Colson 1979).

However, climatic changes are not necessarily gradual. Short climatic oscillations like the Heinrich and Dansgaard-Oeschger events occurred in the late Pleistocene. Yet, it is not clear whether these oscillations are recorded in continental pollen sequences from France and Northern Europe (Guyot *et al.* 1993). Consequently, these oscillations might not have had immediate major effects on vegetation, and by extension, on the abundance and distribution of the terrestrial animal species that feed on them. The "inertia" and slow response of vegetal communities to these short-term changes may be responsible for this (Guyot *et al.* 1993). Thus, at the level of resolution discussed here, these short-term oscillations might be of lesser importance in terms of ungulate diversity than long-term directional changes.

Human population densities, genetic drift, and transitional assemblages

If the above interpretations are correct, a decrease in population density in the early Upper Paleolithic of southwestern France has important implications. A decline in local population densities may have caused small-scale bottlenecks in some Neandertal populations and promoted genetic drift. Genetic drift is a very important concept often downplayed or ignored in the debate, perhaps, because it is difficult to document with archaeological material. Yet, it has been argued that:

> "Because all populations are finite, alleles at all loci are potentially subject to random genetic drift -but all are not necessarily subject to natural selection. For this reason, and because genetic drift constitutes evolution by chance alone, some evolutionary geneticists feel that genetic drift should be the 'null hypothesis' used to explain an evolutionary observation unless there is positive evidence for natural selection or some other factors" (Futuyma 1998:297).

Genetic drift is especially relevant in this discussion, as Neandertal forager groups were almost certainly small, and small populations are demographically vulnerable, due to stochastic processes affecting reproduction (Li and Grauer 1991).

Typically, genetic drift reduces genetic variation. Because it is a random process, this often increases divergence between populations (Futuyma 1998). This process may lead to the rapid fixation of rare alleles, including, in very rare cases, those that are slightly deleterious (Li and Grauer 1991). For all these reasons, genetic drift is a real possibility in the context of declining human population densities in the early Upper Paleolithic of southwestern France and may well explain some, perhaps most, of the biological changes observed during this episode.

Although participation in the modern human reticulate network might have been weaker during the early Upper Paleolithic, there is little evidence that a migration or population replacement occurred. Rather, it appears that the Middle to Upper Paleolithic transition is more parsimoniously explained by a combination of demographic and economic factors acting on local populations, as argued here. Indeed, combined with relatively rapid demographic changes, genetic drift may help elucidate why some of the biological changes observed during the transition appear to be "sudden" in Western Europe.

In relation to the last issue, a decline in human population densities in southwestern France in the early Upper Paleolithic may provide an explanation for the "abrupt" appearance of the Aurignacian in this area. A decrease in population densities probably resulted in the creation of fewer sites and, possibly, a poor archaeological visibility of the assemblages marking the transition between the Châtelperronian and the Aurignacian. In addition, changes were perhaps too rapid at the archaeological scale to be recorded, except in some rare cases. The "Aurignacian 0" occupation possibly documented at Le Piage by J.-G. Bordes (2002) and the Aurignacian 0? occupation from Saint-Césaire might represent such transitional assemblages. Further work may confirm these propositions.

Based on these findings, the Middle to Upper Paleolithic transition in southwestern France is best viewed as an *in situ* evolution of human populations facing increased fluctuations in ungulate procurement, rather than a complete re-colonization of Eurasia and Australia by expanding modern humans. In this regard, the consistent use of some specific classes of faunal material for fuel, combined with striking similarities in retoucher production and subsistence strategies throughout the sequence of Saint-Césaire might be viewed as evidence of cultural continuity. However, it should be kept in mind that ecological constraints probably contributed appreciably to channel decisions in this respect. Nevertheless, the many similarities observed in faunal exploitation at Saint-Césaire over a relatively long time span, approximately 15,000 years, may testify to the evolution of a single human population at this location.

Explaining the Middle to Upper Paleolithic transition

One may argue that high-amplitude fluctuations in food procurement also occurred in periods other than the Middle to Upper Paleolithic transition. In the same vein, high-amplitude fluctuations may not be limited to reindeer and might have been typical of other taxa that were abundant in late Mousterian and Châtelperronian assemblages. For instance, bison is described ethnographically as a fluctuating resource in the Canadian plains (Moodie and Arthur 1976). This is possibly true of horses and red deer as well. However, these arguments would miss the point. What is argued here is not that fluctuations were restricted to reindeer procurement, but rather that fewer ungulate taxa were abundant in the early Upper Paleolithic. This would have increased human group vulnerability to cycles of prey abundance, as fall-back resources would have been fewer. This seems to be the explanation for the low population densities in regions in which foragers are heavily dependent on caribou. The narrow spectrum of ungulates documented in many large Early Aurignacian assemblages, some of which, like Saint-Césaire, show multiseasonal occupations, appears to support such a view.

Although climatic change is an independent variable in the forager system, cultural features are not. In fact, most of the cultural changes documented during the transition are probably tightly interrelated. Therefore, their interaction in an explanatory model should be viewed in a systemic, rather than monocausal, perspective. It is possible that increased fluctuations in food procurement promoted greater social integration, the spread of art, and an expansion of social networks during the Middle to Upper Paleolithic transition (White 1982; Jochim 1987; Gamble 1999). However, because declines in human population densities probably occurred in other periods as well, these propositions do not explain the timing of these cultural changes. The population bottleneck model discussed here simply provides a more viable and more parsimonious explanation for the Middle to Upper Paleolithic transition in southwestern France than replacement hypotheses and better accounts, with fewer assumptions, for *some* biological and cultural changes associated with this episode. However, additional studies will be necessary to provide a more complete explanation for cultural change in the Middle to Upper Paleolithic transition.

CHAPTER 10

FINAL CONCLUSIONS AND RESEARCH PROSPECTIVES

This study has attempted to move the discussion beyond the unproductive Neandertal/modern human dichotomy. A review of the evidence shows that the hypothesis of a modern human migration or demic expansion into Eurasia and Australia during the Middle to Upper Paleolithic transition is highly contentious. The most probable reason for the popularity of the replacement model is its deep historical roots, based essentially upon Breuil's and Boule's adoption of the diffusionist paradigm in the early nineteenth century. Although migrations and demic expansions probably occurred in the late Pleistocene, these are believed to have been small-scale in nature prior to the emergence of farming economies. In that perspective, a new approach to the problem was offered here.

In order to clarify some of these issues, archeological predictions were generated in this study based on the assumption that modern human groups migrated or expanded into Eurasia and Australia during the Middle to Upper Paleolithic transition. These predictions were tested using eight archaeozoological assemblages from Saint-Césaire. The analysis of the Saint-Césaire fauna did not yield evidence of resource depression during the early Upper Paleolithic, which was predicted to occur following a modern human dispersal into Eurasia. Rather, stability and continuity in decision-making were observed with regard to resource exploitation. These conclusions appear to be corroborated by comparisons with the fauna from Grotte du Renne at Arcy-sur-Cure (David and Poulain 1990, 2002) and Abri Pataud (Bouchud 1975; Sekhr 1998). Because these results are in contradiction with the implications derived from the replacement model, it is fairly clear that we need to discuss the Middle to Upper Paleolithic transition according to a new paradigm.

As an alternative, it was argued that these assemblages testify to the *in situ* evolution of local groups that experienced decreasing ungulate diversity and increasing fluctuations in ungulate procurement during the early Upper Paleolithic. This model suggests that a decline in human population densities in southwestern France fueled significant biological and cultural changes. In this scenario, Neandertals would be no more than a peripheral modern human population shaped through natural selection and genetic drift by the local conditions (Thorne and Wolpoff 1981; Wolpoff 1999).

Another conclusion emerging from this study is that adaptation, genetic drift, and natural selection are key issues to the problem. These aspects must be integrated in future attempts at solving the debate on the Middle to Upper Paleolithic transition. Likewise, these endeavors will only be viable if they incorporate findings from evolutionary biology, human genetics, physical anthropology, and archaeology. This is because the solution does not lie in DNA, nor will it be found in a complex description of the Aurignacian 0 reduction sequences, or of a new “hybrid” fossil. The solution will only emerge by integrating the information from each of these approaches. Hopefully, this study has been successful in this respect.

APPENDICES

Appendix 1. MNI counts by species and level for mammal and fish remains.

	Moust (10)		Ejop (8-9)		Châtel? (9)		Châtel (8)		EJO (6-7)		low dens (7)	
Artiodactyla	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
reindeer	4	19.0	5	20.0	2	12.5	6	13.9	5	27.8	2	18.2
bison	6	28.6	6	24.0	4	25.0	12	27.9	4	22.2	1	9.1
red deer	1	4.8	1	4.0	1	6.3	4	9.3	1	5.6	1	9.1
megaceros	1	4.8	1	4.0	1	6.3	.	.	1	5.6	.	.
roe deer	.	.	.	.	.	.	1	2.3	.	.	.	.
wild boar	.	.	1	4.0	1	6.3	1	2.3	1	5.6	.	.
Perissodactyla												
horse	4	19.0	4	16.0	3	18.7	6	13.9	2	11.1	1	9.1
wooly rhino	1	4.8	1	4.0	1	6.3	1	2.3	1	5.6	1	9.1
wild ass	.	.	1	4.0	.	.	1	2.3	.	.	.	.
Proboscidea												
mammoth	1	4.8	1	4.0	1	6.3	1	2.3	.	.	1	9.1
Carnivora												
spotted hyena	1	4.8	1	4.0	.	.	1	2.3	1	5.6	1	9.1
wolf	1	4.8	.	.	1	6.3	1	2.3	1	5.6	.	.
arctic fox	.	.	.	.	.	.	1	2.3	.	.	1	9.1
unspecif. fox	1	4.8	1	4.0	1	6.3	2	4.6	1	5.6	1	9.1
bear	.	.	1	4.0	.	.	.	.	.	.	.	.
polecat	.	.	.	.	.	.	1	2.3	.	.	.	.
pine marten	.	.	.	.	.	.	.	.	.	.	.	.
lynx	.	.	.	.	.	.	.	.	.	.	.	.
badger	.	.	.	.	.	.	.	.	.	.	.	.
cave lion	.	.	.	.	.	.	1	2.3	.	.	.	.
Lagomorpha												
hare	.	.	.	.	.	.	.	.	.	.	.	.
unspec lagom	.	.	1	4.0	.	.	1	2.3	.	.	1	9.1
Pisces												
cyprinid	.	.	.	.	.	.	1	2.3	.	.	.	.
brown trout	.	.	.	.	.	.	1	2.3	.	.	.	.
Total	21	100.2	25	100.0	16	100.3	43	99.5	18	100.3	11	100.1
Total with antlers	21	-	37	-	19	-	52	-	19	-	16	-

1.1. Saint-Césaire. MNI counts by species and level for mammal and fish remains.

	Auri 0? (6)		Auri I (5)		Evol Auri (4)		Evol Auri (3)		Total 10-3	
Artiodactyla	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
reindeer	9	40.9	42	58.3	12	50.0	7	43.8	94	35.1
bison	2	9.1	5	6.9	2	8.3	2	12.5	44	16.4
red deer	1	4.5	1	1.4	1	4.2	1	6.3	13	4.8
megaceros	.	.	1	1.4	.	.	.	.	5	1.9
roe deer	.	.	.	.	.	.	.	.	1	0.4
wild boar	.	.	1	1.4	.	.	.	.	5	1.9
Perissodactyla										
horse	1	4.5	8	11.1	4	16.7	2	12.5	35	13.1
wooly rhino	1	4.5	1	1.4	1	4.2	.	.	9	3.4
wild ass	.	.	.	.	.	.	.	.	2	0.7
Proboscidea										
mammoth	1	4.5	1	1.4	1	4.2	1	6.3	9	3.4
Carnivora										
spotted hyena	.	.	1	1.4	.	.	1	6.3	7	2.6
wolf	1	4.5	2	2.8	1	4.2	1	6.3	9	3.4
arctic fox	1	4.5	1	1.4	.	.	.	.	4	1.5
unspecif. fox	1	4.5	3	4.2	1	4.2	1	6.3	13	4.8
bear	.	.	.	.	.	.	.	.	1	0.4
polecat	1	4.5	1	1.4	.	.	.	.	3	1.1
pine marten	2	9.1	.	.	.	.	.	.	2	0.7
lynx	.	.	1	1.4	.	.	.	.	1	0.4
badger	.	.	1	1.4	1	4.2	.	.	2	0.7
cave lion	.	.	1	1.4	.	.	.	.	2	0.7
Lagomorpha										
hare	1	4.5	.	.	.	.	.	.	1	0.4
unsp. lagom.	.	.	1	1.4	.	.	.	.	4	1.5
Pisces										
cyprinid	.	.	.	.	.	.	.	.	1	0.4
brown trout	.	.	.	.	.	.	.	.	1	0.4
Total	22	99.6	72	100.1	24	100.2	16	100.3	268	100.1
Total with antlers	22	-	77	-	25	-	16	-	304	-

1.1. Saint-Césaire. MNI counts by species and level for mammal and fish remains (continued).

Appendix 2. Analysis of the bird remains from Saint-Césaire by Véronique Laroulandie

Les Oiseaux de Saint-Césaire

Composition du spectre avifaunique

Les Oiseaux de Saint-Césaire appartiennent à six ordres.

Les Ansériformes sont représentés par le Canard pilet *Anas acuta*, la Sarcelle d'hiver *Anas crecca* ainsi que par une Oie *Anser* sp. et un Fuligule *Aythya* sp. d'une espèce indéterminée. Le Canard pilet est représenté dans la couche EJO sup (Aurignacien 0?) par les éléments de la ceinture scapulaire (scapula et coracoïde droit et gauche, fragment de fourchette) ainsi qu'une portion proximale d'humérus droit. Ces vestiges appartiennent probablement au même individu. En témoigne le fait qu'ils ont été trouvés dans le même carré et le même décapage ainsi que la présence à l'intérieur des éléments de la ceinture, exceptée la fourchette, d'os médullaire.

Les rapaces diurnes et nocturnes sont présents dans l'avifaune de Saint-Césaire. Les Accipitriformes sont représentés par deux taxons de grande taille, l'Aigle royal *Aquila chrysaetos*, d'une part dans la couche EGPF (Moustérien a Denticulés), le Vautour, d'autre part dans les couches EJOP inf (Châtelperronien?), EJF (Aurignacien I) et EJM (Aurignacien évolué). Une griffe et une phalange du pied provenant respectivement des couches EJO sup (Aurignacien 0?) et EJF (Aurignacien I) appartiennent à un Strigiforme.

Les Galliformes sont représentés uniquement par deux restes de Lagopèdes *Lagopus* sp., l'un trouvé dans l'ensemble EJO (couches 6-7), l'autre dans l'ensemble EJF (Aurignacien I).

Deux taxons au moins appartiennent à l'ordre des Charadriiformes. Il s'agit d'une part du Mergule main, *Alle Alle,* identifié dans l'ensemble EJO sup (Aurignacien 0?) et d'autre part du Pluvier, *Pluvialis* sp., rencontré en EJO sup (Aurignacien 0?) et EJF (Aurignacien I). Les trois ossements de Mergule nain (une ulna complète, un carpométacarpe et un tibiotarse fragmentaires) possèdent les mêmes coordonnées spatiales, ce qui indique qu'ils proviennent sans doute d'un seul et même individu. Cette espèce est rarement décrite dans le Pléistocène supérieur français, ce qui s'expliquer par le fait qu'elle ne fréquente l'intérieur des terres que lors de conditions anormales (tempêtes). Ainsi que le propose Mourer-Chauviré (1975) pour les vestiges provenant de la Fage, ces restes appartiennent vraisemblablement à un individu égaré.

Enfin les Passériformes sont représentés par le Grand corbeau, *Corvus corax*, et une espèce indéterminée de petite taille dans la couche EJF (Aurignacien I) ainsi que par une espèce de la taille du merle dans la couche EJOP (couches 8-9).

Quelques éléments sur la saison de mort

Un élément remarquable de la faune aviaire de Saint-Césaire est la présence de plusieurs ossements appartenant à des individus immature du point de vue ostéologique (Tableau). Les oiseaux dont proviennent ces restes sont morts durant la bonne saison.

Par ailleurs, l'os médullaire observé dans les ossements de Canard pilet indique également que cet individu, une femelle, est morte durant la période de reproduction. L'os médullaire, qui un développement de phosphate de calcium à l'intérieur des os, constitue une réserve de minéraux pour l'élaboration de la coquille. Au sein d'une population, il se trouve chez les femelles qui pondent. La période durant laquelle cet os est présent se situe avant, pendant et peu après la ponte. La durée des périodes précédant et succédant la ponte n'est pas connue précisément pour cette espèce. Toutefois, au vue des données disponibles pour la poule domestique, une estimation respectivement de une à deux semaines et de une à trois semaines peut être proposée (Lentacker et Van Neer, 1996). Sachant que la période de ponte du Canard pilet s'étale de mars à juin, le moment de l'année durant lequel l'os médullaire est présent se situe approximativement de mi-février à mi-juillet.

Taphonomie

La fragmentation des vestiges est importante : seuls 7 restes sur 64 sont complets ou presque complets. Sans préjuger de la cause, la fragmentation s'est produite sur certains ossements lorsqu'ils été encore frais. En outre, des phénomènes post-depositionnels (pression des sédiments et fouille) sont à l'origine d'une bonne part du fractionnement du corps des os longs.

La lecture des surfaces osseuses n'a révélé aucune trace résultant de l'activité d'un prédateur quel qu'il soit (stries, brûlures récurrentes, peeling, rognage, digestion…). Cette absence peut en partie résulter de la mauvaise conservation de certaines pièces (traces de racines, desquamation), état peu favorable à la préservation des stigmates de prédateurs. Or, l'absence de traces qu'elles soient anthropique ou non-anthropique est difficilement interprétable comme une absence d'activité, en particulier lorsque les ossements sont peu nombreux par espèce et de conservation moyenne. Par exemple, une accumulation aviaire telle que celles des Eglises (Ariège) qui selon toutes vraisemblances résulte d'une activité humaine présente très peu de stigmates anthropiques (moins de 5 %). En raison du faible nombre de vestiges, le recours à des méthodes basées sur la quantification des éléments anatomiques n'est pas envisageable. La question de l'origine de l'accumulation des restes aviaires à Saint Césaire reste donc entière.

Pour la discussion, considérons un instant que les restes d'oiseaux résultent d'un apport anthropique. Dans la perspective de cette hypothèse, l'apport alimentaire constitué par cette ressource fut au mieux très faible relativement aux Ongulés.

Signification paléoclimatique et paléoenvironnementale

Même si la détermination jusqu'au niveau spécifique n'a pas été possible, la présence d'un tarsométatarse de jeune Pluvier dans la couche EJF (Aurignacien I) est importante d'un point de vue climatique. Cet os appartient en effet à un individu mort vraisemblablement au niveau de l'aire de nidification. Or, actuellement, aucune espèce de Pluvier ne nichent en France. Le pluvier argenté, *P. squatarola,* établit son nid dans la toundra arctique du centre nord de la Russie, du nord de la Sibérie et d'Alaska tandis que le Pluvier doré, *P. apricaria*, niche en Norvège, Suède, Finlande, Nord du Royaume-Uni ainsi qu'en Islande. Aujourd'hui, ces deux espèces sont hivernantes en France. Deux autres espèces, le Pluvier américain, *P. dominica,* et le Pluvier fauve, *P. fulva,* sont migratrices exceptionnelles en Europe de l’Ouest. La première niche au Nord du Canada et en Alaska, la seconde dans la toundra sibérienne et à l’ouest de l’Alaska. La présence de ce reste osseux indique donc qu’un climat plus froid que l’actuel régnait au moment de la formation de l’ensemble archéologique EJF (Aurignacien I). Ce vestige atteste également de l’existence d’un paysage ouvert. Cette tendance est confirmée par la présence du Lagopède. La Sarcelle d’hiver apporte à ce tableau une touche d’humidité .

Un environnement froid et découvert existait également lors de la formation de la couche sous-jacente EJO (couches 6-7), en témoigne le Lagopède.

En EJO sup (Aurignacien 0?) plusieurs ossements de Canard pilet appartenant à une femelle morte sur l’aire de nidification indiquent un climat plus rigoureux que l’actuel. Son aire de nidification normale se situe en effet au delà du territoire français, en Europe du Nord et de l’Est. Cette espèce évoque par ailleurs l’existence à proximité du site d’un paysage de dunes ou d’un environnement humide, de marais, de tourbières, d’îles lacustres.

Appendix 3. MNE counts for reindeer, bison, and horse elements.

EGPF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler						
cranial/maxillary teeth	4	1	67	2	90	4
mandible/lower teeth	10	3	77	2	86	10
atlas						
axis						
other cervical vertebra	1	1			1	1
thoracic vertebra	3	1			2	1
lumbar vertebra					1	1
sacrum						
rib	8	1	9	1	15	1
sternum	5	1				
scapula	2	1	1	1	7	2
proximal humerus						
shaft humerus	10	4	8	4	6	4
distal humerus						
proximal radius					1	1
shaft radius	17	5	5	2	2	1
distal radius						
proximal ulna						
shaft ulna	2	1			3	2
distal ulna					1	1
scaphoid						
lunatum						
triquetrum					1	1
pisiform					2	2
capitatum	1	1	1	1		
hamatum	1	1			1	1
proximal metacarpal	1	1	4	4	1	1
shaft metacarpal	12	4	3	4		
distal metacarpal			1	2	2	2
pelvis			2	1	2	1
proximal femur			1	1		
shaft femur	9	5	2	1	6	2
distal femur			1	1		
patella						
proximal tibia			2	2		
shaft tibia	36	6	6	3	46	8
distal tibia					1	1

3.1. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Denticulate Mousterian assemblage (EGPF).

EGPF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar	1	1	3	3	2	1
talus			1	1		
calcaneum	1	1				
cubo-navicular/navicular			1	1		
smaller cuneiform			1	1		
greater cuneiform					1	1
proximal metatarsal	3	3	1	1	1	1
shaft metatarsal	73	7	2	1	13	2
distal metatarsal					1	1
proximal metapodial	1	1	1	1		
shaft metapodial	5	1	3	1	4	1
distal metapodial	1	1				
vestigial metapodial.			10	2		
phalanx 1	2	2	1	1	2	2
phalanx 2	1	1			2	1
phalanx 3					3	2
vestigial phalanges	2	1				
sesamoid			1	1	8	
tooth fragment	2		79		15	
vertebra fragment			1			
Total	214	56	295	46	329	60

3.1. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Denticulate Mousterian (EGPF) assemblage (continued).

EJOP INF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	45	2				
cranial/maxillary teeth	2	1	8	1	8	2
mandible/lower teeth	5	3	15	2	13	3
atlas						
axis						
other cervical vertebra					2	1
thoracic vertebra	1	1				
lumbar vertebra	1	1				
sacrum					1	1
rib	7	1	3	1	8	1
sternum						
scapula	3	2			2	1
proximal humerus						
shaft humerus	2	2	2	1	10	6
distal humerus						
proximal radius						
shaft radius	5	2				
distal radius						
proximal ulna						
shaft ulna						
distal ulna					1	1
scaphoid					1	1
lunatum						
triquetrum						
pisiform						
capitatum						
hamatum						
proximal metacarpal	1	1	1	1	1	1
shaft metacarpal	8	1			2	2
distal metacarpal						
pelvis			2	2	1	1
proximal femur						
shaft femur	5	1			3	1
distal femur						
patella						
proximal tibia						
shaft tibia	14	2	7	4	27	6
distal tibia	1	1				

3.2. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Châtelperronian? assemblage. Antlers excluded from the total.

EJOP INF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar						
talus						
calcaneum						
cubo-navicular/navicular	1	1				
smaller cuneiform			1	1		
greater cuneiform	1	1	1	1		
proximal metatarsal	1	1	1	1	1	1
shaft metatarsal	29	2	1	1	5	2
distal metatarsal						
proximal metapodial	1	1				
shaft metapodial	2	1	1	1	4	1
distal metapodial	1	1			1	1
vestigial metapodial.						
phalanx 1						
phalanx 2						
phalanx 3	1	1			1	1
vestigial phalanges	2	1				
sesamoid					1	1
tooth fragment			30		9	
vertebra fragment						
mandible/maxillary			2			
Total	94	29	75	17	102	35

3.2. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Châtelperronian? assemblage (continued). Antlers excluded from the total.

EJOP SUP	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	142	12				
cranial/maxillary teeth	7	2	9	2	48	5
mandible/lower teeth	22	6	35	5	71	12
atlas						
axis						
other cervical vertebra	1	1	1	1		
thoracic vertebra			4	1	3	1
lumbar vertebra						
sacrum						
rib	40	5	17	1	25	2
sternum						
scapula	2	2	1	1	15	6
proximal humerus						
shaft humerus	9	7	2	2	21	9
distal humerus	1	1				
proximal radius	3	3			3	2
shaft radius	4	1	5	3	11	7
distal radius					1	1
proximal ulna						
shaft ulna					5	4
distal ulna						
scaphoid						
lunatum						
triquetrum						
pisiform						
capitatum						
hamatum	1	1				
proximal metacarpal	1	1			2	1
shaft metacarpal	2	1			5	2
distal metacarpal						
pelvis	2	2	1	1	1	1
proximal femur	3	3				
shaft femur	5	4	4	2	18	8
distal femur						
patella	2	2				
proximal tibia	1	1				
shaft tibia	13	4	4	3	73	19
distal tibia	2	2	1	1		

3.3. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Châtelperronian assemblage. Antlers excluded from the total.

EJOP SUP	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar						
talus					1	1
calcaneum					2	1
cubo-navicular/navicular	1	1				
smaller cuneiform						
greater cuneiform	1	1	1	1		
proximal metatarsal	1	1			11	6
shaft metatarsal	18	1	1	1	26	6
distal metatarsal			1	1		
proximal metapodial						
shaft metapodial	4	1			5	1
distal metapodial			1	1	1	1
vestigial metapodial.			5	1		
phalanx 1	1	1	2	1	3	1
phalanx 2	1	1				
phalanx 3	2	1				
vestigial phalanges	1	1				
sesamoid	3	2	1	1		
tooth fragment	8		44		40	
Total	162	60	140	30	391	97

3.3. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Châtelperronian assemblage (continued). Antlers excluded from the total.

EJOP	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	93	14				
cranial/maxillary teeth	3	1	13	1	11	3
mandible/lower teeth	23	5	18	2	33	6
atlas						
axis						
other cervical vertebra	1	1				
thoracic vertebra	3	2	1	1		
lumbar vertebra						
sacrum						
rib	11	2	7	1	13	1
sternum						
scapula			1	1	4	1
proximal humerus						
shaft humerus	1	1	2	2	9	6
distal humerus						
proximal radius	1	1				
shaft radius	7	3			1	1
distal radius	1	1			1	1
proximal ulna						
shaft ulna	2	1				
distal ulna						
scaphoid					1	1
lunatum						
triquetrum						
pisiform	1	1			1	1
capitatum	1	1				
hamatum	1	1				
proximal metacarpal	2	2				
shaft metacarpal	2	2			1	1
distal metacarpal	1	1				
pelvis	3	2	1	1		
proximal femur	1	1				
shaft femur	1	1	1	1	6	2
distal femur	1	1				
patella						
proximal tibia						
shaft tibia	9	3	3	1	22	9
distal tibia	1	1				

3.4. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the EJOP (8-9) assemblage. Antlers excluded from the total.

EJOP	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar	1	1			1	1
talus	2	1				
calcaneum	2	2			2	2
cubo-navicular/navicular						
smaller cuneiform						
greater cuneiform	1	1				
proximal metatarsal	1	1			1	1
shaft metatarsal	27	3			6	2
distal metatarsal						
proximal metapodial						
shaft metapodial	5	1	2	1	2	1
distal metapodial						
vestigial metapodial.			1	1		
phalanx 1	3	1			1	1
phalanx 2	1	1			3	2
phalanx 3	1	1			1	1
vestigial phalanges	3	1				
sesamoid	1	1				
tooth fragment	4		27			
mandible/maxillary			2		17	
Total	129	50	79	13	137	44

3.4. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the EJOP (8-9) assemblage (continued). Antlers excluded from the total.

EJO INF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	23	4				
cranial/maxillary teeth	1	1	1	1	1	1
mandible/lower teeth	8	1				
atlas						
axis						
other cervical vertebra						
thoracic vertebra						
lumbar vertebra						
sacrum						
caudal					1	
rib	5	1	9	2	5	1
sternum						
scapula	1	1			1	1
proximal humerus						
shaft humerus	1	1				
distal humerus						
proximal radius					1	1
shaft radius			1	1		
distal radius						
proximal ulna						
shaft ulna					1	1
distal ulna						
scaphoid						
lunatum						
triquetrum	1	1				
pisiform						
capitatum						
hamatum						
proximal metacarpal						
shaft metacarpal						
distal metacarpal						
pelvis						
proximal femur						
shaft femur						
distal femur						
patella						
proximal tibia	1	1				
shaft tibia	1	1			3	2
distal tibia						

3.5. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the low density assemblage. Antlers excluded from the total.

EJO INF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar						
talus						
calcaneum						
cubo-navicular/navicular						
smaller cuneiform						
greater cuneiform						
proximal metatarsal			1	1		
shaft metatarsal					1	1
distal metatarsal						
proximal metapodial						
shaft metapodial						
distal metapodial						
vestigial metapodial.						
phalanx 1						
phalanx 2						
phalanx 3	1	1				
vestigial phalanges						
sesamoid						
tooth fragment			1			
Total	20	9	13	5	14	8

3.5. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Châtelperronian assemblage. Antlers excluded from the total.

EJO SUP	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	63	4				
cranial/maxillary teeth	9	2	1	1	1	1
mandible/lower teeth	23	3	2	1	6	2
atlas			1	1		
axis						
other cervical vertebra						
thoracic vertebra	1	1				
lumbar vertebra	3	1			1	1
sacrum	1	1				
rib	53	4	12	1	5	1
sternum	2	1				
scapula	1	1	1	1	1	1
proximal humerus						
shaft humerus	9	5				
distal humerus						
proximal radius						
shaft radius	15	6			1	1
distal radius	1	1				
proximal ulna	1	1				
shaft ulna	5	2				
distal ulna						
scaphoid	1	1				
lunatum						
triquetrum	1	1				
pisiform	1	1				
capitatum	1	1				
hamatum	2	2				
proximal metacarpal	2	2				
shaft metacarpal	9	3				
distal metacarpal	1	1				
pelvis	1	1	1	1		
proximal femur	2	2				
shaft femur	9	2				
distal femur						
patella						
proximal tibia	2	2				
shaft tibia	45	15	1	1	1	1
distal tibia						

3.6. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Aurignacian 0? assemblage. Antlers excluded from the total.

EJO SUP body part	reindeer NISP	 MNE	horse NISP	 MNE	bison NISP	 MNE
malleolar						
talus	4	3				
calcaneum						
cubo-navicular/navicular	1	1				
smaller cuneiform						
greater cuneiform						
proximal metatarsal	7	6				
shaft metatarsal	94	8			2	1
distal metatarsal	1	1				
proximal metapodial						
shaft metapodial	13	1				
distal metapodial	2	1				
vestigial metapodial.						
phalanx 1	11	4				
phalanx 2	4	1				
phalanx 3	3	3				
vestigial phalanges						
sesamoid	5	3				
tooth fragment	3		3		1	
Total	349	95	22	7	19	9

3.6. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Aurignacian 0? assemblage (continued). Antlers excluded from the total.

EJO	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	48	5				
cranial/maxillary teeth	5	1	3	1	2	1
mandible/lower teeth	22	5	3	1	8	3
atlas						
axis						
other cervical vertebra	1	1	3	1		
thoracic vertebra						
lumbar vertebra	1	1				
sacrum						
rib	17	2	7	1	12	1
sternum						
scapula	1	1	1	1	1	1
proximal humerus						
shaft humerus	1	1			1	1
distal humerus						
proximal radius	1	1			1	1
shaft radius	6	3	1	1	1	1
distal radius						
proximal ulna						
shaft ulna	1	1				
distal ulna						
scaphoid						
lunatum	1	1				
triquetrum						
pisiform						
capitatum						
hamatum	1	1				
proximal metacarpal					1	1
shaft metacarpal	6	1				
distal metacarpal						
pelvis	1	1				
proximal femur						
shaft femur	1	1	2	1		
distal femur			1	1	1	1
patella						
proximal tibia						
shaft tibia	21	4	1	1	4	2
distal tibia	1	1	1	1		

3.7. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the EJO (6-7) assemblage. Antlers excluded from the total.

EJO body part	reindeer NISP	reindeer MNE	horse NISP	horse MNE	bison NISP	bison MNE
malleolar	1	1				
talus						
calcaneum	1	1				
cubo-navicular/navicular						
smaller cuneiform						
greater cuneiform						
proximal metatarsal	1	1			2	2
shaft metatarsal	55	4				
distal metatarsal						
proximal metapodial						
shaft metapodial	4	1				
distal metapodial			1			
vestigial metapodial.						
phalanx 1	3	1				
phalanx 2	1	1				
phalanx 3						
vestigial phalanges						
sesamoid	3	2				
tooth fragment	5		8		3	
Total	162	39	32	10	37	15

3.7. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the EJO (6-7) assemblage (continued). Antlers excluded from the total.

EJF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	643	47				
cranial/maxillary teeth	63	6	32	2	6	2
mandible/lower teeth	147	22	45	8	16	5
atlas	3	2	1	1		
axis	2	2				
cervical vertebra	7	4				
thoracic vertebra	3	2	7	4	8	4
lumbar vertebra	5	2	1	1	11	5
sacrum					3	1
rib	427	23	174	13	86	9
sternum	1					
scapula	20	8	5	3	7	2
proximal humerus	1	1				
shaft humerus	102	43	6	1	2	2
distal humerus	5	4	1	1		
proximal radius	29	11	4	1		
shaft radius	205	43	7	4	1	1
distal radius	4	4	2	2	1	1
proximal ulna	3	2				
shaft ulna	31	5			2	2
distal ulna	-	-				
scaphoid	9	8				
lunatum	8	7				
triquetrum	2	2				
pisiform	3	3				
capitatum	7	7				
hamatum	1	1				
proximal metacarpal	16	10	2	1		
shaft metacarpal	102	35	3	1	3	2
distal metacarpal	6	6	2	2		
pelvis	23	10	13	3		
proximal femur	10	10	3	1		
shaft femur	93	33	8	5	4	3
distal femur	11	6	2	1		
patella	6	6				
proximal tibia	11	5			1	1
shaft tibia	373	73	9	7	10	5
distal tibia	8	5	7	5		

3.8. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Aurignacian I (EJF) assemblage. Antlers excluded from the total.

EJF	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar	5	5				
talus	18	12				
calcaneum	11	6				
cubo-navicular/navicular	8	6	1	1	1	1
smaller cuneiform	1	1				
greater cuneiform	3	3				
proximal metatarsal	32	19	7	5		
shaft metatarsal	806	64	3	5	1	1
distal metatarsal	3	2	2	3		
proximal metapodial	2	1	1			
shaft metapodial	64	1		1		
distal metapodial	9	4				
vestigial metapodial.	1		8	2		
phalanx 1	40	32	4	2		
phalanx 2	23	9	2	2		
phalanx 3	12	8	1	1		
vestigial phalanges	8	1				
sesamoid	17	9	1	1		
tooth fragment	7		21		1	
vertebra fragment	6					
Total	2823	594	385	89	164	47

3.8. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Aurignacian I (EJF) assemblage (continued). Antlers excluded from the total.

EJM	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
antler	250	10				
cranial/maxillary teeth	21	4	10	2	2	1
mandible/lower teeth	64	11	19	4	5	2
atlas			1	1	1	1
axis						
other cervical vertebra	1	1	1			
thoracic vertebra	1	1	3	2	3	2
lumbar vertebra						
sacrum	1	1				
rib	47	4	34	3	42	2
sternum						
scapula	9	3			3	2
proximal humerus			1			
shaft humerus	26	12	2	2	2	2
distal humerus						
proximal radius	2	2			1	1
shaft radius	50	8	2	1	3	3
distal radius	2	2	1	1		
proximal ulna						
shaft ulna	9	3			1	1
distal ulna						
scaphoid	1	1				
lunatum						
triquetrum						
pisiform	1	1				
capitatum	1	1			1	1
hamatum	1	1				
proximal metacarpal	5	5	4	4		
shaft metacarpal	13	5	1	3	1	1
distal metacarpal	2	2				
pelvis	5	2	4	2		
proximal femur	1	1	1			
shaft femur	22	19	3	1		
distal femur	1	1				
patella	2	2				
proximal tibia	1	1	2	1		
shaft tibia	80	21	4	4	8	2
distal tibia			1	1		

3.9. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Evolved Aurignacian EJM assemblage. Antlers excluded from the total.

EJM	reindeer		horse		bison	
body part	NISP	MNE	NISP	MNE	NISP	MNE
malleolar	1	1				
talus	1	1				
calcaneum	5	5	1	1		
cubo-navicular/navicular	3	3				
smaller cuneiform						
greater cuneiform	2	1				
proximal metatarsal	4	2	1	1	1	1
shaft metatarsal	154	14	2	1	1	1
distal metatarsal	2	2	1	1		
proximal metapodial						
shaft metapodial	41	1	1	1		
distal metapodial	2	2	1	1		
vestigial metapodial.			5	1		
phalanx 1	9	5	1	1	1	1
phalanx 2	2	2				
phalanx 3	1	1				
vestigial phalanges	1					
sesamoid	3	2				
tooth fragment			4		2	
mandible/maxillary			2			
Total	600	157	113	40	78	24

3.9. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Evolved Aurignacian EJM assemblage (continued). Antlers excluded from the total.

EJJ body part	reindeer NISP	 MNE	horse NISP	 MNE	bison NISP	 MNE
antler	97	2				
cranial fragment/maxillary teeth	15	4	8	1	5	1
mandible/lower teeth	22	7	15	2	4	1
atlas			1	1	2	1
axis						
other cervical vertebra	1	1				
thoracic vertebra	2	2	1	1		
lumbar vertebra						
sacrum						
rib	15	4	12	1	7	1
sternum						
scapula	1	1	3	2	2	1
proximal humerus						
shaft humerus	9	5	1	1	3	2
distal humerus						
proximal radius						
shaft radius	11	3	1	1		
distal radius			1	1		
proximal ulna						
shaft ulna	2	1				
distal ulna						
scaphoid	1	1				
lunatum						
triquetrum	1	1				
pisiform						
capitatum						
hamatum						
proximal metacarpal	2	2	1	1		
shaft metacarpal	8	3			1	1
distal metacarpal	1	1				
pelvis	2	1	1	1		
proximal femur	1	1				
shaft femur	11	5	1	1	1	1
distal femur						
patella						
proximal tibia						
shaft tibia	30	8	1	1	3	2
distal tibia	2	2				

3.10. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Evolved Aurignacian EJJ assemblage. Antlers excluded from the total.

EJJ body part	reindeer NISP	 MNE	horse NISP	 MNE	bison NISP	 MNE
malleolar						
talus						
calcaneum	3	2			1	1
cubo-navicular/navicular	1	1				
smaller cuneiform						
greater cuneiform	3	3				
proximal metatarsal	1	1			1	1
shaft metatarsal	67	6			5	3
distal metatarsal						
proximal metapodial	1	1				
shaft metapodial	7	1	1	1		
distal metapodial						
vestigial metapodial.			4	1		
phalanx 1	2	1	1	1	1	1
phalanx 2						
phalanx 3						
vestigial phalanges						
sesamoid	1	1				
tooth fragment	3		4		3	
Total	226	70	57	18	39	17

3.10. Saint-Césaire. Skeletal representation in reindeer, bison, and horse in the Evolved Aurignacian EJJ assemblage (continued). Antlers excluded from the total.

Appendix 4. Fetal age and corresponding diphyseal length in horse.

	Humerus			Radius			Metacarpal	
age in days	diaphyseal length	reference	age in days	diaphyseal length	reference	age in days	diaphyseal length	reference
35	3.8	H	74.9	6.1	G	74.9	2.8	G
63	7.5	H	79.8	9.9	G	76.8	6.1	G
77	12.5	H	85.6	9.9	G	79.8	6.9	G
105	19.0	H	89.7	14.1	G	85.6	6.3	G
140	33.0	H	94.7	17.4	G	89.7	9.4	G
161	48.0	H	96.1	16.3	G	95.0	12.1	G
175	55.0	H	98.8	18.8	G	96.1	9.9	G
203	63.0	H	100.7	21.0	G	98.8	11.3	G
231	85.0	H	112.0	25.9	G	100.7	13.0	G
245	95.0	H	149.7	37.5	G	111.2	16.8	G
259	112.0	H	150.2	34.5	G	149.9	21.8	G
294	132.0	H	153.8	37.2	G	149.7	24.6	G
308	167.0	H	154.1	43.6	G	153.5	23.4	G
			166.7	50.2	G	153.8	26.8	G
			174.4	54.3	G	166.4	35.9	G
			180.2	59.0	G	173.8	37.2	G
			186.5	60.7	G	180.2	37.2	G
			229.6	116.1	G	186.5	40.6	G
			234.3	116.4	G	229.6	102.9	G
			234.9	111.2	G	234.6	96.8	G
			253.5	131.9	G	234.9	101.2	G
			257.4	150.6	G	253.3	123.6	G
			269.5	144.0	G	257.4	142.6	G
			271.1	148.7	G	269.8	139.3	G
			271.1	155.9	G	271.4	141.0	G
			274.4	151.2	G	271.7	138.2	G
			276.6	158.9	G	277.2	143.2	G
			277.7	155.0	G	279.4	141.0	G
			278.8	153.1	G	280.5	155.6	G

4.1. Fetal age in days and corresponding diaphyseal length in the horse foreleg. Data from Habermehl (1975, as cited in Prummel 1989) and read from the graphs of Guffy *et al.* (1970). G = Guffy *et al.* 1970, H=Habermehl 1975.

age in days	Humerus diaphyseal length	reference	age in days	Radius diaphyseal length	reference	age in days	Metacarpal diaphyseal length	reference
			279.1	158.3	G	284.1	140.1	G
			279.4	160.8	G	284.3	150.1	G
			284.1	156.1	G	294.5	156.1	G
			284.1	161.1	G	294.0	159.2	G
			293.7	165.5	G	294.0	162.2	G
			296.2	170.2	G	303.6	160.6	G
			300.0	175.4	G	303.8	164.1	G
			303.6	169.9	G	304.1	166.9	G
			303.6	173.8	G	305.2	180.4	G
			303.8	177.4	G	318.1	177.7	G
			307.4	182.1	G	325.0	205.2	G
			307.7	187.9	G	331.6	195.0	G
			317.6	180.4	G	331.6	198.1	G
			325.3	210.5	G	331.6	209.4	G
			331.3	200.3	G	331.9	218.8	G
			331.3	205.0	G	35	1.8	H
			331.6	207.4	G	63	5	H
			331.6	211.3	G	77	10.5	H
			331.9	222.1	G	105	14.2	H
			63	8	H	140	28	H
			77	15	H	161	40	H
			105	22	H	175	48.5	H
			140	40	H	203	60	H
			161	58	H	231	79	H
			175	68	H	245	111	H
			203	78	H	259	136	H
			231	102	H	294	155	H
			245	122	H	308	200	H
			259	147	H			
			294	168	H			
			308	211	H			

4.1. Fetal age in days and corresponding diaphyseal length in the horse foreleg (continued). Data from Habermehl (1975, as cited in Prummel 1989) and read from the graphs of Guffy *et al.* (1970). G = Guffy *et al.* 1970, H=Habermehl 1975.

	Femur			Tibia			Metatarsal	
age in days	diaphyseal length	reference	age in days	diaphyseal length	reference	age in days	diaphyseal length	reference
35	4.2	H	74.9	5.2	G	74.6	3.6	G
63	8.3	H	75.7	8.8	G	76.6	6.9	G
77	15.0	H	79.3	9.9	G	79.6	6.6	G
105	23.0	H	85.6	9.9	G	85.4	7.2	G
140	41.5	H	89.8	14.3	G	89.5	10.5	G
161	58.0	H	95.3	17.7	G	92.5	15.2	G
175	67.0	H	96.9	16.0	G	94.7	12.4	G
203	89.0	H	98.3	19.3	G	97.2	11.0	G
245	118.0	H	101.9	21.0	G	98.8	13.2	G
259	140.0	H	112.3	27.0	G	101.9	13.2	G
294	159.0	H	150.9	34.5	G	112.1	21.2	G
308	212.0	H	150.6	37.2	G	150.9	28.1	G
			155.0	35.3	G	150.9	30.9	G
			154.7	41.9	G	154.7	30.6	G
			167.6	48.0	G	154.7	33.1	G
			175.1	53.2	G	167.6	42.1	G
			180.8	53.2	G	175.1	48.5	G
			188.3	58.2	G	181.1	49.0	G
			235.6	107.3	G	187.5	51.0	G
			235.9	112.3	G	235.9	123.7	G
			241.1	107.3	G	235.9	126.7	G
			254.6	128.8	G	240.8	118.2	G
			257.9	146.5	G	254.6	149.9	G
			262.3	147.0	G	262.3	162.0	G
			268.6	150.1	G	270.6	160.6	G
			272.2	144.0	G	269.7	170.5	G
			272.2	151.4	G	272.8	158.7	G
			278.8	154.5	G	280.5	170.2	G
			280.2	152.0	G	280.7	174.4	G
			280.7	156.1	G	281.0	177.1	G

4.2. Fetal age in days and corresponding diaphyseal length in the horse hindleg. Data from Habermehl (1975, as cited in Prummel 1989) and read from the graphs of Guffy *et al.* (1970). G = Guffy *et al.* 1970, H=Habermehl 1975.

	Femur			Tibia			Metatarsal	
age in days	diaphyseal length	reference	age in days	diaphyseal length	reference	age in days	diaphyseal length	reference
			280.5	158.9	G	280.7	180.2	G
			285.1	151.7	G	280.7	184.8	G
			285.1	156.7	G	285.4	165.0	G
			295.3	160.8	G	285.7	182.6	G
			298.6	171.9	G	295.6	186.2	G
			300.3	166.3	G	298.3	199.7	G
			301.7	175.2	G	302.2	191.2	G
			305.0	171.3	G	305.5	189.8	G
			305.2	176.6	G	305.5	195.0	G
			307.2	181.2	G	305.5	200.0	G
			308.5	183.4	G	307.4	210.2	G
			319.5	180.4	G	308.8	198.6	G
			327.2	199.7	G	320.6	214.3	G
			331.6	200.3	G	327.2	214.3	G
			333.3	202.8	G	335.5	228.7	G
			334.1	219.9	G	335.5	231.1	G
			334.9	200	G	337.4	233.9	G
			334.9	213.2	G	337.7	230.0	G
			63	8.3	H	35	2.1	H
			77	15	H	63	5	H
			105	23	H	77	11.5	H
			140	42	H	105	17	H
			161	59	H	140	32	H
			175	69	H	161	44	H
			203	90	H	175	57	H
			245	129	H	203	80	H
			259	155	H	245	119	H
			294	180	H	259	154	H
			308	235	H	294	182	H
						308	236	H

4.2. Fetal age in days and corresponding diaphyseal length in the horse foreleg (continued). Data from Habermehl (1975, as cited in Prummel 1989) and read from the graphs of Guffy *et al.* (1970). G = Guffy *et al.* 1970, H=Habermehl 1975.

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