Exploring hominins and animals in the Swabian Jura: Study of the Paleolithic fauna from Hohlenstein-Stadel

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Summary

Caves from the Swabian Jura region in Germany have produced one of the richest archaeological records in the Paleolithic. During the Middle and Upper Paleolithic period, the fossil record in Eurasia shows a biological break between archaic and modern humans, but differences in culture, behavior and demography remain a topic of debate. This study documents the subsistence pattern and the use of cave by Neanderthals and modern humans through the analysis of faunal remains from Hohlenstein-Stadel and compares the assemblages with other sites in the Swabian Jura.

Faunal remains from Hohlenstein-Stadel indicate a mixture of carnivore, cave bear and hominin activities, resulting in a complex depositional history. The mortality of cave bear occurred naturally during the winter hibernation independently of hominin occupations. Prey remains further indicate that both hominins and non-human predators visited the site. The cave during the Middle Paleolithic served as a den for carnivores, namely hyenas, and a site of short term occupation for Neanderthals, which is documented by the presence of burnt faunal material and lithic artifacts. During the Aurignacian, the faunal remains show relatively few signatures of human activity related to subsistence practices, which also coincide with decreasing abundance of carnivores. The increased antler fragments and the ivory figurine of Lionman suggest a possible role of Hohlenstein-Stadel as a non-habitation site for modern humans.

The comparison of several sites in the Swabian Jura reveals regional patterns of hominin subsistence behavior and the use of caves by cave bears, carnivores and hominins. Horse is the most abundant herbivorous taxon in the Middle Paleolithic and the Aurignacian, targeted both by hominins and carnivores alike. There is a significant increase in the

abundance of reindeer in the Aurignacian, which corresponds to the cooler climate at the beginning of the early Upper Paleolithic.

Cave bears continue to dominate in certain cave localities, which demonstrates that the abundance of ursids did not greatly alter between the two Paleolithic periods. The decrease of middle and large sized carnivores, predominantly hyenas, and the damage made by non-human predators across all sites indicates that the role of carnivores in the accumulation of faunal material during the Aurignacian diminished on a regional scale. Inversely, anthropogenic modification increases significantly across most sites from the Middle Paleolithic to Aurignacian, pointing to the greater contribution of prey remains by modern humans. Further, there is some evidence for cave bear exploitation at sites during the Aurignacian. These trends possibly attest to intensified use of sites, indicating greater group size of modern humans and/or longer residential time.

The difference in the subsistence behavior of Neanderthals and modern humans is not influenced by cognitive abilities, but reflects changes in the environment of the Swabian Jura. Significant distinction between the two hominin species manifests not in terms of prey choice or hunting strategies, but instead through increased use of caves by modern humans compared to their predecessors. Modern humans utilized the sites differently from Neanderthals, which possibly affected the local carnivore population and can account for the unique symbolic behavior and cultural repertoire which emerged during the Aurignacian.

Zusammenfassung

Höhlen aus der Region Schwäbische Alb in Deutschland haben eine der fundreichsten archäologischen Aufzeichnungen im Paläolithikum erbracht. Zwischen dem Mittel- und Jungpaläolithikum zeigen die Fossilien in Eurasien einen biologischen Bruch zwischen archaischen und modernen Menschen. Aber Unterschiede in Kultur, Verhalten und Demographie bleiben ein Thema der Diskussion. Diese Studie dokumentiert die Subsistenzmuster und die Nutzung einer Höhle durch Neanderthaler und moderne Menschen mit Hilfe einer Faunenanalyse aus dem Hohlenstein-Stadel und vergleicht sie mit anderen Fundstellen auf der Schwäbischen Alb.

Die Faunenreste aus dem Hohlenstein-Stadel stellen eine Mischung aus Aktivitäten von Fleischfresser, Höhlenbären und Menschen dar, die eine komplexe Sedimentationsgeschichte ergeben. Die natürliche Mortalität der Höhlenbären während ihrer Winterruhe ist unabhängig von der Besiedlung der Menschen entstanden. Die Beutereste in der Höhle zeigen, dass beide, nämlich Menschen und andere Raubtiere die Höhle nutzten. Während des Mittelpaläolithikums diente die Höhle als Horst für Fleischfresser, hauptsächlich Hyänen, und als Platz für kurze Aufenthalte von Neanderthalern, wie man am Vorkommen von verbranntem Knochen und Steinartefakte erkennen kann. Die Tierreste aus dem Aurignacien zeigen relativ wenig Hinweise auf menschliche Aktivitäten, die auf Subsistenz-Praktiken hinweisen, und die mit einem Rückgang der Raubtiere zusammenfällt. Die erhöhte Anzahl von Geweihfunden und die Elfenbeinfigur des Löwenmenschen sprechen für eine besondere Rolle des Hohlenstein-Stadel im Vergleich zu anderen Fundstellen.

Der Vergleich von mehreren Fundstellen auf der Schwäbischen Alb zeigt regionale Muster des menschlichen Subsistenzverhaltens und der Nutzung der Höhlen durch Höhlenbären, Raubtiere und Menschen. Pferd ist das häufigste herbivore Beutetiere im

Mittelpaläolithikum und im Aurignacien, auf das es sowohl Menschen als auch Carnivoren abgesehen hatten. Während des Aurignaciens gibt es eine deutliche Zunahme von Rentieren, die möglicherweise einer kühleren Klimaphase zu Beginn des frühen Jungpaläolithikums entspricht.

In bestimmten Höhlen dominieren Höhlenbären in beiden Paläolithischen Perioden, das zeigt, dass sich die Wahl eines geschützten Platzes für die Winterruhe über die lange Zeit nicht geändert hat. Die Abnahme der mittelgroßen und großen Fleischfresser, hauptsächlich der Hyänen, und der Rückgang der Zerstörung, die durch Raubtiere in allen Fundplätzen erfolgte, zeigt, dass die Rolle der Raubtiere in der Akkumulation von Faunenresten im Aurignacien zurückgeht. Umgekehrt erhöht sich die Zahl der menschlichen Modifikationen deutlich in den meisten Funstellen des Aurignaciens und weist auf einen größeren Beitrag von Beutetieren durch den modernen Menschen hin. Weiterhin gibt es Hinweise auf die Nutzung von Höhlenbären an einigen Fundstellen während des Aurignaciens. Dieser Trend ist möglicherweise ein Hinweis auf eine intensivere Nutzung der Fundstellen, was auf eine größere Gruppengröße und /oder längere Begehungszeiten hinweisen könnte.

Der Unterschied im Subsistenzverhalten von Neanderthalern und modernen Menschen ist nicht durch kognitive Fähigkeiten beeinflusst, sondern spiegelt vor allem Veränderungen in der lokalen Umwelt der Schwäbischen Alb wieder. Deutliche Unterscheidung zwischen den beiden Menschenformen manifestiert sich nicht in der Auswahl der Beutetiere, sondern in der intensivierten Nutzung der Höhlen durch den modernen Menschen im Vergleich zu seinen Vorgängern. Moderne Menschen nutzten die Fundplätze anders als Neanderthaler, was möglicherweise Auswirkungen auf die Fleischfresser-Populationen hatte und dadurch möglicherweise die einzigartige Symbolik und Kunst im Aurignacien hervorbrachte.

Contribution

As in any research, this work has benefited from help from many individuals.

Farnaz Boroushaki labeled and helped sort the faunal material from the previous excavation to facilitate identification.

Dr. Claus-Joachim Kind from Landesamt für Denkmalpflege in Baden-Württemberg headed the excavation from 2009-2011 and allowed access to the faunal material.

Thomas Beutelspacher worked with Dr. Claus-Joachim Kind in recovery of the faunal material and to correlate stratigraphy from the excavation in 1939 to the recent excavation.

The faunal identification and subsequent analysis have been conducted by myself, Keiko Kitagawa.

1 Introduction

Caves from the Swabian Jura region in Germany have produced one of the richest archaeological records in the Paleolithic. Extensive excavations and research starting from the 19th century inform us about the settlement patterns and behavior of hominins in this area of Central Europe during the Paleolithic periods. These cultural phases represent a crucial transition in which Neanderthals and modern humans occupied and frequented the sites. The fossil record shows a biological break between archaic and modern humans, but the differences in culture, behavior and demography remain a topic of debate. This study aims to document past hominin adaptations through an analysis of the zooarchaeological record from the cave of Hohlenstein-Stadel and a comparison with the faunal material from neighboring sites.

Neanderthals and modern humans

The question surrounding the uniqueness of modern humans is linked to an ultimate interest in understanding how and why their behavior and cognition led to their successive dispersal into previously uninhabited areas as well as the eventual emergence of agricultural lifeways and the development of social complexity. The coexistence of several hominin species or subspecies such as Denisovan (Krause et al., 2010; Meyer et al., 2014; Meyer et al., 2012; Reich et al., 2010) has been proven by recent advances in genetic studies. Among extinct hominins that existed at the same time, Neanderthals have often been well studied due to the abundant fossil remains and their wide geographic distribution, namely Europe and the Middle East, which has been subjected to more intensive investigation. The record of Neanderthal occupations allows for an adequate comparison with that of modern humans.

Known for anatomically robust features, Neanderthals first appeared in the paleoanthropological record roughly around 200 ka (Clark, 2002; Harvati, 2010; Hublin, 2009; Smith et al., 1989). Their predecessors, *H. heidelbergensis*, show a gradual appearance of Neanderthal features pointing to a local evolution of the *Homo* lineage in Europe, the Near East and Western Asia roughly beginning around 600 ka. Their southern limit is in the Near East and their eastern limit is southern Siberia according to paleogenetic studies (Green et al., 2010; Green et al., 2006; Reich et al., 2010; Skoglund and Jakobsson, 2011). On the other hand, *Homo sapiens sapiens* emerged around ~200-150 ka in Africa and migrated as far as the Arabian Peninsula. They later dispersed into Eurasia, reaching Australia at least by 50 ka and migrating into Europe later (Hoffecker, 2009b; Klein, 2008; Mellars, 2006; Stringer, 2002). Scant evidence of early *Homo* fossils means that the exact timing of their spread into Europe still remains unclear (Bar-Yosef, 2006; Churchill and Smith, 2000; Hublin, 2012; Mellars, 2004; Trinkaus, 2005).

Recent advances in the research of Neanderthals and anatomically modern humans have been made in the field of genetics (Abi-Rached et al., 2011; Briggs et al., 2009; Green et al., 2010; Green et al., 2006; Krause et al., 2010; Krause et al., 2007; Noonan et al., 2006). Studies show that modern humans outside of Africa and Neanderthals share 3-5 % of their genes (Green et al., 2010). The genetic data support the hypothesis that the two species of *Homo* interbred, most likely in the Middle East. This discovery, however, does not necessarily support a scenario in which interbreeding occurred in Europe after Neanderthals settled and modern humans spread to Europe. A study by Dalén et al. (2012) indicates that the mitochondrial DNA from Neanderthals that survived in Western Europe after 48 ka has a lower variation when compared to individuals existing prior to 48 ka and to those from Eastern Europe. The most parsimonious explanation for this trend is that the population pool and the genetic diversity began to decrease around 50 ka. The timing suggests that the slow decrease in the population size occurred before modern humans began to occupy Europe around 45 ka.

When archaeological sites lack paleoanthropological findings, the designation of those who occupied the sites is determined based on the material culture. However, such designations become unclear during the period of transition from the Middle to early Upper Paleolithic. Transitional cultures that exist after the Middle Paleolithic and predate the emergence of the early Upper Paleolithic, namely the Aurignacian, are often a topic of debate. Around twenty transitional industries emerged on a regional scale in Europe and Western Asia (Anikovich et al., 2007; Brantingham et al., 2004). Some cultures include the Bachokirian in Bulgaria, Bohunician in the Czech Republic and Poland, Châtelperronian in France and northern Spain, Lincombian/Ranisian/Jerzmanowician in northern Europe, Szeletian in central Europe and Uluzzian in southeastern Italy and Greece.

One prominent example is the Châtelperronian technocomplex, found mostly in southwestern France and northern Spain (Bar-Yosef and Bordes, 2010). This archaeological culture is known for the production of personal ornaments and organic artifacts associated with Neanderthals (Morley, 2006; Soressi et al., 2013). Deposits with Châtelperronian assemblages are limited in number, and their dating and association with fossil remains remain controversial, but the current consensus views Neanderthals as the makers of the Châtelperronian industry (Gravina et al., 2005; Higham et al., 2010; Mellars et al., 2007; Zilhao, 2006).

Furthermore, recent findings show that the dispersal of anatomically and behaviorally modern humans into Europe occurred earlier than once assumed. Investigations in Grotta del Cavallo, Italy, have recently demonstrated that a hominin tooth once associated with the Uluzzian industry shows closer to affinity to modern humans based on morphometric analysis (Benazzi et al., 2011). The site is dated to roughly 40 ka (45-43,000 cal BP), making this one of the oldest pieces of evidence for the presence of modern humans in Western Europe (Benazzi et al., 2011). These two instances underline the variability that exists among transitional industries and suggest that they cannot be assigned to one *Homo* species unless they are securely associated with hominin fossils.

Symbolic behavior is one of the key behavioral traits in the debate concerning Neanderthals and modern humans. A general consensus states that the emergence of art exhibited by ornamentation, cave painting and portable figurines is a clear hallmark of ‘modernity’ rarely observed from the Middle Paleolithic. Some views hold that the production of artistic motifs and artifacts is uniquely associated with modern humans while others argue that modern and archaic humans independently developed symbolic behavior (Zilhão, 2007). Furthermore, certain artistic expressions are regionally restricted. Many of the elaborate cave paintings are located in caves in the Franco-Cantabrian region (Straus, 1987) , indicating that manifestations of symbolic behavior are at times localized and not uniformly practiced by all modern human groups in Europe. Restricted distribution may infer that differences result from varied social systems or demographic patterns and not from cognitive capabilities.

The extinction of Neanderthals, which occurred around 30-28 ka, is also of major archaeological interest (Harvati, 2010; Pettitt, 1999; Roebroeks, 2008). The Neanderthal population began to contract gradually from the east over a period of 10,000 years, last surviving in the Iberian Peninsula (Finlayson et al., 2006). The MIS 3, as described below, was a period of instability, and researchers have sought to give an ecological explanation for the demise of the archaic *Homo*. Studies that consider climate as the major determinant argue that it triggered the dispersion of modern humans westwards into Europe, and forced Neanderthals into refugia and extinction, implying that Neanderthals and modern humans had some form of contact and interaction, which adversely affected the archaic populations (Finlayson, 2005; Finlayson and Carrion, 2007; Skoglund and Jakobsson, 2011). According to some studies, the transition from the Proto-Aurignacian to Early Aurignacian cultures, marking the appearance of modern humans, chronologically correlates with the beginning of

Heinrich Stadial 4, which is marked by an abrupt transition to cold and dry conditions (Banks et al., 2013; Teyssandier, 2008; Teyssandier et al., 2010).

Although environmental changes may have enabled modern humans to flourish, the negative effect of such climatic shifts on Neanderthals has not been successfully documented. Neanderthals survived various climatic fluctuations in the past, which is one of reasons why researchers associate the extinction of Neanderthals with the appearance of modern humans. Some archaeologists have questioned this approach, noting that the change in the distribution of the *Homo* species does not correspond well with the paleoclimatic record during this period (d’Errico and Sánchez Goñi, 2003).

The resolution of the archaeological record may be too coarse for addressing unresolved issues, but there are different interpretations on the matter of exchange and interactions among modern humans and Neanderthals. Areas such as the Swabian Jura show no evidence of interaction (see below) while the range of the *Homo* species temporally and geographically overlapped in other areas, possibly allowing for some form of contact. In regions or site localities where the temporal and spatial distribution of Neanderthals and modern humans overlap, the questions of exchange, interbreeding, cultural assimilation and competition between the hominin groups still remain open.

Zooarchaeological studies on the Middle and early Upper Paleolithic assemblages also help inform and shape our understanding of Neanderthals and modern humans. Analysis of sites with both occupations has increased over the years (Adler et al., 2006; Gaudzinski-Windheuser and Niven, 2009; Grayson and Delpech, 2003; Grayson and Delpech, 2006; Hoffecker, 2009a; Morin, 2008; Starkovich, 2012; Stiner, 2009b; Stiner et al., 2012; Stiner et al., 2000). When the faunal data are considered on a broader scale, assemblages are characterized by variability and regional patterns. Subsistence practices that reflect unique and ‘modern’ behavior of Upper Paleolithic humans are not readily apparent.

Grayson and Delpech’s (2003) work on Grotte XVI, France, indicates that no behavioral change can be detected in the manner with which hominins acquired and transported their prey to the site. The abundance of different ungulates gradually increases, and the remains of reindeer show an inverse correlation with the decreasing summer temperature. Thus, the authors refute the notion that behavioral shifts account for the changes in the composition of the faunal assemblage. The underlying implication is that the economic principles that drive the hunting of ungulates do not alter over time and the change is dependent upon varying environments and available resources.

On the other hand, the work of Stiner and colleagues demonstrates the broadening of diet around the Mediterranean Rim (Starkovich, 2012; Stiner and Munro, 2011; Stiner et al., 2000). The authors observe the use of small game such as mollusk, tortoise, hare and bird. The use of aquatic resources persists in the Middle Paleolithic and decrease thereafter while the number of terrestrial animals increased during the Upper Paleolithic period. Furthermore, Hoffecker (2009) also observes notable diversification of resources in two regions of Eastern Europe during the Middle and Upper Paleolithic period and points to increased exploitation of small mammals, fish and birds by modern humans. Subsistence practices remain regionally variable and both continuity and change appear to persist. Thus, the faunal data suggest that hominins’ flexibility and ability to adapt to diverse resources probably existed before the arrival of modern *Homo sapiens* in Eurasia.

Interaction of animals and humans in the Paleolithic

One of the fundamental questions in faunal research revolves around subsistence strategies and diet. As such, hominins as predators and their relationship with their prey are a main focus in Paleolithic zooarchaeology. The consumption of meat and the development of hunting as a method of food procurement have direct implications for hominin evolution and biology (Aiello and Wells, 2002; Aiello and Wheeler, 1995; Froehle et al., 2013; Macdonald et al., 2009).

At the same time, past animal remains are not solely the result of exploitation and processing by hominins. Traces of non-human predators including physical modification of their prey as well as their carcasses occur in Paleolithic deposits. These signatures in the zooarchaeological record shed light to ways in which hominins potentially interacted with non-prey animals and add another dimension to the study of past human behavior and evolution. Faunal assemblages reveal how hominins and animals coexisted in the landscape and provide opportunities to study indirect and direct interaction.

Signatures of carnivores prevailed in the zooarchaeological record during the Paleolithic. The evidence of direct interaction between hominins and carnivores is rarely documented in the archaeological record until the middle of the Upper Paleolithic although some exceptions exist (Blasco et al., 2010; Gabucio et al.; Rosell and Blasco, 2009). Nonetheless, non-human predators played a crucial role in the evolution of hominins and likely affected the biological and cultural adaptations of early *Homo* (Aiello and Wheeler, 1995; Aiello and Wheeler, 2003; Ambrose, 2001; O'Shea, 2009).

Medium and large sized carnivores became active competitors as hominins began to incorporate ungulates in their diet and actively pursue large game. On the one hand, studies focus on the behaviors and interaction of top-tiered predators to understand the nature of ecological guild and niche partitioning among the carnivores (Lewis and Werdelin, 2010; Turner et al., 2008; Van Valkenburgh, 2001; Werdelin and Lewis, 2005, 2013). On the other hand, the shift in the diet of hominins has triggered debates on the nature of subsistence activity (i.e. hunting and/or scavenging) among early *Homo* and the degree to which carnivores contributed and modified faunal remains at Lower Paleolithic sites in eastern Africa (Blumenschine, 1986; Blumenschine and Pobiner, 2007; Bunn et al., 1986; Domínguez-Rodrigo and Barba, 2006). Therefore, understanding the taphonomic effects of carnivores is a way to extrapolate archaeological signals from faunal assemblages (Brain, 1981; Cleghorn et al., 2007; Selvaggio and Wilder, 2001).

Hominins and large carnivores also occupied a similar ecological niche in that they utilized natural shelters when they were present in the landscape (Stiner, 1994). Caves provide protection for carnivores to consume prey, avoid competition and rear their young. Bears also occupy sheltered areas during the period of hibernation. Fauna from the caves are the focus of the research presented here as the archaeological record is better preserved in an enclosed context and deposits from caves result from long-term occupation, increasing the likelihood of its preservation. As such, we infer that carnivores and hominins had similar needs for resources and space ever since hominins began to regularly exploit animals for resources and as hominins dispersed in areas where they encountered new faunal communities and adapted to different ecological systems (Stiner, 2002).

Understanding how caves were occupied by hominins and carnivores is often based on isolated cases of single sites. Few studies have focused on the pattern of cave use by carnivores and hominins on a regional scale, with some notable exceptions. Mussi (2001) and Straus (1982) compiled data at a larger scale, namely parts of Italy and Cantabria in Spain, to study patterns of carnivore representation in assemblages spatially and temporally. While most interactions cannot be tracked using fossil records alone, an attempt to track the use of caves and exploitation of prey by carnivores and hominins beyond one or two sites can potentially shed light on the ecological relationship between them and detect trends that speak to differences in the adaptation of archaic and modern humans to their environment. The study presented here consists of faunal analyses from the caves in the Swabian Jura during the Middle and early Upper Paleolithic. We sought to observe regional patterns in the changes of cave use by considering carnivore abundances, bone modification and exploitation of carnivores by humans.

Thus, the presence of carnivores is often incorporated into zooarchaeological analyses from a taphonomic approach, but the question becomes ecological in nature in the framework of hominin evolution. Notably, researchers are interested in studying whether carnivores and hominins altered their behavior due to their presence and competition. The common occurrence of carnivores suggests that carnivores and humans had overlapping ecological niches. Thus, it is of paleontological, ecological and archaeological interest to explore how carnivores and humans as competitors evolved over time (Kitagawa et al., 2012).

The aim of the present study

There are several reasons for conducting this research. First, the faunal assemblage of Hohlenstein-Stadel, which has been studied previously by Gamble (1979, 1999) will be reassessed with a focus on taphonomic analysis. Further, a sample of material from recent excavations will be incorporated here to evaluate the effect of the recovery method on the animal remains and augment the existing dataset. Combined data from two excavations enable us to compare the material with other sites and document the patterns of subsistence practices and site use on a regional scale. The faunal data across multiple sites add to the general understanding of adaptation practiced by Neanderthals and modern humans. Difference and similarity among the faunal assemblages in turn contribute to the interpretation of Hohlenstein-Stadel as a site in the region.

Faunal remains from archaeological contexts reveal subsistence patterns and dietary choices of hominins who inhabited various ecological landscapes and were part of the local faunal communities. The patterns of subsistence and the diachronic trend are documented. Paleolithic deposits, which mostly consist of palimpsests, elicit insight into the subsistence behavior on a long term and the relationship of hominins and the natural environment. Further, studying the past interaction of carnivores and humans has implications for understanding evolution and paleoecology of hominins in prehistory. This research explores and discusses human/carnivore interaction and their frequent use of caves and rockshelters in Central Europe.

The work here is thus informed by the questions presented above, relating to the ways of subsistence and human adaptation to the natural environment, on the one hand, and studying hominins and the interaction with other animals on the other. The ultimate objective is to track continuity and change in the faunal assemblages over the major cultural phrases and to document similarities and differences among Neanderthals and modern humans through the study of animal remains.

Summary

The Swabian Jura is an archaeologically defined area with evidence for continuous occupation of archaic and modern human populations during the Middle and Upper Paleolithic. It is also an area distinguished by one of the earliest and richest Aurignacian assemblages in Central Europe. The faunal analysis of the material in the region provides insights into the subsistence activities of hominins, enabling us to track temporal trends and the use of caves by hominins as well as by other animals in understanding settlement patterns.

The organization of the work is as follows: Chapter 2 deals with the background of the general setting, including the geology, geography, past environment as well as the cultural history of the Swabian Jura. Chapter 3 summarizes the history of research and excavation at Hohlenstein-Stadel and provides a brief description of the other sites in the region. Chapter 4 discusses the fauna and the methods employed in this study. Chapter 5 presents the results from the faunal analysis of Hohlenstein-Stadel, followed by a comparison of the faunal data with other sites in the Swabian Jura to understand the pattern on a regional scale in Chapter 6. A general summary and conclusion will then follow.

2 The Swabian Jura: Background

Geography and Geology

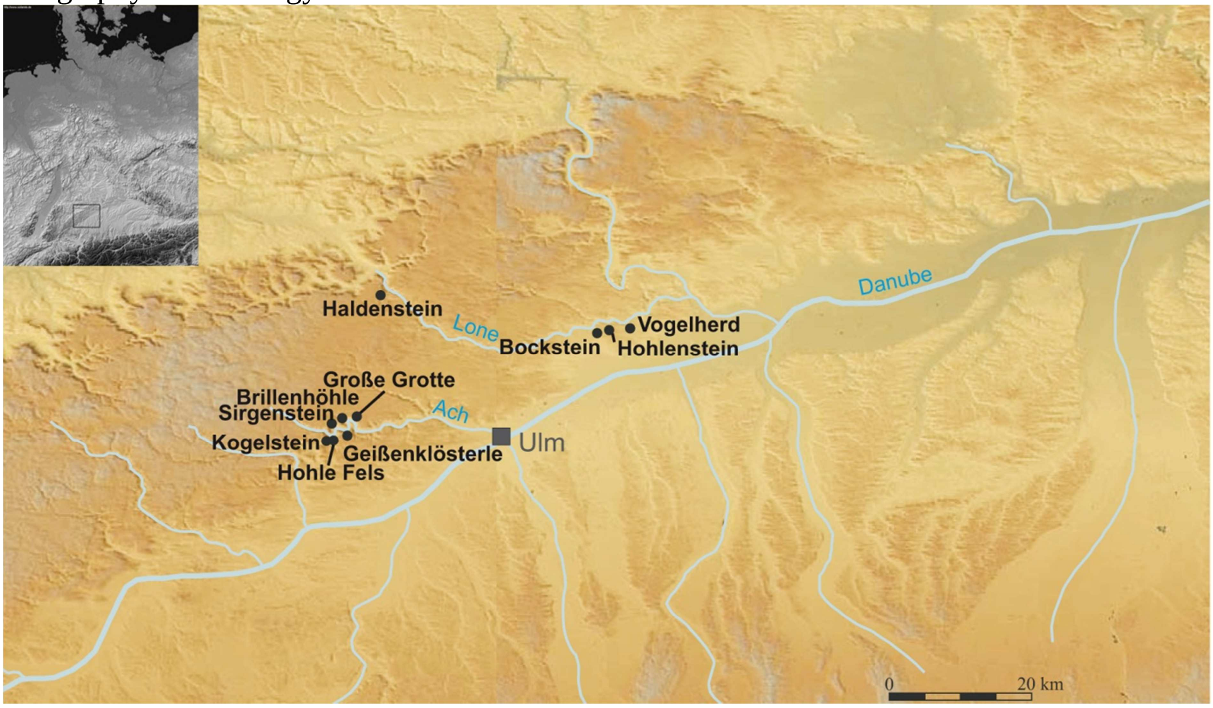


Figure 2.1 Topographical map of the Ach and Lone valleys with the names of the major Paleolithic sites.

The Swabian Jura, also known as the Swabian Alb, is located in the southwestern area of Central Europe and represents the largest karst system consisting of calcareous massifs in Germany. It is part of the Jurassic limestone belt that stretches from the Swiss and French Jura mountains to the west and the Franconian Alb to the east, approximately 220 km in length and 80 km in width. Ranging between 450-1000 m asl, it consists of an escarpment and a dry upland plateau. Geographically, the Swabian Jura is bounded by the Upper Danube Valley that cuts through the Alpine Foreland Basin to the south and by the meteorite crater of Nördlinger Ries to the northeast. The plateau is tilted slightly towards the Upper Danube Valley due to the cuesta landscape and is marked by the uplifted flank (*Albtrauf*) on the northern side. Further, the northern area consists of a hilly landscape (*Kuppenalb*), whereas the south is characterized by a low relief landscape (*Flachenalb*) (Geyer and Gwinner, 1991; Kaufmann and Romanov, 2008).

The caves are geologically found in the White Jura (Malm Ɛ), which consists of massive limestone (*Massenkalk*) and bedded marl complexes of reef facies (*Schwammfazies)* (Geyer and Gwinner, 1991; Miller, 2009). The sea of Theys (former Mediterranean) formed in the Upper Jurassic Period, and the sedimentation of limestone and dolomites led to the formation of the Swabian Jura (Abel et al., 2002; Geyer and Gwinner, 1991). Shallow karstification occurred during the Cretaceous and Early Tertiary periods (Abel et al., 2002). The North Alpine Molasse Basin formed during the early Eocene, transgressed over the Jura and prevented further karstification leaving shallow marine deposits in the foreland (Abel et al., 2002). It receded in the Middle Miocene and left a shoreline known as *Klifflinie* (cliff line). The line runs along the Alb and defines the boundary between the *Kuppenalb,* which resulted from the exposure of the reef, and the *Flachenalb,* which formed with the recession of the molasse and erosion.

After the molasse disappeared, water began to flow into the Danube River. Some tributaries such as the Lone River experienced a flow reversal due to the opening of the riff in the Rhine River, resulting in further incision (Strasser et al., 2010). The present landform of southwestern Germany is mostly the result of Alpine tilting, which occurred during the Middle-Late Miocene to Pliocene and the uplift of the foreland crust by 1-3° in the Middle Pleistocene. The Swabian Jura also underwent further karstification and formed rock formations and caves that resulted from the uplifting of the plateau during the Late Miocene and Pliocene, and the incision of rivers such as the Aare-Danube River that cut into the carbonate plateau (Abel et al., 2002; Strasser et al., 2010).

Further, the phreatic water from the Pliocene and Early Pleistocene led to the formation of underground cave systems in the massive Jurassic limestone dolomites (Diedrich, 2013). The continuous karstification and entrenchment has led to discharge of smaller tributaries into the subsurface (Abel et al., 2002). Escarpments exist on the southern area of the Jura that resulted from the incision and migration of the Danube River southwards during the late Miocene and the early Pleistocene. The caves around the Danube became inactive by the Pleistocene and the tributaries gained more water. The current river drainage system formed during the Riss Glacial period (200-130 ka) and the Danube River fluctuated with the advances of the glaciers in the Alps (Abel et al., 2002). Some claim that the landscape of the Ach and Lone valleys have been relatively stable since the beginning of the Pleistocene, but some note that there may have been some changes such as a river migration in the Lone Valley (Barbieri, pers. comm.). Sites are located predominately in the valleys of the Lone and Ach. Due to tectonic activities, Jurassic chert is more commonly found in the eastern area of the upland (Burkert and Floss, 2005).

The Ach and Lone Valleys

The Lone Valley lies several kilometers north of the Danube River. It runs approximately 30 km long and parallel to the Danube. The Lone River originates from the source of karst groundwater in the village of Urspring on the border of the eastern *Flachenalb,* and flows east into the Brenz River, which then drains into the Danube River. The Lone River today runs seasonally when there is heavy precipitation or when enough snow melts into the karst water table that feeds into the river. Most of the water from the source is fed into the karst system. The northern edge of the Danubian Basin runs roughly 4 km to the south (Krönneck, 2012). In the past, the Lone was one of the major streams in the Jura that fed into the Danube River (Strasser et al., 2009). The vegetation was probably dominated by an open steppic landscape with slightly humid conditions, as it was part of the Molasse Basin (Hahn et al., 1985). There are nine sites with seven Paleolithic deposits (Hahn et al., 1985) including Haldenstein (Bolus, 2004), the Bockstein complex (Wetzel et al., 1969), Hohlenstein-Stadel (Beck, 1999; Wetzel, 1961), Hohlenstein-Bärenhöhle (Wetzel, 1961) and Vogelherd (Riek, 1934). Most sites are found at an elevation ranging between 478-500 m asl.

The Ach Valley lies roughly 10-15 km away from the Lone Valley. It formed as the Danube River flowed through and incised the plateau, with the Danube River leaving the valley after the Riss Glacial Maximum. In the Early Pleistocene, the river flowed 80 meters higher than the present valley floor. As a result, the valley is more than 150 m below the surrounding plateau surface, creating high reliefs in some areas (Miller, 2009). The Ach River is roughly 3 m wide and runs in the valley year round, draining into the Blau River, a tributary that runs into the Danube River. Many sites in the Ach Valley lie between 556-580 m asl. The nearest outcrop of chert is roughly 3 km away (Floss and Kieselbach, 2004). The valley bottom was 40 m lower and filled with gravel and sand after the Riss Glacial period. It was 5-10 m lower at the end of the Pleistocene (Goldberg et al., 2003; Wagner, 1979). The main archaeological sites include Geißenklösterle, Hohle Fels, Kogelstein (Böttcher et al., 2000; Kind, 2000), Sirgenstein (Schmidt, 1912), Brillenhöhle (Riek, 1973) and Große Grotte (Wagner, 1983a; Weinstock, 1999).

The Past environment: trends in Central Europe during MIS 5-3

Environment serves as an important background for the evolution of humans and often played a crucial role in shaping hominin behavior. The climatic data of Central Europe from the MIS 5-3 (110-27 ka) will be discussed in this section. The proxies for global climate change from various sources have gained greater resolution and dating methods with increased accuracy have enabled researchers to correlate environmental records with archaeological deposits. On a global scale, continuous paleoenvironmental archives include ice cores from Antarctica and Greenland, marine and lake cores, loess deposits and cave speleothems. Several environmental records allow a glimpse into the past environment in Central Europe during the period of the Middle and early Upper Paleolithic. The pollen data, which are often the conventional terrestrial record for paleoclimatic reconstruction, provide a detailed picture of past vegetation (Antoine et al., 2001; Müller et al., 2003).

The Pleistocene period, especially for 1.8 million years ago (Ma), witnessed repeated glaciation (lasting roughly 100 k on average) and interglacials (lasting 15 k) (Birks, 2008). The environment in middle and high latitudes of the northern Hemisphere was mostly dominated by steppe-tundra (also known as the mammoth steppe), an ecosystem with no present analog, and served as an environmental setting for hominins occupying Central Europe during glacial conditions (Gamble, 1986; Guthrie, 1982, 1990). The origin is not clear, but this biome is first identified in the Yukon region and emerged between 2-1.6 Ma (Harington, 2011; Schweger, 1997). The geological setting and the climatic conditions have been present by 2 Ma while the fossils of the fauna that represent the ecosystem are present since 1.6 Ma (Kahlke, in press). Kahlke (in press) has argued for an earlier genesis of tundra-steppe at the beginning of the Pleistocene ~2.6 Ma with the formation of a circumpolar tundra belt caused by decreased sea levels, change in the ocean currents and increased continentality. The extent of tundra-steppe was the largest probably during the last Glacial period, starting from 110 ka until the Last Glacial Maximum around 24 ka.

The landscape of tundra-steppe was characterized by an arctic environment with open grasslands. There was moderate moisture with little precipitation, permanent permafrost and thin snow cover. Several authors note that tundra-steppe vegetation developed on loess, which is rich in minerals and nutrients. The loess surface with high insolation was conducive to high biological productivity and provided diverse forage (Guthrie, 1982; Vereshchagin and Baryshnikov, 1992). While the seasonal fluctuation of temperature and humidity is not easy to track, it is presumed that the permafrost in the soil partially thawed during the summer, which allowed herbaceous plants to grow (Vereshchagin and Baryshnikov, 1992). The vegetational community was composed of a mix of grasses, sedges, herbs, shrubs in addition to lichens, forbs and mosses (Birks, 2008; van Geel et al., 2008a). Such conditions in turn have sustained a diverse faunal community, especially large herbivores. Kahlke (in press) attributes the origin of the vertebrates to fauna from Asian steppe and Arctic tundra, which migrated into the tundra-steppe. The community is referred to as the *Mammuthus–Coelodonta* faunal complex (Kahlke, 1999, in press).

The initial phase of MIS 5 or MIS 5e (127-115 ka) was the Eemian Interglacial phase characterized by globally warm and moist conditions. The loess-paleosol sequences in the Lower Danubian corridor show intense pedogenesis during this period (Fitzsimmons et al., 2012). MIS 5e was characterized by one of the warmest and most humid climatic phases in the last 1 million years except for the Holocene (Fitzsimmons et al., 2012). In the Alpine Foreland, deciduous trees such as elms and oaks and mixed forests prevailed (Müller, 2000; Preusser, 2004). During the final phase of the Last Interglacial, the vegetation was dominated by coniferous trees (Preusser, 2004). The pollen spectrum from the Füramoos pollen core in southern Germany indicates forests with conifer trees (Müller et al., 2003).

Climatic deterioration prevailed immediately after the interglacial phase. Each stage from MIS 5d-5a (115-74 ka) corresponds to the interstadial (5c/5a) or stadial phases (5d/5b) with cycles of climatic fluctuations. An interstadial phase initially referred to a warm period without the expansion of temperate forest, which characterized the interglacial vegetation, because of its relatively short duration (West, 1961). Interstadial and stadial time periods witnessed reforestation and deforestation intermittent with the development of steppe-tundra biomes (Preusser, 2004). Such cycles are documented in geological profiles with episodes of soil development and erosion (Antoine et al., 2001).

The Dansgaard-Oeschger events occurred on a global scale during the Last Glacial Period, which correspond to MIS 5d-2 (110-12 ka) (Dansgaard et al., 1993; Genty et al., 2010; Spötl and Mangini, 2002). The events refer to a series of recurring climatic fluctuations and are characterized by an abrupt warming (Greenland Interstadial) and gradual cooling

(Greenland Stadial) (Dansgaard et al., 1993). The climatic oscillations were first identified in the ice cores (Grootes et al., 1993) and are often documented in terrestrial archives of the Middle Weichselian (MIS 4-3) (Boettger et al., 2009). One of the D-O events was recorded in a peat deposit in eastern Germany some time during the MIS 4 and early MIS 3, and the botanical and zoological analyses indicated a minimum July temperature of 12-14 °C (Bohncke et al., 2008). Terrestrial record studied by Boettger et al. (2009) shows abrupt warming during the transition from the last interglacial to glacial condition (Early Weichselian) in Central Europe. An overview of several records from the Alpine indicates the flora during most of the interstadial periods were dominated by open boreal forest with pine, spruce, birch and *Larix* (Fletcher et al., 2010).

Heinrich events were sudden cold climatic episodes that are associated with the formation of ice-rafted debris deposits in the North Atlantic (Heinrich, 1988). First identified in the marine sediments, Heinrich events are better documented in the marine records than the terrestrial ones (Bond and Lotti, 1995). A core from the Bay of Biscay represents one of the few marine cores in the middle latitude between 44-50 °N (Fletcher et al., 2010; Sánchez Goñi et al., 2008). In this record, the decrease of pines and higher values of steppic flora correspond with the occurrences Heinrich events and differ from other stadials (Fletcher et al., 2010).

The loess record from MIS 4 (74-60 ka) shows greater accumulation of loess, indicating dry and cold climates (Fitzsimmons et al., 2012). MIS 4 was characterized by the increase in non-arboreal pollens, suggesting a replacement of forests by steppe and tundra, and a development of deltaic deposits, which are interpreted as advances of glaciers onto the Alpine foreland (Early Würmian) (Preusser, 2004). During MIS 4, arboreal taxa became extinct in the area north of the Alps (Müller et al., 2003).

The Nussloch loess profile in southwestern Germany serves as a crucial paleoenvironmental archive on a millennial scale with a continuous record from the Last Interglacial and Glacial period in Central Europe (Antoine et al., 2009; Antoine et al., 2001; Kadereit et al., 2013) . In this sequence, MIS 4 was represented by thick loess deposits interrupted by weathering horizons. Such patterns correspond to a cold and arid environment represented by the loess formation and a warmer and humid condition represented by chemical weathering. Mollusk abundance correlates with a $\delta\ ^{18}$O signal from Greenland ice cores, suggesting warmer conditions during the interstadial periods (Moine et al., 2008). Other sedimentary records in the region track this trend (Kühn et al., 2013). A series of drill cores in the Unterangerberg Terrace has also yielded an environment reconstruction of the Eastern Alps in Austria (Starnberger et al., 2013). Conventional pollen analysis and dating in lacustrine sediments revealed the following environmental fluctuations. The end of the Interglacial was characterized by a relatively abrupt cold spell, suggested by episodes of strong fluvial aggradation with sparse vegetation. Before the onset of MIS 4, the boreal forest with *Picea* was prevalent. The forest disappeared in MIS 4, which was documented by a low pollen concentration (Starnberger et al., 2013).

Some terrestrial paleoenvironmental records show gaps in the record during the MIS 3 period (60-27 ka), as deposits were eroded away during the Last Glacial Maximum (Fiebig and Pacher, 2006). Thus, a number of sedimentary records that span during MIS 3 are characterized by a hiatus in pollen accumulation until the end of the glacial period, and not many pleniglacial deposits are located in northwestern Europe (Caspers and Freund, 2001; Müller et al., 2003). However, several sources of paleoenvironmental archives help us reconstruct the past environment in temperate Central Europe.

Open forests characterized the early phase of MIS 3 starting around 60 ka. The malacofaunal assemblage recovered from the loess-paleosol sequence in Dolní Věstonice dating to ~55-40 ka shows that it was dominated by a humid and steppe environment (Antoine et al., 2013). Loess in the Middle Danubian corridor demonstrates a wet and mild condition relative to the previous stage. The soil is not intensively weathered, documenting no climatic deterioration (Fitzsimmons et al., 2012). Analysis of pollens from cores in the foreland of the Eastern Alps 30-50% of arboreal pollen shows that the tree vegetation developed in the interstadial, dating to ∼55 and 45 ka (Starnberger et al., 2013). In lowland Switzerland, the pollen record indicates that the open woodland prevailed in 54 ka (Preusser et al., 2003). The Nussloch sequence in southern Germany shows a mild climate with a decrease in loess accumulation and soil formation (Antoine et al., 2001; Kadereit et al., 2013). Füramoos indicates a mild climate during the interstadial periods dated to 51,000 and 44,000 BP, respectively (Müller et al., 2003).

In contrast, the landscape of the MIS 3 stadials was covered by grasses and shrubs and only 10-20% of pollen originated from trees such as pines and birches (Starnberger et al., 2013). At Niederweningen, a paleontological site with rich mammoth remains in the Swiss Alps, arboreal pollen proportion of 20-40% suggest open grassland vegetation ~50-45 ka (Drescher-Schneider et al., 2007). In the Alpine foreland, MIS 3 was characterized by an unstable climate with cool conditions, but a lack of ice in the Swiss Alps (Turk, 2012). In lowland Switzerland, the period of 50-48 ka was marked by forest steppe vegetation and the decrease in temperature, which is inferred from coleopteran assemblages (Preusser et al., 2003).

Work by Huijzer and Vandenberghe (1998), which combines evidence from eolian, fluvial and glacial deposits as well as botanical and faunal data, provides a comprehensive review of the climate in Central Europe during this period. The interval of 50-45 ka was characterized by cold conditions in which the warmest months were still within the range of freezing temperature. This climatic trend was interrupted around 43-42 ka when there was a thermal spike known as the Upton Warren Interstadial and was marked by the spread of arboreal vegetation. Organic remains including microbotanical remains in the fluvial/eolian deposit from Niederlausitz, eastern Germany, also indicate a treeless landscape dominated by low-shrub tundra during 42-40 ka with relatively high summer temperatures which may correspond to the Upton Warren Interstadial period (Bos et al., 2001).

From 41-38 ka, the continental condition with cold, arid winters prevailed again with the expansion of glaciers along the Norwegian coast (Huijzer and Vandenberghe, 1998). Glacial conditions are marked by the presence of ice-wedge casts, lasting until 38 ka, and a mean temperature of 10-11 °C and -20 °C for warm and cold months (Bos et al., 2001; Caspers and Freund, 2001). The 38-28 ka interval is marked by tundra biome with low shrubs and grasses (Bos et al., 2001). The climate between 36-32 ka was marked by warming with permafrost degradation with a stable landscape inferred from loess deposits in the time before Europe entered the coldest phase in 27 ka.

In all, the climate was in flux throughout the late Middle and early Upper Paleolithic in temperate Europe. There is no general consensus on the duration on the oscillation except on a millennial-scale, as observed in stalagmites (Genty et al., 2003; Genty et al., 2005). The authors remark on the increased oscillation after 40 ka, partially attributed to better resolution of the data in contrast to other sources on the paleoenvironmental record, which may show temporal lags (Genty et al., 2003; Genty et al., 2005). Caspers and Freund (2001) discuss the similarity between vegetation around 50-28 ka and the earlier Weichselian periods, which corresponds to the Middle Paleolithic period. Their interpretation suggests that despite continual climatic fluctuations in mid-latitude Europe, stadial periods were marked by colder conditions resulting in a similar array of vegetation that did not significantly alter between each interval. Cycles of climatic oscillation are particularly well documented in the temperate region of Europe throughout the last Interglacial to Glacial period with tundra-steppe environments during the glacial and stadial periods, interchanging with woodland/forests during interstadial periods.

Past environments in the Swabian Jura

Few paleoenvironmental archives independent from archaeological sites exist in the Swabian Jura. Some of the closest archives, as mentioned above, include the Nussloch terrace deposit (Antoine et al., 2009; Kadereit et al., 2013) , the terrace near the Eastern Alps in Austria (Starnberger et al., 2013), Pleistocene deposits in the Swiss Alps region (Drescher-Schneider et al., 2007), the Füramoos pollen sequences (Müller et al., 2003), roughly 150 km away from the Swabian Jura. They depict mostly steppe-tundra vegetation on the landscape with occasional open forests.

Most of the paleoenvironmental records in the Swabian Jura itself derive from caves with Paleolithic deposits. The reconstruction of the past climatic patterns is based on several lines of evidence including microfauna, avian fauna, macrobotanical remains as well as micromorphological samples from archaeological deposits (Böttcher et al., 2000; Krönneck, 2012, in press; Miller, 2009; Ziegler, in press). Some of these data are discussed here.

During the Late Pleistocene, the Swabian Jura is mostly characterized by a steppe-tundra biome with some woodland, especially since the Last Glacial period. The spectra of fauna attest to a landscape typical of continental Europe in the middle latitude. The analysis of middle and large-sized fauna from the site complex of Bockstein indicates that steppes with woodland prevailed during the Middle Paleolithic and persisted throughout the Aurignacian (Krönneck, 2012). Although faunal composition can be influenced by the hominin choice of prey, it indicated that the taxonomic representation did not alter significantly over the period of transition.

Microfauna document smaller climatic oscillations compared to larger mammals that represent averaged climatic signals from the Paleolithic periods. The inventory of microfauna from Kogelstein in the Middle Paleolithic demonstrates that the area was characterized by a mosaic environment with different ecozones (Böttcher et al., 2000). Arctic species such as collard lemming (*D. gluliemi)*, brown lemming (*L. lemmus)* and narrow skulled vole (*M. gregalis)* account for less than 10% of the assemblage, whereas animals inhabiting temperate steppe and open forests make up the greater proportion of the assemblage. The gradual decrease of temperate species documents a shift from the interstadial to stadial condition (Böttcher et al., 2000). This trend is also reflected in the assemblage of land mollusks, which is marked by a lack of glacial species (Böttcher et al., 2000).

The microfaunal assemblage from Geißenklösterle depicts a fine-grained picture of the Middle Paleolithic and the Aurignacian (Ziegler, in press). In several MP layers, the environment largely witnessed a milder climate with a decreasing tundra element and increasing boreal species, evidenced by the scarcity of *Dicrostonyx*. The average summer temperature is relatively high. The trend is consistent from the MP to the Lower Aurignacian, but the microfauna representing tundra biome dominated the assemblage during the Middle Aurignacian (Ziegler, in press). Consistent with larger mammals, the transition from the Middle Paleolithic to the Aurignacian shows no direct evidence of abrupt climatic change.

The avian faunal assemblage is represented by taxa that inhabit steppe-tundra, temperate steppe and coniferous forest and species that live in the vicinity of lakes during the Middle Paleolithic (Böttcher et al., 2000). At Geißenklösterle, the assemblage is mostly dominated by birds that inhabit tundra biome and a small proportion is represented by woodland species during the Aurignacian (Krönneck, in press). Such a proportion points to a continental climate with arid conditions that was common through Central Europe (Krönneck, in press). Therefore, the climate in the Swabian Jura was mostly characterized by more temperate and warmer conditions during the interstadial phases of MIS 4 and 3.

Geological and micromorphological analyses from Geißenklösterle and Hohle Fels offer another reconstruction of the environment with some intersite variability (Conard et al., 2006; Miller, 2009). In Geißenklösterle, micromorphological samples taken from the transition between the Middle Paleolithic and the Aurignacian are marked by an episode of erosion, indicating an abrupt shift from a mild and moderately humid climate to a colder and drier climate (Miller, 2009). While the general trend is comparable at Hohle Fels, the change appears to be gradual with a mild climate lasting through to the beginning of the Aurignacian, which is then followed by a cooler climate. These studies demonstrate that climatic changes did occur, but the exact timing of environmental shifts and their effect on hominins remain to be investigated.

Pollen and charcoal remains from the sites of Geißenklösterle and Hohle Fels show a period of warm weather, which correlates with an increase of arboreal pollen around 42,000-40,000 cal BP, followed by evidence of sparse tree cover during 39,000-37,500 cal BP (Riehl, 1999). Increased tree pollen suggests another episode of woodland expansion during the middle of the Aurignacian that continues until the end of 33,000 BP. Filzer (1969) analyzed the pollens from the upper Middle Paleolithic deposits of Bockstein and identified *Pinus*, *Picea* (spruce), *Betula* (birch) *Corylus* (hazel bushes) and *Ulmus* (elm), which reflects mild climate with diverse trees.

In all, the paleoenvironmental record shows that the steppe environment mostly prevailed in the Swabian Jura with some woodland and riverine forests. To date, an abrupt shift in the climate between the Middle Paleolithic and the Aurignacian is documented only by micromorphological studies of Geißenklösterle (Miller, 2009), while other lines of evidence mostly support a relative stable climatic condition during the transitional period followed by a climatic fluctuation within the Aurignacian period. From the middle of the Aurignacian, the cooler climate prevailed and persisted through to the Gravettian period around 27,000 BP.

Prehistory in the Swabian Jura: The Chronostratigraphy

Middle Paleolithic

The Middle Paleolithic is a period known for the emergence of Neanderthals, which is dated to roughly ~200 ka, but some technological attributes that are common in the lithic industries appear earlier, between 250-300 ka. While Neanderthals are one of the most common hominin fossils in the paleoanthropological record, there are indications that the population was relatively small and the density of occupation remained low based on genetic analyses (Dalén et al., 2012; Green et al., 2010).

The emergence of the Middle Paleolithic industries is distinguished by the development of the Levallois technique for core preparation and the standardization of flakes for tool production, which are culturally specific, such as bifacial tools or blades (Delagnes et al., 2007; Richter, 2011). That said, there is a large variability in lithic assemblages in the Middle Paleolithic, triggering debates among archaeologists to explain the diversity (Binford and Binford, 1966; Bordes, 1961). This period is also characterized by the emergence of ‘technocomplexes’ limited to a particular temporal and geographical range (Gamble, 1986). Tools that are made on flakes such as scrapers and points appear more frequently. Further, composite tools also became a part of the cultural repertoire in the Middle Paleolithic around 150 ka (Ambrose, 2001; Wadley, 2010). The archaeology of Middle Paleolithic in Europe continues into the later phase of MIS 3 as the Neanderthals survived in the southern Iberia until 40-30 ka (Finlayson et al., 2006).

The lithic industry from the Middle Paleolithic in Central Europe is characterized by a large temporal and regional variability. Towards the end of the Middle Paleolithic, the Micoquian complex appears in Central Europe. The site that served as the type locality, La Micoque, is situated in France and its assemblage is characterized by the common occurrence of bifacial tools in contrast to the late Mousterian (Rosendahl, 2011; Ruebens, 2007a). It appears that Micoquian is a unique development in the Middle Paleolithic and not a result of a continuous tradition from the Acheulean industry of the Lower Paleolithic (Kozłowski, in press). Another tool type, known as the *Keilmesser* group, is now a preferred term as it encompasses other variants of tool forms and since the technocomplex may not be temporally and technologically related to La Micoque (Conard and Fischer, 2000; Rosendahl, 2011).

Keilmesser in particular refers to the bifacial backed knife, which was recovered in large numbers at Bockstein (Conard and Fischer, 2000). This form of tool is found in Germany and some northwestern and central European sites. Interestingly, Kind has further argued that there are ‘mixed’ assemblages with Micoquian and Mousterian components and thus these two technocomplexes are not mutually exclusive (Kind, 1992; Ruebens, 2007a). To date, the *Keilmesser* (Micoquian) technocomplex has been recovered from central Europe while mixed assemblages have been found in central and northwestern Europe (Ruebens, 2007b, 2013).

In addition, (Bosinski, 1967) distinguished leaf points, or *Blattspitzen*, as a characteristic tool type (Bolus, 2004). They are usually thin and elongated bifacial tools. Leaf points have been found in Vogelherd, Große Grotte (Wagner, 1983a) and Haldenstein Cave (Riek, 1938) and Geißenklösterle in the Swabian Jura, but are not well dated. Stratigraphically, it overlies the *Keilmesser* group and chronologically is found before the appearance of the Upper Paleolithic industries. Leaf points are one of the tools that distinguish late Middle Paleolithic industries. Since leaf point assemblages only appear at the end of the Middle

Paleolithic, they can be interpreted as a transitional industry in parts of central Europe. *Blattspitzen*, or the leaf point complex, is chronologically placed at the end of the Middle Paleolithic or as a transitional period (Bolus, 2004).

In the Swabian Jura, the earliest occurrences of hominin settlement remain to be securely dated. A fossil specimen from Hohlenstein-Stadel is a clear evidence of Neanderthal occupation in the region (Kunter and Wahl, 1992), but hominin remains from sites such as Steinheim, Bad Cannstatt and Reilingen demonstrate that predecessors of Neanderthals occupied southern Germany well before 200 ka (Czarnetzki, 1999; Czarnetzki and Pusch, 2001; Dean et al., 1998; Haidle and Pawlik, 2010). It is still not clear how early Neanderthals settled into the area, but the recovery of straight-tusked elephant from Vogelherd confirms that early hominins resided in the Swabian Jura at least by the last Interglacial period between 130-115 ka (Hahn et al., 1985; Niven, 2006).

Typical tools in the *Blattspitzen* group or other late Mousterian complexes are not found ubiquitously in the Swabian Jura with the exception of Bockstein (Bolus, 2004; Conard et al., 2012). Instead, the typical lithic assemblage from the area can be broadly coined as Swabian Mousterian with no equivalence of a similar lithic technocomplex in other geographical regions (Conard et al., 2012). The assemblage shows a low level of standardization with highly reduced Levallois components and is not defined by a particular tool type (Beck, 1999; Conard, 2011). Thus, there is no clear occurrence of a transitional industry in this region.

The lithic raw material is dominated by the Jurassic grey chert, found in the vicinity of the caves, and Bohnerz brown chert, found in the southern Swabian Jura in the river deposits (Burkert and Floss, 2005; Çep et al., 2011). In addition to the Jurassic chert, another important raw material of the region is radiolarite, which originated in the Alps and is found in river deposits of the Danube and moraine gravels (Floss and Kieselbach, 2004). In most cases, the local grey chert is the most commonly exploited raw material, and other sources were rarely used. Preference for the grey chert may point to Neanderthal's use of a relatively small territory, or the abundance of the local raw material, or to the high degree of hominin mobility that did not permit transportation of exotic raw materials over long distance.

While the use of organic artifacts for the Middle Paleolithic period is still debated, some sites have produced bone, antler and ivory remains that are unambiguously modified in the Middle Paleolithic (Villa and D'Errico, 2001). There are few examples of bone points and retouchers from Vogelherd (Riek, 1934) and Große Grotte (Wagner, 1983a) found from a Middle Paleolithic context. Besides, there is scarce evidence of use of organic remains for the production of artifacts in this region.

The earliest evidence of Neanderthal occupation in this region still remains to be securely dated. The presence of straight-tusk elephant associated within a stratified layer at Vogelherd (Niven, 2006) points to milder climate and wooded vegetation and suggests possible occupation during the Interglacial Period (MIS 5, 130-70 ka). Further, the archaeological horizon from Bocksteintörle (AH X) indicates an occupation layer during warm interglacial conditions (Krönneck, 2012; Lehmann, 1954; Wetzel, 1957), but the earlier Middle Paleolithic occupation remains to be directly dated. ESR dating is currently being conducted on bovid and equid teeth from Hohlenstein-Stadel and Geißenklösterle by C. Falgueres and M. Richard to understand the duration of occupation at the sites.

The oldest date using electron spin resonance (ESR) dating on teeth enamel came from the latest Middle Paleolithic layer (AH IV) from Geißenklösterle and yielded a mean age of 43.3±4 ka (Richter et al., 2000). There are additional results of ^{14}C dating for Hohlenstein-Stadel that point to older dates. While the dates near the limit of radiocarbon dating, and uncertainty in the calibration remains, the recent dating suggests a minimum age of ~50,000 cal BP for Hohlenstein-Stadel and 48,600±3200 BP for Geißenklösterle (AH VII) (Beutelspacher et al., 2011; Higham et al., 2012). The youngest Middle Paleolithic occupations at most sites in the Swabian Jura date to approximately 40 ka (Conard and Bolus, 2003; Richter et al., 2000). These dates generally coincide with the end of the Mousterian industries in Western Europe and their replacement by the Aurignacian culture.

Transition to the Aurignacian

The emergence of the Aurignacian in the Swabian Jura coincides with the evidence of the earliest fossil remains occurring around 43-42 ka (Higham et al., 2011). The Uluzzian culture may slightly predate the appearance of the Aurignacian culture by 1,000-2,000 years (Benazzi et al., 2011).While the coexistence of the Uluzzian and Aurignacian technocomplexes remains to be resolved, current data support the hypothesis that one of the earliest populations of humans with fully developed Aurignacian culture settled in the Swabian Jura (Conard and Bolus, 2003, 2008; Higham et al., 2012).

There are no fossil remains found in association with the industry, pointing to a lack of direct evidence that links the makers with the early Upper Paleolithic culture. Nonetheless, the fossil remains of modern humans were recovered at Kent’s Cavern, England, dated to 43-42,000 cal BP (Higham et al., 2011), Grotta del Cavallo, SE Italy, dated to 43-42,000 cal BP, (Benazzi et al., 2011) and Peştera cu Oase, southwestern Romania, dated to 36-34 ka (Trinkaus et al., 2003). These dates span the period when the early Aurignacian culture first emerged in Europe. We thus assume that this culture represents the dispersal of modern humans in Eurasia.

Demonstrated by recent series of new measurements, the Aurignacian begins immediately after the end of the Middle Paleolithic and the ages of the two cultures overlap at the scale of radiometric dating (Conard and Bolus, 2003, 2008). The youngest Middle Paleolithic and the earliest Aurignacian date to 40 ka (calibrated to 42,000 cal ^{14}C BP) (Higham et al., 2012). The earliest Aurignacian in the Swabian Jura is dated to 42,000 cal ^{14}C BP from Geißenklösterle based on the AMS dating method using ultrafiltration and improved background correction (Higham et al., 2012). Improvements in dating technique consistently resulted in dates that are older than the material, which are treated without ultrafiltration (Higham et al., 2012). This date conforms to the TL dating, 41 ka, which was produced from the same basal layer of the Aurignacian (Richter et al., 2000).

While no temporal gap between the last Neanderthals and the arrival of modern humans is observed, the coexistence of Neanderthals and modern humans has not been documented in this region. The absence of direct contact is supported by sterile layers that exist between the upper most MP basal Aurignacian layers and by micromorphological analysis showing erosional disconformity between the cultural horizon of the Middle Paleolithic and early Upper Paleolithic at Hohle Fels and Geißenklösterle (Conard et al., 2006; Miller, 2009). The depositional history argues against the co-occurrence of Neanderthals and modern humans in the Swabian Jura. Thus, the archaeological record in the region has not produced evidence indicating contacts and possible competition between Neanderthals and modern humans, leaving the cause for the Neanderthal disappearance still unresolved.

Several models have been proposed to explain the transition from the Middle to the Upper Paleolithic in the region. The Danubian Corridor model put forth by several researchers posits that one of the earliest waves of modern humans migrated through the river valley of the Danube, with the caves of the Swabian Jura representing one of the earliest settlements of a fully developed Aurignacian technocomplex in Europe (Conard and Bolus, 2003, 2008; Conard et al., 2006)). New series of dates appear to confirm this hypothesis as the beginning of the Early Aurignacian occupation precedes other sites in Europe (Higham et al., 2012; Richter et al., 2000). Further, the *Kulturpumpe* model considers the different causes including the interaction between archaic and modern populations, climatic stress or demographic patterns as forces triggering the development of Aurignacian culture in the Swabian Jura (Conard and Bolus, 2003). To date, the hypotheses on climatic stress and demographic patterns remain to be explored.

The emergence of Aurignacian culture marks a clear break in the prehistoric record of the Swabian Jura. The lithic assemblages are often characterized by tools such as scrapers and burins, and the production of artifacts is mostly dominated by blade production using unidirectional knapping techniques (Bolus, 2003; Conard et al., 2006). The lithic technology in the Aurignacian, which lasts until 32 ka, remains relatively consistent over time. According to Bolus (2003), two horizons, or the Lower and Upper Aurignacian, show variability in the abundance of certain tool types, with greater diversity in the type of organic tools in the Upper Aurignacian period. However, the continuity from the lower to upper period overrides the variability.

Moreover, the Aurignacian is distinguished through the material culture of symbolic expression, a key marker of the early Upper Paleolithic culture in the Swabian Jura (Conard et al., 2006). Prehistoric art expressed in different media and forms in the Aurignacian clearly points to an emergence of a new cognition, behavioral repertoire and cultural system. Mobiliary art is one of the earliest and most abundant examples of Aurignacian symbolism in the Swabian Jura (Conard, 2003; Conard, 2009). This is in contrast to other forms of symbolism, which are documented earlier in southern Africa (Henshilwood et al., 2009; Marean et al., 2007; McBrearty and Brooks, 2000). The oldest anthromorphic ivory figurine known as Venus has been recovered from Hohle Fels and is dated to 35 ka (Conard, 2009). Additionally, two sculptures are anthropic, while other figurines are shaped in the form of animals. Representations of animals in three dimension or in semi-relief point to the significance of these fauna such as mammoth, horse, waterfowl, lion, bison, possible fish and other unidentifiable mammals (Conard, 2010; Floss and Rouquerol, 2007).

Personal ornaments have also been recovered in great quantity at the sites of Geißenklösterle, Hohle Fels and Vogelherd, where the Aurignacian occupations were more intense and excavated (re-excavated for Vogelherd) with an improved recovery technique using water screening and sorting (Conard et al., 2009b; Wolf, 2013). Ornaments were produced either from ivory following a standardized production sequence or *chaine d'operatoire* on teeth of animals such as cave bears, foxes and reindeer (Kölbl and Conard, 2003; Vanhaeren and d'Errico, 2006). Double perforated beads and knob-shaped beads are two common forms found uniquely in the Swabian Jura region, demonstrating a degree of regionality or group identity that occupied the area (Wolf, 2013). Some of the figurative art pieces have rings or holes with polished use-wear, indicating their use as suspended pendants (Conard, 2009). The figurative objects are at times interpreted as products resulting from cultural memory and ideology among the groups practicing the Aurignacian culture (Porr, 2010).

Another component in Aurignacian symbolic culture points to the earliest evidence of musical tradition in the Paleolithic. Flutes were produced either by perforating long bones of raptors or through a complex process using ivory fragments (Conard, 2009; Conard et al., 2006; Münzel et al., 2002). Discoveries of incised and notched fragments from Geißenklösterle and Vogelherd date to ~35 ka, which is contemporaneous with the earliest Venus figurine from Hohle Fels. This is the earliest known instrument in the Paleolithic and shows that music was practiced by the Aurignacian period. This also has implications for language capability and cognition of modern humans (d'Errico et al., 2003). To date, the material culture of symbolism, geographically limited to the Swabian Jura, is significant due to its richness and to an early date for the fully evolved Aurignacian culture.

Organic tools become incorporated in the artifact inventory, including bone points with a split base (Conard et al., 2006; Liolios, 2006). Ivory was an important raw material for the inhabitants of the Swabian Jura particularly during the Aurignacian, as numerous debitage have been recovered and many organic artifacts were produced from mammoth tusks. Fragments of aged ivory were used and softened before the processing by soaking the pieces in water (Wolf, 2013). Numerous fragments of ivory debris demonstrate that the production of elaborate organic tools was part of a cultural repertoire practiced on site in the caves. These include tools such as baton pierces, projectile points, and split bases among other ivory fragments with use-wear. The increase in the use of organic material for production of functional tools as well as non-utilitarian artifacts is another hallmark of behavioral modernity documented in the Swabian Jura. The organic technology clearly distinguishes the Middle Paleolithic, which has only a few organic tools, and the Aurignacian, which has produced a wide array of bone, antler and ivory tools (Conard et al., 2006; Wolf, 2013).

The Aurignacian period is also characterized by a change in settlement patterns following the Middle Paleolithic (Conard, 2011; Conard et al., 2012). Conard and colleagues assessed the intensity of occupation based on the density of artifacts per m^2. Data suggest that there is a clear increase in archaeological finds from the Middle Paleolithic to Aurignacian at sites where both cultural layers are present (Conard et al., 2012). Modern humans are represented by a higher artifact density than in the Middle Paleolithic, evidenced by the increased number of lithic artifacts, burnt bones, charcoal and modified bones in the Aurignacian layers (Conard, 2011; Conard et al., 2012). Such patterns may reflect increased population or longer residential times at caves in the early Upper Paleolithic period. This may have triggered cultural innovations and a new set of symbolic behavior during the

Aurignacian expressed in forms of ‘art’. Conard (2011) posits that Neanderthals may have had a smaller ‘cultural niche’ and did not adapt cultural means to a changing natural environment.

The Later Upper Paleolithic: The Gravettian and Magdalenian

The majority of evidence for Gravettian occupation in the Swabian Jura originates from the Ach Valley with the exception of Bocksteintörle (Conard and Moreau, 2004; Moreau, 2009). While some cultural layers between the Aurignacian and Magdalenian were well accepted, the term Gravettian was not employed in the Swabian Jura until Hahn’s work at Geißenklösterle. He began using the term aided by his communication with French prehistorians (Hahn, 1988). Gravettian occupations are documented at the sites of Sirgenstein (Liolios, 2006), Brillenhöhle (Riek, 1973), Geißenklösterle (Hahn, 1988) and Hohle Fels (Conard and Moreau, 2004; Moreau, 2009).

The earliest Gravettian dates shortly after the end of the Aurignacian around 30,000 years ago. No clear geological and temporal break between the Gravettian and Aurignacian exists and there is a transitional layer in Hohle Fels. Some tool types show overlaps, which suggest a gradual *in situ* transition from the Aurignacian to Gravettian culture. This hypothesis requires further investigation as the taphonomic processes could have led to mixing between the horizons (Conard and Moreau, 2004; Moreau, 2009).

Archaeological data point to intense occupation between 29–27 ka. Backed bladelets, burins, end scrapers and splintered pieces are among the common tools. In addition, the use of projectiles such as Gravette points becomes part of the tool assemblage. In the Gravettian layer of Geißenklösterle, 30% of the tool assemblage consists of bladelets for the manufacture of projectiles. Studies of lithic refits have shown that the same group of hunter-gatherers occupied Geißenklösterle and Brillenhöhle in the Ach Valley (Moreau, 2009).

The raw material of the lithics indicates that people began exploiting non-local sources that were previously unseen in the region (Burkert and Floss, 2005; Çep et al., 2011; Floss and Kieselbach, 2004). In the Gravettian period, there are two raw materials that are found far from the Ach and Lone valleys. One raw material is a fine grained, red Jurassic chert (also known as ‘Bohnerz’ jasper) that is altered through iron ore deposits and occurs in the restricted area of the Upper Rhine Valley south of Freiburg 180 km to the west. Another raw material is a banded tabular chert found in the Franconian Alb, east of the Nördlingen Ries Basin roughly 160 km in distance (Burkert and Floss, 2005; Floss and Kieselbach, 2004). There are also a lower Jurassic black alpine quartzite in the river deposits in the southern lowland and an Upper Triassic ‘Keuper’ chert that is found along the northern edge of the Swabian plateau (Floss and Kieselbach, 2004).

The use of local Jurassic chert decreases although it still dominates the lithic assemblage in the Gravettian period. Instead, the use of radiolarite that comes from the southern lowland (10-20 km away) increases (Burkert and Floss, 2005; Floss and Kieselbach, 2004). The abundance of exotic raw material indicates a movement of people along the Danubian corridor (Floss and Kieselbach, 2004). The inventory of tools and the debitage shows that most lithics produced from non-local raw material were brought to the Swabian Jura region as blanks or tools lacking the different stages of the reduction sequence.

Organic artifacts are found in abundance, but differ from that of the Aurignacian. There are many personal ornaments made from ivory and tear drop forms become more common during the Gravettian. The form of the ornaments also becomes diverse and includes perforated teeth and shell. Further, antler and bone tools become common, including bone points and awls (Conard and Moreau, 2004; Moreau, 2009).

The absence of clear evidence for the Gravettian period in the Lone Valley except for in one horizon in Bockstein is puzzling. However, some dates of faunal remains indicate that the Gravettian periods are represented in the Lone Valley, such as the brown bear canine from VH, but are potentially mixed with the Magdalenian period (Niven, 2006). The extinction of cave bears is dated to 25,560±130 BP in the Swabian Jura, which coincides with the Gravettian phase (Münzel et al., 2011). Thus, the occurrences of cave bear remains in the Magdalenian period needs to be explored by systematic study of the depositional history.

The Magdalenian period, which begins around 17,100±1500 BP (Weniger, 1989; Weniger, 1987), or 15,000 calBP according to new dates from Hohle Fels (Taller et al., 2012), follows a hiatus during the Last Glacial Maximum, during which time no evidence of human settlement is documented. An alternative explanation states that sediment between the Gravettian and Magdalenian was not preserved at many caves that experienced heavy erosion during the LGM. Nonetheless, it is likely that the caves were not intensely occupied by Solutreans, if present, relative to the prior Paleolithic period. A regional scale study suggests that people migrated from the refugia in the southern or western areas and repopulated southern Germany including the Swabian Jura region (Jochim et al., 1999).

The trend for raw material procurement continues from the Gravettian period with greater emphasis on non-local material such as tabular chert from the Franconian Alb or Keuper chert from the river deposits. In all, raw material that is further than 100 km away becomes prevalent (Burkert and Floss, 2005). Various bone and antler tools, such as projectile points, harpoon and bone needles, were thus recovered from Hohle Fels, exemplifying a typical Late Magdalenian assemblage (Taller et al., 2012). The Magdalenian assemblage contains worked pieces of jet and ivory, as well as perforated snail shells and teeth. Limestone fragments with painted red dots were recovered, representing one of the oldest pieces of evidence for artistic use of pigment in this region (Conard and Uerpmann, 2000).

Most sites show a predominance of reindeer and more than 89% of faunal assemblages are represented by reindeer, followed by horses (Weniger, 1987). Reindeer antler remains indicate that the killing of ungulates occurred around autumn to winter, with some smaller sites revealing evidence for summer and spring occupations. The Magdalenian still appears to be heavily dominated by grassland with some presence of forests which increase after the Bølling. In the Swabian Jura region, the sites appear also to have been shortly occupied during the summer with a focus on horse hunting. The sites are small in comparison to other neighboring regions (Weniger, 1987). Further, the proportion of fish in the subsistence increases substantially from the Gravettian period, demonstrated by harpoons as well as diverse fish remains at Hohle Fels (Conard et al., 2013; Owen, 2013; Torke, 1998). Owen notes that “the spectrum of fish recovered from the Magdalenian sites of southwest Germany suggests a much longer fishing season and an emphasis on fish other than salmon” (2013: 95), hinting at the diversification of the Paleolithic diet, most evident during the Late Upper Paleolithic.

Summary

The Swabian Jura is the largest karst system in southwestern Germany with limestone outcrops forming caves that became stabilized in the Pleistocene period. Sites are concentrated in the Ach and Lone valleys, which comprise the majority of the Paleolithic record. Paleoenvironmental archives from the region of western Central Europe during MIS 5-3 indicate climatic fluctuations beginning with interglacial conditions followed by interstadial and stadial periods. Interstadial periods are marked by mild conditions with greater abundance of arboreal vegetation, while the stadial periods indicate mammoth steppe with cold and arid conditions.

The prehistory of the Swabian Jura starts in the Middle Paleolithic. The fossil evidence shows that Neanderthals settled in the area at least by the Interglacial period (Niven, 2006) with relatively nondiagnostic artifact assemblages. Their presence continues until ~40 ka. The Aurignacian culture, with no equivalent cultural repertoire, appeared early in Europe by 40 ka (43-42,000 cal BP). The organic artifacts increased and diversified, which range from functional bone, antler and ivory tools to artifacts with symbolic significance including figurative artworks, ornaments and musical instruments. Gravettian culture is more prevalent in the Ach Valley, and the study of the artifact assemblage points to both continuity in artifact production, on the one hand, and changes in some of the cultural tradition including the manufacturing of body ornaments, on the other. The Magdalenian period represents the last phase of the Upper Paleolithic, after a period of hiatus in the archaeological record, with a likely increase in territorial range or the exchange of artifacts and ideas among cultural groups.

3 Sites in the Swabian Jura

This chapter will introduce the sites of the Swabian Jura that are included in the following analysis. Hohlenstein-Stadel is discussed in detail as this study, along with previous studies by Gamble (1979, 1999), is the first comprehensive work on the fauna material and the main focus of research presented here. Other sites of the Swabian Jura, including Vogelherd, Bockstein, Hohle Fels, Geißenklösterle and Kogelstein, are described more briefly as other primary sources provide in-depth description of the research history and archaeological record of each site.

Hohlenstein and the history of research

Hohlenstein is one of the limestone outcrops on the south side of the Lone Valley that contains four separate deposits: Stadel, Bärenhöhle, Kleine Scheuer and Ostloch (Fig. 3.1). The outcrop is situated roughly 3 km away from the village of Asselfingen, which is situated to the SE of the site complex, and lies roughly 2-5 m above the valley floor. Hohlenstein-Stadel is one of the important sites with Paleolithic material in the Swabian Jura with a few key differences. Lying 470 m asl, the cave lies slightly higher than Bärenhöhle with the mouth facing to the north toward the valley. It consists of a gallery that stretches ~50 m long and 1-3 m wide (Gamble, 1979). Hohlenstein-Stadel is one of the few caves whose presence was recorded in the historic period. A 1.2 m wall known as ‘Ulmer Mauer’ was constructed in 1591 at the entrance of the cave to prevent the use of cave. The excavations took place 30 m from the mouth of the cave.

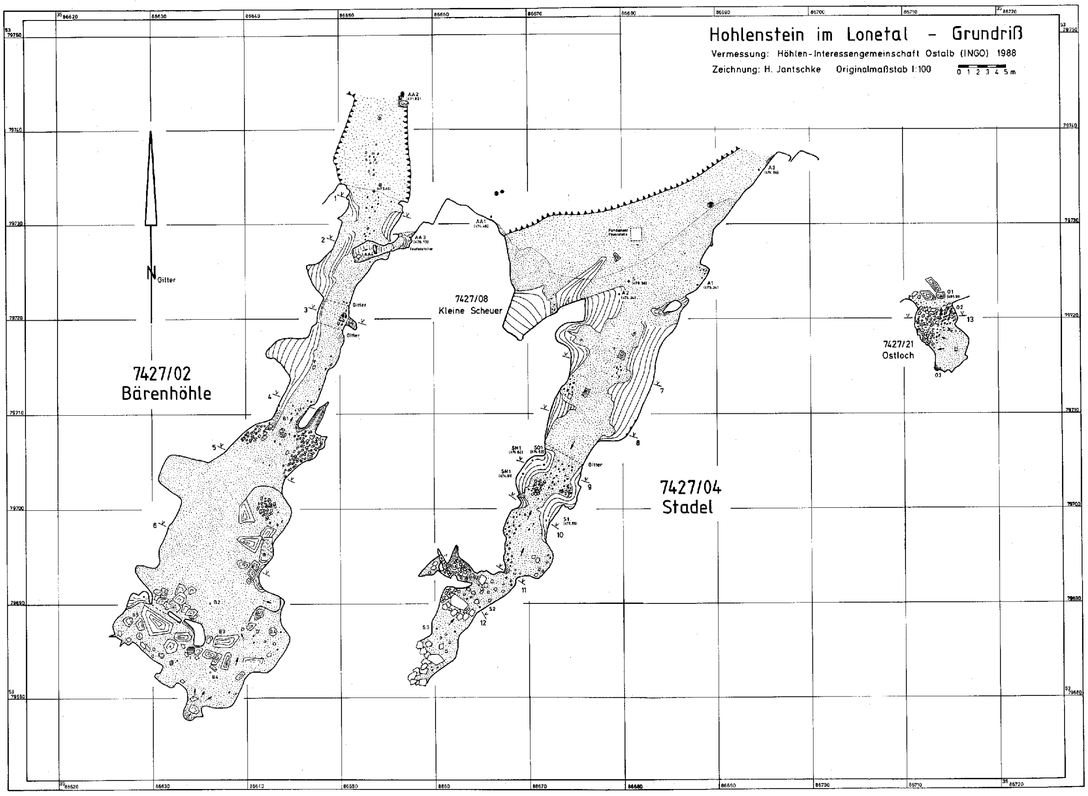


Figure 3.1 Map of Hohlenstein complex. From the West: Bärenhöhle, Kleine Scheuer, Stadel and Ostloch (Schmid et al., 1989).

Hohlenstein-Stadel

Hohlenstein-Stadel has been investigated by a number of researchers for over a century. Artifacts have been recovered by O. Fraas in 1866 after his initial excavation in Bärenhöhle (Fraas, 1862). Other investigations were conducted by O. Fraas along with L. Bürger in 1886 and by R. R. Schmidt in 1908 near the opening of the cave (Jahnke, 2013; Wetzel, 1961). The exact locations of the excavation later run by R. R. Schmidt and G. Kraft in 1925 have not been documented, although the excavators noted that they recovered 60 cm of ‘primitive artifacts’ in association with cave bear, mammoth and horse (Beck, 1999).

3.2 Entrance of Hohlenstein-Stadel on the left and Kleine Scheuer on the right (Photo courtesy of Kurt Wehrberger, Ulmer Museum)

Other sites at Hohlenstein

Ostloch is a small rockshelter located in the eastern end of the outcrop. Wetzel (1961) claimed to have excavated the area, but the details of the archaeological context and findings are not published. However, he noted that the sediment from the base of Ostloch is similar to that of Stadel.

Kleine Scheuer is a rockshelter, or abri, located between Stadel and Bärenhöhle and, compared to the two caves, is a smaller overhang yielding microfaunal remains and artifacts from the Magdalenian occupation in yellow clayey sediment dating to roughly 13,250 BP. It was initially investigated by R. R. Schmidt who excavated roughly 60 cm of sediment in 1908. The finds mostly consisted of microfauna and nondiagnostic Upper Paleolithic lithic tools. E. Koken analyzed the fauna. A larger excavation was conducted in May 1923 by E. Soergel-

Rieth and W. Soergel who studied the area for paleontological and archaeological finds. R. R. Schmidt later returned with G. Kraft in 1925. It was partially excavated by Wetzel and Völzing in 1937 alongside with Stadel's excavation. After WWII, J. Hahn and Wighart v. Koenigswald investigated the area in 1974 to reassess the previous work (Hahn and Koenigswald, 1977).

The most extensive excavation by W. Soergel and E. Soergel-Rieth in 1923 has been well documented (Soergel-Rieth, 2011). It involved the removal of the first 70 cm of sediment, followed by the removal of artificial layer in 5 cm thick Hieb (spit) resulting in 26 Hiebs with archaeological and geological finds. The stratigraphy was 2 m deep and exposed the entire sequence to the bottom of the bedrock. Published in E. Soergel-Rieth's manuscript (originally written in 1923, published in 2011), it begins with humus mixed with limestone for the most upper level (60 cm), followed by a 3-cm thick rot clayey layer. Underneath the layer lies a horizon with black humus mixed with clay and charcoal with a depth of 4 cm. Roughly 14 cm of yellowish clay underlies the layer, followed by yellow clay with large limestone where most of the artifacts as well as faunal remains were recovered with a total depth of 120 cm. This is followed by yellow and lighter clay (15 cm) and stone with lighter yellow clay (15 cm).

Most of the recovered microfauna as well as avian remains derive from the yellow clayey layer, which they named the '*Nagetierschicht'* (rodent layer). The spectrum of microfauna shows that rodents preferring tundra, such as arctic lemmings (*Dicrostonyx torquatus*), and steppe, such the narrow-headed vole (*Microtus gregalis*), prevailed during most of the period with few wooded areas in the surrounding (Soergel-Rieth 2011).

They have relatively little evidence for human activities in the area. The excavation in 1923 yielded a fire place 100-110 cm below the surface with burnt bone fragments, which were identified to ptarmigan and fox teeth (Soergel-Rieth 2011). Some small chert and one knife–like tool have been recovered. One of the well-known findings from the site is a limestone rock painted with two parallel lines of dots using red ochre. The find was recovered 125-130 cm below the surface in the yellow clay layer. The rock is a Jura limestone most likely transported by humans from the river (Soergel-Rieth 2011). The discovery of similar painted stones indicates that such artifacts were prevalent among the Magdalenian people who occupied the Swabian Jura (Conard and Uerpmann, 2000). The find also represents one of the early pieces of evidence of painting and abstract symbolism in Central Europe (Conard and Uerpmann, 2000).

The cave of Hohlenstein-Bärenhöhle (467 m asl) lies 2 m above the valley and 25 m west of Hohlenstein-Stadel. It stretches 69 m long, 10 m wide and 7 m high and runs parallel with Stadel in the SW-NE orientation. This is the site first investigated by O. Fraas and where the first Paleolithic artifacts were discovered in the Swabian Jura, beginning the tradition of archaeological research in the region. Fraas had received information from a forester, who found animal remains from near the cave due to the burrowing of badgers. The cave has two large chambers. Fraas, a geologist and a paleontologist, reported around 400 individuals of cave bears based on the counts of cranial remains recovered at the site (Fraas, 1862). Other animals, though few in number, included mammoth, horse, bison/aurochs, elk, red deer and roe deer. A total of 98% of the animal remains derived from cave bears, which he interpreted as evidence of cave bear hunting and exploitation by humans. Later, he returned to the site in 1866 to recover and study artifacts such as lithics, modified bones and teeth pendants in three different cultural layers (Beck, 1999; Wetzel, 1961).

Bärenhöhle was later excavated by R.R. Schmidt in 1908. Small sondages were also excavated by R. Wetzel and a geologist, Otto Völzing, alongside with Stadel's excavation in 1937-38. After WWII, two sondages were opened in 1954 and 1956 by Wetzel, followed by a systematic excavation during 1957, and in 1959-61 with Marie-Luise Taute-Wirsing (Beck, 1999). Weinstock (2000) has recently studied the fauna to explore the mortality profile and demographic pattern of the bear population.

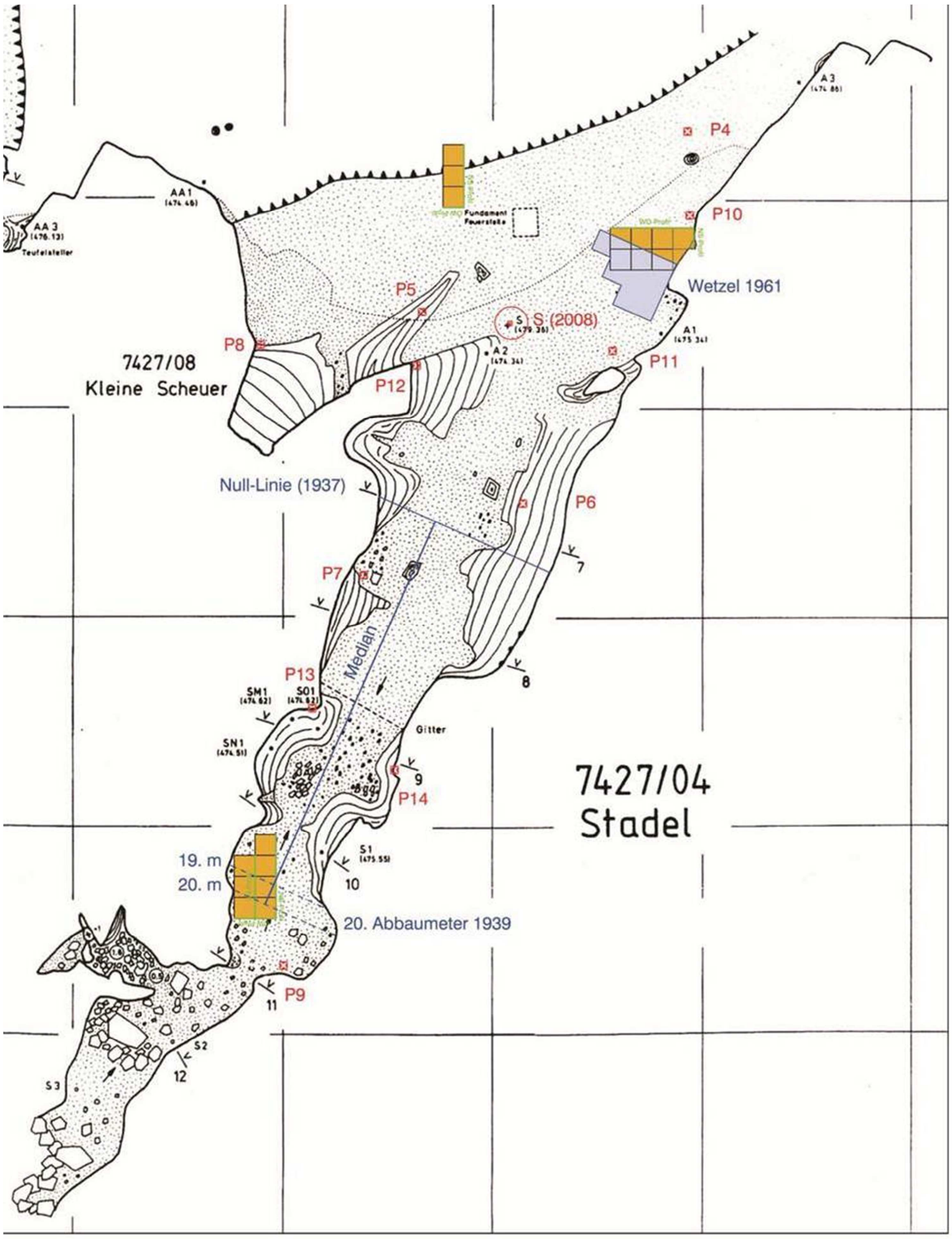


Figure 3.3 the map of Hohlenstein-Stadel and the excavated area. Yellow areas indicate recent excavations. The Blue lines indicate areas excavated by R. Wetzel. Image from Kind and Beutelspacher (2010)

Robert Wetzel's Excavation of Hohlenstein-Stadel

The first systematic excavation in Stadel began on 19th September 1935. Robert Wetzel, an anatomy professor from the University of Tübingen, conducted research in the

1930s and 1950-60s, recovering the majority of artifacts from the site. He initially excavated a 2 x 2 m test trench, followed by two other test trenches in the mouth of the cave behind the Ulmer wall during the first season in 1935. The trench yielded iron and bronze artifacts, *Pfeilspitze* from the Neolithic period in addition to lithics from what he later called ‘Red Mousterian’, with the most upper layer appearing to be disturbed and mixed (Beck, 1999; Wetzel, 1961).

From 1937, O. Völzing joined Wetzel in conducting systematic excavations in a larger area to observe the horizontal distribution of artifacts. With additional help from A. Bamberger, they concentrated on the area behind and under the Ulmer wall. A burial pit, found in the vicinity of the wall, was 70 cm deep. The buried individuals included a female, a male and a child aged between 2-4 years old, represented by three crania, mandibles and cervical vertebrae, which were directly dated to 7835±80 C^{14} BP in the Mesolithic period (Haas, 1991; Orschiedt, 1998; Wetzel, 1961). The skulls have traumatic marks from blows to the head and traces on the vertebrae showed that the individuals were decapitated (Orschiedt, 1998). The individuals rested on top of stones covered in ochre. In addition, the female skull was associated with perforated Cyprinid fish (*Rutilus meidingeri*) teeth with traces of usewear and pigments used as adhesives (Rigaud et al., 2013).

Further, in an area two meters behind the wall, the excavators in 1937 discovered human remains from 54 individuals dating to the early Neolithic period. These remains were named *Knochentrümmer* (literally, bone debris), found in a pit along with lithic and faunal remains. They were in the context of secondary burial covered by a combustion feature and other anthropogenic modification dating to 7 ka (Orschiedt, 1998; Wetzel, 1961). These findings point to the use of the cave for ceremonial as well as burial purposes for the Mesolithic and Neolithic people.

O. Völzing was mostly responsible for the excavation at the site in 1938 and 1939 with Wetzel until the excavation abruptly terminated on 25th August 1939 with the outbreak of the Second World War. After the war, Wetzel reopened the cave with O. Völzing in 1956-57 and 1959, with M-J. Taute-Wirsing in 1960, and with Johannes Wetzel in 1961. By the end of 1960, most infills of the cave stretching 22 m from the mouth of the cave were fully excavated and later refilled. Wetzel notes that around 2.7 m of sediment were removed from the original surface of the sediment in 1937. In the end, in addition to the artifacts from recent prehistory, the excavators were mainly able to distinguish two layers of red and black Mousterian. In 1961, the area outside of the mouth of the cave, or '*Vorplatz'*, was the focus of the excavation work.

In 1937-39, the workers divided the area in meters known as the *Abbaumeter* from an arbitrary null point seen in the Figure 3.3 (instead of quadrants) and excavated within these meters that run across the hall of the cave. Artificial layers of 20 cm, or spit or *Hieb,* served as the vertical unit of excavation and were used to define the position of the artifacts and animal remains. The artifacts were often labeled with *Abbaumeter*, *Hieb* and the date of excavation. At the end of 1939, the excavation extended to the 6th *Hieb* of the 20th *Abbaumeter*. In most areas, the excavation reached the Aurignacian deposits, and the day before the end of the excavation, Wetzel and his workers recovered the figurine known today as the *Löwenmensch* (described below). For all the *Abbaumeter*, excavators reached the 12th spit (roughly 2.2-2.4 m deep), in some areas reaching as far as the 14th and 15th spit (roughly 2.6-3 m) (Gamble, 1979; Beck, 1999).

In 1957, a similar excavation method was employed, but this time using a different null point, which was 10 m closer to the entrance of the cave. This difference has confused researchers, such as Wagner, who used *Abbaumeter* from 1957 to estimate the original position of the *Löwenmensch* (or lion man) in an attempt to recover missing fragments of the figurine. Further, the later excavations did not assign spits; instead, geological layers such as Black Mousterian were employed to refer to the archaeological finds. In 1956-1961, many areas were excavated to the bottom of the cave, exposing a Middle Paleolithic deposit and a basal layer with relatively few artifacts and animal remains that Wetzel described as culturally sterile.

In 1961, Wetzel with the help of M-L Wirsing investigated the area in front of the mouth of the cave (referred to as *Vorplatz*) in addition to the inner area of the cave. He defined the deposit as Black Mousterian, which was 1 -1.5 m thick with several sub-horizons distinguished by the color of sediment varying from dark brown to pale gray, followed by a brown/black and black horizon, which was this color mostly due to large quantities of charcoal and manganese oxides.

They recovered lithic artifacts such as scrapers and blades that were used, displaying rounded edges. The lithic assemblage consisted of unstandardized flakes with various retouches, mostly produced with the Levallois technique. Wetzel (1961) notes that the excavation recovered two bone compresseurs or retouchers from the Black Mousterian, but these pieces have not yet been restudied to assess carnivore damage. Wetzel notes that, while his excavation at Bockstein yielded a large number of lithics, the evidence of human occupation in front of the cave entrance at Hohlenstein-Stadel yielded a few artifacts.

In 1983, E. Wagner, along with the Denkmalpflege of Baden-Württemberg, attempted to excavate an area where the *Löwenmensch* figurine was recovered in order to determine whether this area had remained intact. However, due to the change in the designation of *Abbaumeter* from 1930 to the 1950s, the team excavated several meters closer to the mouth of the cave relative to the original position of figurine (Beck, 1999). The excavation yielded remains of cave bear, horse, aurochs and hyena, as well as an ivory fragment that was interpreted as a female (Wagner, 1983b). The fragment was later reanalyzed and does not appear to be modified by humans (Jahnke, 2013).

Few data indicate that some mixing did take place either through biotic factors as well as through recovery and curational processes. The dating of bones in the same *Hieb* as the *Löwenmensch* suggests that there were material from the Magdalenian period mixed with faunal remains from the Aurignacian period (Schmid et al., 1989). This could partially be due to a recent fox den that was documented by Völzing and Wetzel in the 1930s. Further, two fragments of ivory originating from the 19th *Abbaumeter*, 8th *Hieb* and 12th *Hieb* refit together, indicating that mixing had occurred. The false assignment of *Hieb* during excavation also cannot be excluded from consideration.

Recent Excavations by the University of Tübingen

In search of open-air sites, a project from the University of Tübingen led to systematic surveys of Paleolithic deposits outside of the cave. One of the projects involved excavating an area 10-40 m^2 in front of Hohlenstein towards the floodplain of the valley in 1997-98 (Bolus et al., 1999). This excavation allowed researchers to evaluate the extent to which the cave deposit was transported outside of the sheltered area. Three excavation surfaces were excavated down to a depth of 5 m. Two excavated areas show that cave sediment from Bärenhöhle and Stadel moved with gravitation down the slope.

The stratigraphic profile from three excavated trenches shows that the upper most level consists of Holocene humus followed by a layer of yellow-brown silty loam, while in some profiles there are dark brown clay and brown clayey sediment (Bolus et al., 1999). Rounded limestone is found consistently throughout these upper horizons. In the lower horizons, most sediment consists of gravels with limestone. The layers are mostly not demarcated and transition is gradual. There are a number of lithic artifacts from the upper horizon while fauna remains are found throughout the separate layers. There are various tools that are typologically Neolithic and Mesolithic, with a few Paleolithic tools also being recovered. Some tools may have undergone cryoturbation as indicated by the tool edges. The presence of ceramic fragments also indicates that there is considerable mixing in the sediment.

Excavators recovered no Holocene fauna in the upper levels but found Pleistocene fauna from the lower levels. Horse and reindeer dominate the remains identified taxonomically, with many shed antlers from young reindeers appearing often in the assemblage. There are a few cave bears and wolves present. The artifacts and animal remains were found outside of their original geological context, making it a challenge to place them in a clear chronostratigraphy.

The fauna was analyzed by Geiling (2012). Results indicate that horse and reindeer dominated the assemblage, with half or more represented by antlers. There are some bear remains as well, which indicate that part of the sediment is comprised of sediment from the caves of Bärenhöhle and Stadel (Geiling, 2012). Weathering affected many bone remains, and the surface of the material was not well preserved, although few cutmarks were identified. In particular, there is at least clear evidence of defleshing with parallel cutmarks on the spine of thorathic vertebra from a bear, which also supports Münzel's study on fauna from Hohle Fels, which led her to conclude that bears were opportunistically exploited by humans. Based on the high frequency of antlers (MNI = 18), Geiling (2012) argues that hominins collected outgrown antlers on the landscape to use for tool production.

Recent Excavations by the Denkmalpflege of Baden-Württemberg

The Denkmalpflege of Baden-Württemberg, under the direction of Claus-Joachim Kind and Thomas Beutelspacher, has been running the most recent excavations at the site, from 2008 to 2013. . Its aim was to document the extent of the previous excavations and the geological context of the artifacts in addition to recovering other fragments of the *Löwenmensch*. The overall objective was to better understand the work of R. Wetzel and to assess the state of the site so that it, along with other archaeological sites in the Swabian Jura, would be considered under the auspices of UNESCO World Cultural Heritage (Kind and Beutelspacher, 2010). In order to protect the area for future investigation, work surface for this new excavation was limited to the previously excavated area.

Fieldwork thus consisted of recording the excavation from Wetzel's work, including the extent and the spatial distribution of the refills and the intact sediment after the last year of excavation in 1961. This took place both outside of the cave near the entrance and within the rear end of the cave. Later, excavation of the refills was carried out in disturbed and intact sediment, with the recovery of faunal and artifact remains, as well as with waterscreening of the sediment using 2-mm sieve size and sorting of the finds recovered through waterscreening.

The excavation in 2008-09 initially took place at the *Vorplatz* or on the terrace in front of the cave entrance, which was investigated by Wetzel in 1961. A sector from a surface area of 8 m^2 with refills and intact sediment was opened to document the geological context and taphonomic history in and in front of the cave in addition to the documentation of Wetzel's excavation. In total, 4 m^2 of undisturbed sediment was excavated to the depth of roughly 2 m below the original surface. A number of layers show complex depositional processes, which were studied by T. Jahnke (2013).

Excavators identified 11 geological layers with 8 layers containing cultural artifacts (Jahnke, 2013). Stratigraphic layers identified within the cave produced a chronology with major cultural periods including the Middle Paleolithic, Aurignacian and Magdalenian. It begins with the humus filled sediment, followed by cultural horizons from the Magdalenian, Aurignacian and Middle Paleolithic (Beutelspacher et al., 2011; Jahnke, 2013; Kind and

Beutelspacher, 2010). In addition, excavation involved the opening of three m^2 and a1.5-m deep sondage in the N/S orientation roughly 10 m west from the main trench. This sondage produced no artifacts, indicating extensive disturbance of sediment.

Micromorphological studies indicate that there was no indication of high power water flow from the inner area of the cave (Jahnke, 2013; Miller, personal comm.). Instead, the sediment originating from the cave most likely was transported through solifluction after the deposition of sediment at the end of the Middle Paleolithic (Kind and Beutelspacher, 2010). In all, the stratigraphy reveals complex depositional and taphonomic processes occurring at the mouth of the cave (Jahnke, 2013; Kind and Beutelspacher, 2010).

In 2009-2013, the team excavated the intact layers from the inner cave. The refills from excavations in the 1930s were partially excavated, and excavators noted reddish brown sediments in the refill, which most likely derive from the Aurignacian horizon. The recovery of refilled sediments yielded notable artifacts, such as perforated teeth of various animals including fox (canines and incisors), wolf (premolar), giant or red deer (canine) and one worked ivory pendent. These artifacts from refills corroborate the hypothesis that this refill derives from the Aurignacian sediment (Beutelspacher et al., 2011; Kind and Beutelspacher, 2010).

The excavation first began with 2.5 m² of surface, which was later enlarged to ~ 6 m² (Beutelspacher et al., 2011). On 25 Aug 1939, Wetzel's team halted their work as they approached the bottom of the Aurignacian layer (6 *Hieb*) in the 20th meter and left the area intact through the subsequent excavation. The team from the *Denkmalpflege* began the work with the intact sediment from the area where excavation in 1939 stopped and where the *Löwenmensch* was recovered, seeking to recover fragments that may add to the figurine. Further, the team sought to obtain samples for redating the stratigraphy in order to understand the nature of the transition from the Middle to early Upper Paleolithic (Beutelspacher et al., 2011).

The recent excavation has revealed that the Magdalenian horizon has been completely dug out from the previous excavations. Thus far, new work revealed a sparse presence of hominins at the site. Some kind of combustion feature in the cave, due to small fragments of burnt bones and charcoals, existed during the Middle Paleolithic. The lithic artifacts from the Aurignacian include small flakes, but lack any clear tools.

The excavation uncovered ivory pieces that potentially fit with the *Löwenmensch*. Over 650 ivory fragments were used to digitally fit with the figurine using 3D scanning (Beutelspacher et al., 2011; Ebinger-Rist and Wolf, 2013). The figurine underwent restoration through the removal of wax and adhesives and was re-pieced together (Beutelspacher and Kind, 2012; Ebinger-Rist and Wolf, 2013).

Dating and Stratigraphy

The micromorphological work of the site is currently underway, which will provide us with additional information on the geological context of the site, but a brief summary of known facts is described below. The sediment derives mainly from three sources, which include sediment accumulated above the Hohlenstein complex, moving through the fissures of limestone massif. Part of the sediment is eolian in origin as some loess component is present. Lastly, the weathering of limestone with humidity results in the decomposition of lime and clayey sediment in the matrix.

Other geological features include limestone blocks, often recovered from these cave contexts, showing that frost wedging occurred regularly (Riek, 1934), affecting the inner structure of the cave. Limestone blocks resulting from frost wedging occur commonly throughout the layers and at times become rounded from weathering. Bohnerz is clay with iron concretions that is wide spread in the caves of the Swabian Jura (Ufrecht, 2008). Rounded quartz pebbles have also been recovered especially from the lower to basal layer of the site. The origin of these pebbles still remains unclear, but was likely deposited partially when the karst system was still active (Beribieri, pers. comm.).

The stratigraphy from the site was documented by the original excavators. O. Völzing described the stratigraphy based on the color and consistency of sediments, and drew profiles from several excavated sectors, most of which are reproduced by D. Beck (1999). According the profiles from 1937-39, Völzing identified one Neolithic layer overlying the Magdalenian layer as well as two Aurignacian horizons, two thick layers from the Middle Paleolithic and one sterile level at the base. R. Wetzel recommenced excavations in the 1950s starting around 2.78 m below the original surface from 1930. He continued with the documentation of the stratigraphy and formed a composite profile based on drawings from 1930 and from the 1960s with some slight differences. Namely, the original depth of the excavated material differs from the 1930s and 1960s (Beutelspacher, pers. comm.). According to Beck (1999), the excavated area was possibly disturbed on the surface and thus appears as an inconsistency in the profile.

Nonetheless, a reopening of the site revealed that the documentation of the stratigraphy was relatively accurate. The profile drawings from Völzing reflect a precision in his documentation technique. The team from the Denkmalpflege reconstructed the stratigraphic profile by combining the data from the previous and modern excavations. A small pocket of intact sediment attached to the western cave wall and the discoloration of the wall resulting from the sediment shows the limit of the sediment and the original surface before the initial excavation was established.

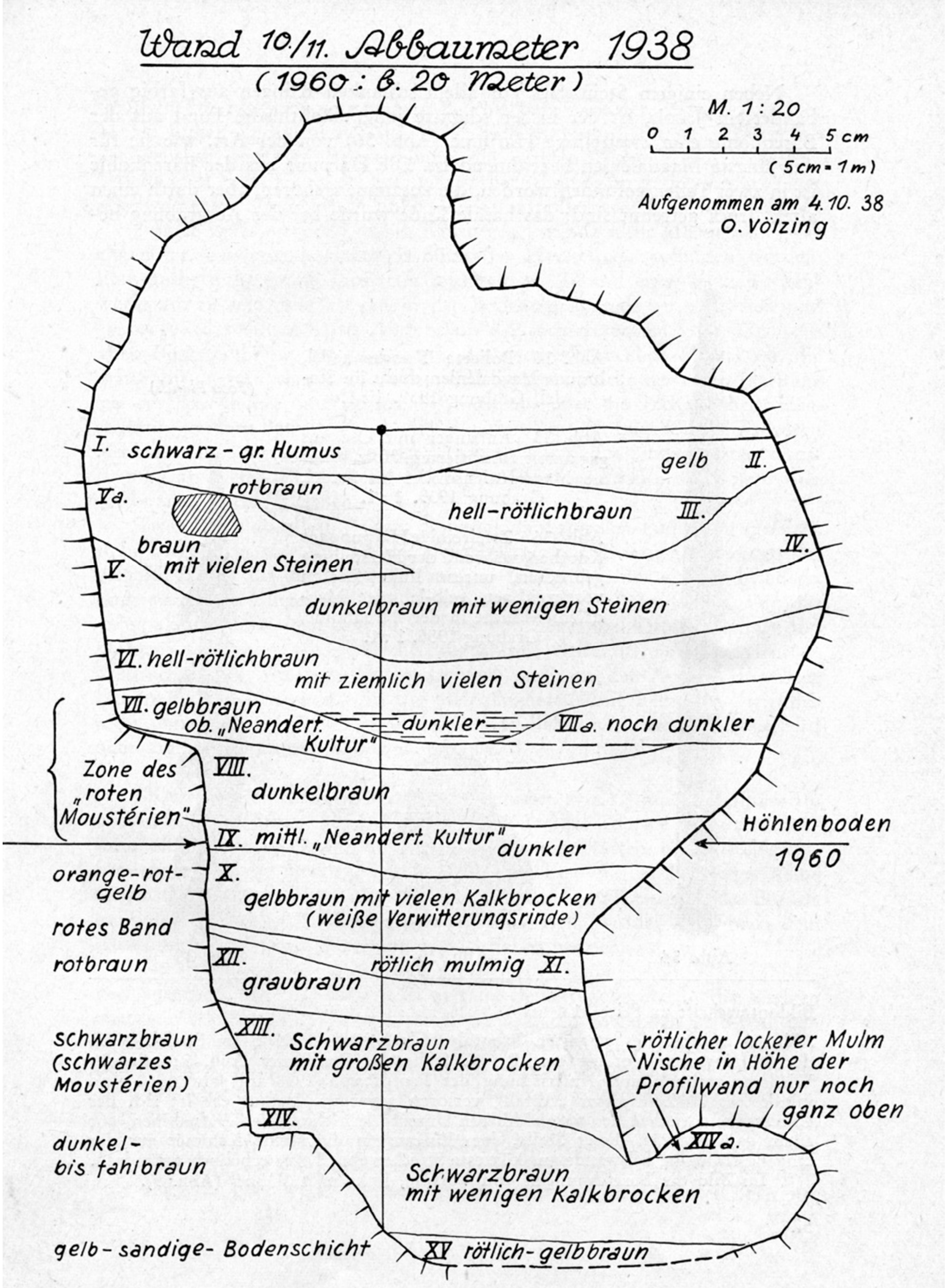


Figure 3.4 Original profile created by Völzing and Wetzel between Abbaumeter 10/11 (Wetzel 1961)

Geological horizon	Cultural horizon	Sediment	Cultural assignment
A	I	black-gray humus	Neolithic
C	II	Yellow	Magdalenian
D1	III	lighter reddish brown	
D2	IV	red brow	
D3	V	dark brown, few stones	Aurignacian
D4	Va	brown, many stone	
D5	VI	light reddish brown, many stones	
E1	VII/VIIa	yellow brown	Upper Mousterian
E2	VIII	dark brown	Red Mousterian
E3	IX	dark brown	Red Mousterian
E4	X	yellow brown, many limestone fragments	Red Mousterian
E5	XI	reddish, loose	
E6	XII	gray brown	
F1	XIII	black brown, large limestone pieces	Black Mousterian
F2	XIV	Black brown, few limestone pieces	Black Mousterian
G	XV	yellow-brown	

Table 3.1 Stratigraphy described by Wetzel and Völzing from the profile 10/11m *Abbaumeter* (in Beck, 1999: 48-49, Profile 39, Fig 35).

Figure 3.4 shows the original profile created by Völzing and Wetzel. Table 3.1 summarizes the description of the sediment and cultural assignment of each layer (Wetzel, 1961). The lowest level forms the basal layer with yellow, sandy sediment (XV). It produced few artifacts and is mostly sterile with only a few faunal remains. No known faunal material has been systematically recovered from Wetzel’s excavation.

This level was then followed by two major Middle Paleolithic horizons identified by Wetzel’s team. Black Mousterian layers (XIV-XIII), excavated during the late 1950s and 1960s, form a clear cultural unit with manganese-rich sediment. The color of the sediment varied from black at the upper sub-horizon to dark brown and pale gray in the lower sub-horizon of the horizon. The faunal material shows distinctive black stains and was also heavily mineralized. It is not included in the sample of this study. The Red Mousterian layers (X- VIII), here referred to as the Red Middle Paleolithic, overlie the Black Mousterian and were partially excavated in 1938 and after the war. The Red Mousterian has produced a number of lithic artifacts produced using the Levallois technique (Beck, 1999; Wetzel, 1961).

Further, two Upper Paleolithic cultural horizons were documented. The Aurignacian (V) is characterized by red-brown loam sediment with limestone fragments (Schmid et al, 1989; Wetzel, 1961). To date, no clear Gravettian layer has been documented. Following the Aurignacian, the Magdalenian (III) is characterized by the yellow loam deposit, with ^{14}C dates from this layer ranging from 13,550 ±130 BP and 13,110±160 BP (Hahn, unpublished, in Gamble 1979).

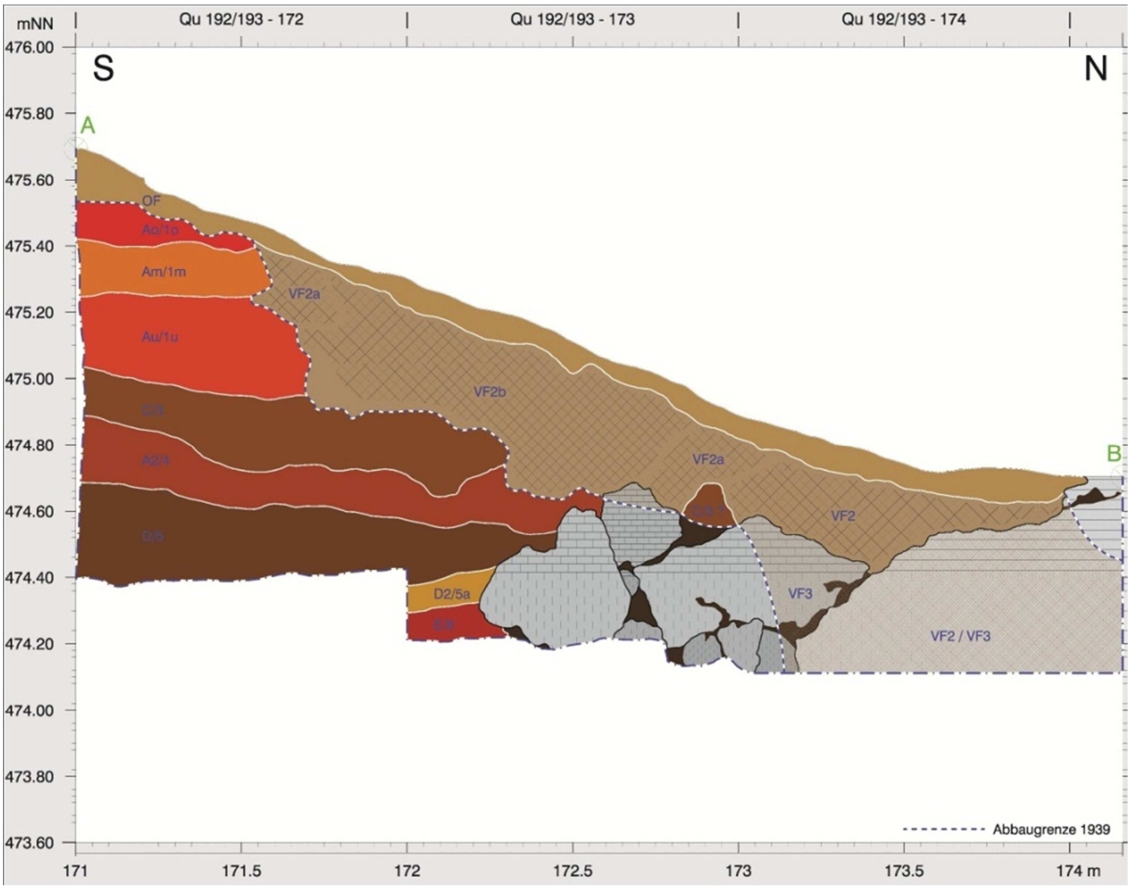


Figure 3.5: Stratigraphic profile of Hohlenstein-Stadel running N/S. Quadrants 192/193-172 to 192/193-174 from modern excavations are represented (Beutelspacher et al., 2011).

Geological Horizon/ Archaeological Horizon	Horizon of Wetzel 1961 (Profile 39)	Cultural assignment	Sediment
VF		Backdirt from 1939	Reddish / grayish brown
Ao/1o	IV	Aurignacian	Dull reddish brown, clayey silt
Am/1m	Va	Aurignacian	Brown, clayey silt, many limestones
Au/1u	V	Aurignacian	Dull reddish brown, clayey silt
C/3	VI	Upper Middle Paleolithic	Dull brown, silty clay
A2/4	VII+VIIa	Upper Middle Paleolithic	Dull reddish brown / brown, clayey/silty
D/5	VIII	Red Middle Paleolithic	Dull brown, silty clay
D4/5b*1	VIII	Red Middle Paleolithic	Brown, silty clay
D2/5a*2	VIII	Red Middle Paleolithic	Bright brown, clayey silt
E/6	IX	Red Middle Paleolithic	Brown, clayey silt
F/7	X	Red Middle Paleolithic	Dull brown, clayey silt
G/8	X	Red Middle Paleolithic	Yellowish brown, clayey silt
H/9*2		Backdirt from 1939	Reddish brown
J/10	XI	Lower Middle Paleolithic	Dull brownish orange, silt
K/11	XII	Lower Middle Paleolithic	Grayish brown (mix of G (+J) and L), silt
L/12	XIII+XIV	Lower Middle Paleolithic	dark grayish brown, silt
M/13	XV	Sterile	Yellowish brown, sandy silt

Table 3.2 Stratigraphy based on the recent excavation (from Kind and Beutelspacher, 2010; Beutelspacher et al., 2011, Beutelspacher and Kind, 2012, Beutelspacher, n.d.).
Comment: *1D4/5b is probably a part of D/5. *2 localized

There are 13 horizons identified by the recent excavation (Tab. 3.2, Fig. 3.5). The basal horizon (M/13) and the Black Mousterian (K/11 and L/12) are easy to distinguish from the current observations of the stratigraphy. Layer K/11 is characterized by relatively abundant finds of lithic artifacts, yielding the earliest evidence of hominin occupation at the site.

Layers overlying the ‘Black Mousterian’ including layer G/8 and F/7 were not securely correlated to either the Black or Red Middle Paleolithic. In the G/8 layer, the sample size of faunal remains is relatively small. Since the sediment of F/7 is not characterized by black coloration, it is assumed that this layer was subsumed to the Red Middle Paleolithic in Wetzel’s excavation. Artifacts are also rare in these two layers. Here, I group these layers with the rest of the Red Middle Paleolithic assemblage with an assumption that they need to be revisited. The material from G/8 will not largely alter the overall pattern in the zooarchaeological assemblages and it is for now plausible to presume that F/7 was considered a part of the Red Middle Paleolithic. The Red Middle Paleolithic also consists of several horizons from E/6, D4/5d, and D/5. The artifact density is higher in D/5 than in E/6. Lithic finds are relatively sparse, but exist in all intact layers of the excavation. In this study, these five layers were grouped as one cultural unit to aid in studying the temporal variation in faunal remains.

The Upper Middle Paleolithic layers A2/4 and C/3, which appear in some sources of Wetzel as part of the Upper Red Middle Paleolithic, are differentiated as more precise dating is possible and because the correlation between the older and more recent excavation is clear. A2/4 produced a considerable lithic assemblage while C/3 yielded relatively scant evidence of human occupation. However, few artifacts still indicate that this layer was not culturally sterile, unlike similar geological layers represented by other sites of the Swabian Jura (more discussed below). Therefore, there does not seem to be a complete absence of hominin presence at the site.

The Aurignacian horizons (Au/1u, Am/1m, Ao/1o) as noted from previous observations by Völzing, are characterized by reddish brown sediment. These horizons have been the focus of recent investigations particularly concerning the recovery of the early Upper Paleolithic artwork. Nonetheless, the number of lithic artifacts recovered from the recent excavation has been limited. The Magdalenian, Mesolithic and Neolithic layers were not documented in this recent excavation and were completely removed by previous excavations.

A series of C^{14} dates corroborate with the general chronology and assignment of cultural layers. There is currently no secure date for the earliest occupation in the Middle Paleolithic period. Based on the stratigraphy and the artifacts, the lower deposits at Stadel are considered to be Middle Paleolithic, but the exact duration of the Middle Paleolithic occupation still remains to be assessed. ESR dating on the equid and bovid teeth is currently being undertaken by M. Richard and C. Falgueres. Ziegler's initial analysis of the microfauna from the strata that potentially corresponds to the 'Black' Middle Paleolithic shows that the faunal spectrum reflects a relatively warm climate (Jahnke, 2013). If true, this places the layer in the Interglacial Period (110-70 ka) and also corroborates with an early occupation in Vogelherd (Niven 2006).

The E/6 horizon dates to around 50 ka (Table 3.4). Due to limits in the radiocarbon dating technique, it is likely the value represents a minimum date. Dates from D/5-C/3 range between 41.9-39.8 ka, suggesting that Neanderthals occupied the cave shortly before the arrival of modern humans. This date corresponds with dates from other sites, such as Geißenklösterle in the Ach Valley, whose date falls around 43 ka BP based on ESR dating on enamel tooth (Richter et al., 2000).

Lab Number	Archeological horizon	Cultural assignment	Material	Modification	Collagen (%)	Date uncalibrated
KIA 8951	19m spit 6	Aurignacian	Reindeer humerus	Impact	13,6	31,440±250
H 3800-3025	20m spit 6	Aurignacian	mixed bone sample			31,750 + 1,150/-650
ETH-2877	20m spit 6	Aurignacian	reindeer ulna + wolf astragalus			32,000 ± 550
KIA 13077	20m spit 6	Aurignacian	reindeer radius	fresh break	7,6	32,270 +270/-260
KIA 8949	19m spit 7	Aurignacian	reindeer? Long bone	fresh break	17,2	33,920+ 310/-300
KIA 8950	19m spit 7	Aurignacian	elk metatarsal	fresh break	8,1	36,910 +490/-460
KIA 8948	19m spit 8	Middle Pal	horse? Long bone	Impact	9,1	41,710 +570/-530
KIA 8947	19m spit 9	Middle Pal	horse long bone	fresh break	10,2	42 410+ 670/-620
OxA-18455	19m spit 9	Middle Pal	horse long bone (2nd measurement of KIA8947)	fresh break	10,2	47,100 ± 900
KIA 8946	19m spit 10	Middle Pal	reindeer metapodial	fresh break	15,4	39,970 +490/-460
KIA 8945	19m spit 11	Middle Pal	long bone	fresh break	11	40,220 +550/-510

Table 3.3 Dating of material from the excavation of 1939 from Conard and Bolus (2008)

Labor-Nr.	GH	CH	Cultural assignment	14C BP	Cal BP (oxcal)
ETH-41231	Ao	1o	Aurignacian	31950 ± 210	35589 - 36906
ETH-41232	Am	1m	Aurignacian	33390 ± 245	37286 - 38835
ETH-38797	Au	1u	Aurignacian	35185 ± 270	39421 - 41105
ETH-38798	C	3	Middle Paleolithic	39805 ± 420	43103 - 44555
ETH-38799	A2	4	Middle Paleolithic	41920 ± 545	44523 - 46187
ETH-38800	D	5	Middle Paleolithic	40560 ± 480	43577 - 45238
ETH-41234	E	6	Middle Paleolithic	46440 ± 1050	out of range

Table 3.4 Dating from recent excavations 2009-2011 (Beutelspacher et al., 2011; Kind, unpublished).

A series of dates published by Conard and Bolus (2003, 2008) yielded relatively young ages from the Middle Paleolithic horizons (Table 3.3). The reason for the young dates remains unclear, but it may point to subtle differences in the processing of dating material at various laboratories. Further, these dates underline the relative small temporal gap between the Middle Paleolithic and the early Upper Paleolithic at the site.

The A/1 Horizon represents the Aurignacian period. The C^{14} dating suggests occupation of modern humans from 35-32 ka (40,000 to 36,000 cal C^{14} BP). Discrepancy is also observed in the same samples of horse long bone from Stadel that were sent to two different radiocarbon laboratories, resulting in differences of around 5,000 years (Conard and Bolus, 2003, 2008). The Aurignacian period at Hohlenstein-Stadel alone documents the occupation of modern humans from roughly 40-36,000 BP. Dates from the recent excavation fit in the conventional timeframe of the Aurignacian in the Swabian Jura, but it appears that the occupation at the site ceased 3-4,000 years before the transition from the Aurignacian to the Gravettian culture.

Artifacts from the Middle Paleolithic

The lithic assemblages from the Middle Paleolithic deposits of Stadel and Bärenhöhle, housed in the Ulmer Museum, were studied by Dunja Beck (1999). The assemblage consists of 1358 lithics, with 23.9 % exhibiting retouch. Tools are relatively small in number and cannot be assigned to a particular technocomplex or industry. The raw material of the lithics was dominated by the local Jura chert found roughly 12 km from the site, and making up 62% of the assemblage. Beck interprets the assemblage as resulting from short, sparse occupations of the site by Neanderthals.

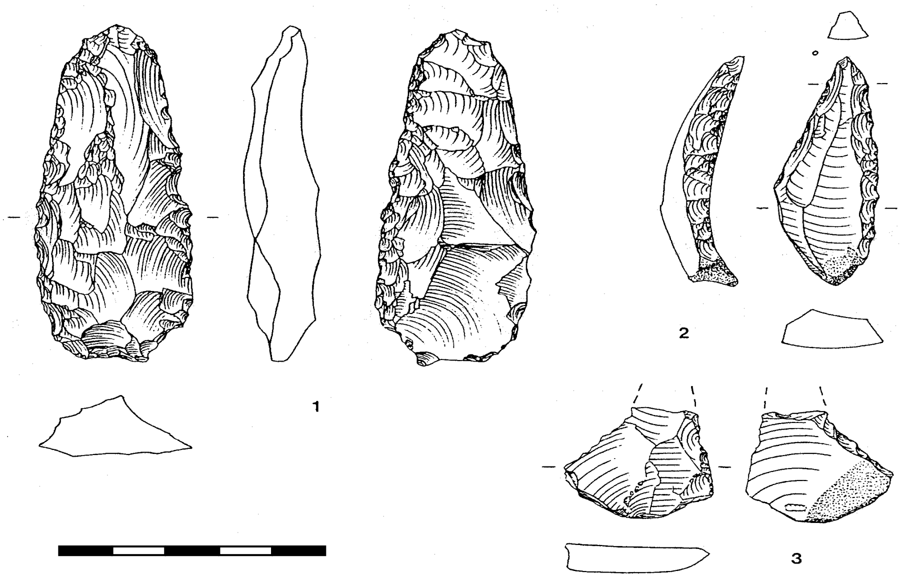


Figure 3.6 Lithic artifacts from Beck's analysis: 1 *Doppelspitze*, (Double point) 2-3 *Spitzen* (Point) (Beck, 1999).

Relatively few diagnostic tools were identified from the recent excavation except for a handful of cores and retouched tools. Some rounded flint pieces are nondiagnostic and are not considered as artifacts, because flints are found in relative close vicinity to the site and can occur naturally in the deposit.

Artifacts from the Aurignacian

J. Hahn analyzed the Aurignacian artifacts which make up a small assemblage (Schmid et al., 1989). In total, 313 lithics from Wetzel's excavation of 1935-39 were studied. The dominant raw material, or roughly 75% of the lithics, were gray chert found from the local area (Jurassic chert 4-7 km away on average), followed by white chert as well as green and red brown radiolite. A total of 37% of the lithics showed damaged or rounded edges, possibly due to cryoturbation, which will later explain the rounding of faunal remains. Nine artifacts appear to be modified with frost and 14 lithics showed evidence of fire treatment. Blades and flakes are the most common types of artifacts while small debris and shatter were rarely found, probably due to the lack of sieving that would have allowed for the recovery of smaller artifacts. Fifty-six of the total artifacts were tools, with 120 retouched blades and bladelets and 23 cores. The flint nodules are found commonly in the limestone beds in the Jura (Bukert and Floss, 2005). Other material such as radiolite and quartzite are found from fluvial deposits.

Organic tools include spear points made from antler and ivory, awls and retouchers totaling 58 artifacts. There were also six perforated fox canines as well as one rounded ivory pendant (Hahn, 1989). In addition, perforated fox canine, wolf incisors, and reindeer incisor were recovered from the Aurignacian refill (Beutelspacher et al., 2011) (Figure 3.7). Hahn suggests that the lithics from the Aurignacian layer are more comparable to the lower Aurignacian of Geißenklösterle (1988), although sculpted ivory suggests otherwise (Bolus, 2003). Hahn (1989) deduced from the modification of bones that the assemblages of artifacts and animal remains were not immediately buried after their deposition. Organic artifacts and fauna show clear carnivore modification.

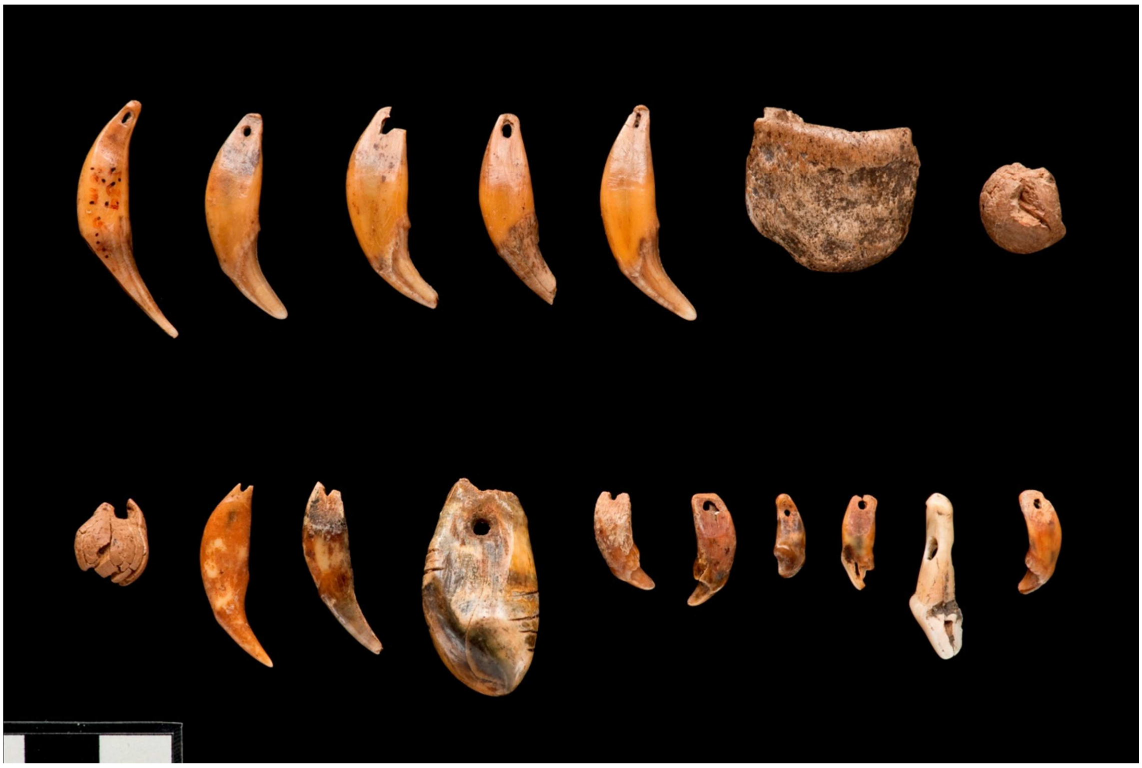


Figure 3.7 Personal ornaments from the Aurignacian at Hohlenstein-Stadel (Photo courtesy of Kurt Wehrberger, Ulmer Museum)

The *Löwenmensch*

The Swabian Jura is known for producing one of the earliest evidence for symbolic behavior that includes the use of artistic representation and music emerging with the arrival of modern humans in Eurasia. For instance, the cave of Hohle Fels yielded the earliest female figurine, known as the Venus, and flutes that are dated to the Aurignacian period (~42 cal BP) (Conard, 2009; Conard et al., 2009a). Among other sites in the Swabian Jura, Hohlenstein-Stadel also produced an important figurine that has few equivalents in prehistoric art.

Known as the *Löwenmensch*, or lion man, the figurine consists of a head of a lion (*Panthera leo spelaea* without a mane) and a body of a man (Figure 3.8). With a length of 31.1 cm (Ebinger-Rist and Wolf, 2013), it is the largest example of portable art made in ivory from the Paleolithic period. The figurine was recovered from the excavation by Völzing in 1939 the day before the project abruptly ended 27 m behind the dripline, 20 m behind the null point from the initial excavation seasons. The statue was found in the 6th spit which is roughly 1 to 1.2 m below the original surface.

Figure 3.8 Ivory sculpture of the *Löwenmensch* (Lion man), a therianthropic creature with human and lion traits from the Aurignacian of Hohlenstein-Stadel, 31.1 (Photo courtesy of Kurt Wehrberger, Ulmer Museum).

While Wetzel noted his discovery in a letter shortly after the excavation to a colleague, the figurine, in fragments, was stored away with bone and teeth remains and was forgotten until Joachim Hahn in 1968 and 1969 took a systematic inventory of lithics and fauna to discover worked ivory fragments. He pieced together over 200 fragments to recreate the figurine, which remains as a unique example of a therianthropic figure depicted in Paleolithic art. Dating on bones found from the same level securely dates the figurine to 32,000 BP, placing it in the upper Aurignacian period (Conard and Bolus, 2003; Schmid et al. 1989).

Several investigations attempted to reveal the production process of the lion man. The lion is made from the right tusk of either a 12-15 year-old juvenile or from a female mammoth, and the head is oriented towards the end of the tusk while the pulp cavity defines the inner part of the legs (Wolf, 2013). The outer surface of some areas is teeth cement, but most of the cement was removed so that the maker could work with the dentine of the tusk. The surface of the figurine shows some wear due to the depositional context and patches of manganese stains.

In a later excavation in 1960, excavators also recovered an unworked tusk from the left side from a juvenile mammoth that measured roughly 50 cm. The tusk originates between the 20 and 21 *Abbaumeter* and shows damage incurred from the excavation with fresh breaks. The edge of the ivory also shows possible cutmarks, although possible scoring marks left by carnivores are also present. The lion man was likely created using ivory that paired with this tusk or a tusk of comparable size. However, the original vertical position of the tusk and the figurine is roughly 40 cm apart, which obscures the cultural designation of the unmodified tusk. Some have suggested that the tusks may have been buried during the Middle Paleolithic and later uncovered during the Aurignacian period.

Experimental work undertaken to reconstruct the lion man necessitated extensive time (320 hours required) and effort. New excavations have also revealed ivory fragments that fit to the figurine. The statue is both incomplete and displaying wear, which are thought to reveal damage received during its recovery in the 1930s when the use of hand held hoes was a common tool for excavation. However, recent analysis and refitting of the *Löwenmensch* have indicated that the edges of breakage were weathered and not sharp. Thus, it is most likely that it was damaged before its recent recovery in 1930 (Wolf, pers. comm.). Several worked ivory fragments from recent excavations recovered from the refills were digitally pieced together with the figurine using a 3D scanner (Kind and Beutelspacher. 2011).

The use or meaning of the figurine can only be assumed since any form of symbolic expression and any cultural context from the past cannot readily be inferred. Some note the significance of the combination of human and animal traits. Similar figurine from Hohle Fels has been interpreted as a smaller version of the Lion man, 25.5 mm in length, but the felid and human traits are more distinct in this figurine. While some ivory figurines found from the same period in the Swabian Jura captures animals in a realistic form, this figurine manifests an imagined creature artistically rendered by the manufacturer. The lion man clearly represents the diversity and richness in the symbolic expression of the Aurignacian culture that has no precedence in the Swabian Jura.

Hominin remains

As noted before, there are several human remains dating to the Mesolithic and the Neolithic period. In addition, there is one remain from a Neanderthal, the sole find of hominin remains in the Swabian Jura. This consists of a right femur shaft, ca. 25 cm long that was excavated by Wetzel and Völzing in 1937 from the black clayey layer of the Middle Paleolithic period (Black Mousterian) (Figure 3.9). Both ends of the shaft are gnawed by a mid-sized carnivore, possibly from hyena, and are also highly rounded. The specimen is also highly mineralized, which can be evidenced from its weight. From the previous analysis, it considered a male roughly 1.6 m in height (Kunter and Wahl, 1992).

Figure 3.9 Femur shaft from a Neanderthal excavated by Wetzel and Völzing (© Flora Gröning / Neanderthal Museum / Ulmer Museum from NESPOS).

DNA analysis has been conducted by the Max-Planck Institute in Leipzig, confirming that the femur belongs to a Neanderthal. The results indicate that there is also considerable contamination resulting from historic and recent periods, possibly due to post-recovery processing such as washing. Resampling and reanalysis of the gene is under way to better sequence the material.

Figure 3.10 Juvenile human teeth. Canine and lower 3rd premolar.

Two hominin teeth were recovered from recent excavations (Figure 3.10). They are two permanent premolar teeth with unmineralized enamel indicating that they derive from juveniles, most likely of one individual. These findings are not easy to place temporally. The teeth were recovered close to the refilled sediments and spatial integrity is not confirmed. One tooth represents a canine and the other represents a lower P_3. Both teeth were not yet erupted as the root of the teeth remains undeveloped and probably derives from the same individual aged to 5-7 years old. The teeth are currently under analysis, but a variation in the morphology of premolars in recent and archaic hominins such as Neanderthals may prove that the positive identification remains equivocal. Direct dating and genetic analysis could further help reveal whether the specimens belong to modern humans or Neanderthals and their accurate age.

Other Sites in the Swabian Jura

Caves in the Swabian Jura represent one of the most well-documented Paleolithic settlements in central Europe. The archaeological deposits were well known from the late 19th century and have been investigated ever since. In this section, deposits with Middle Paleolithic and Aurignacian cultural layers are discussed in greater detail. The main deposits considered for comparison include Vogelherd and Bockstein from the same valley of the Lone and Hohle Fels, Geißenklösterle and Kogelstein from the Ach Valley. They all consist of caves or rockshelters that were occupied through the Middle and Upper Paleolithic, with the exception of Kogelstein, which has yielded evidence of a Middle Paleolithic occupation only.

Lone Valley: Bockstein and Vogelherd

Vogelherd is located 478 m asl and at 18 m above the valley floor with three entrances. It is situated on a small hill that offers an ideal view of the Lone Valley, intersecting another valley and lying roughly 1 km east of Hohlenstein-Stadel. The cave is accessible from three interconnected entrances with openings toward the north, south and southwest. The northerly and the southwest openings are connected by a 25 m long passage up to 7 m wide.

After the discovery of lithic artifacts that the badgers dug out of the cave in 1931, the site, roughly equivalent to 300 m^3, was fully excavated by G. Riek at the University of

Tübingen in 1931 over the course of 12 weeks (Riek, 1934). Wagner excavated a test pit in 1978 (Wagner, 1981). N. Conard's excavation of refills in front of the cave from 2005-2012 recovered additional artifacts including worked ivory, ornaments, and figurines that previously went unnoticed (Conard and Malina, 2006; Conard et al., 2008). It is one of the first sites with evidence of Aurignacian art in the region, as the artifacts were recovered and documented by G. Riek (1934).

Riek (1934) identified in total four cultural layers from the Middle Paleolithic (IX-VI), two Aurignacian layers as well as two Magdalenian layers. The Gravettian layer appears to be absent, but the perforated bear canine is at the limit of the beginning of the Aurignacian and could fall in the Gravettian period. Riek recovered human remains (known as Stetten) from the Aurignacian layer, but they were directly dated to the late Neolithic period, demonstrating the intrusive nature of the human burial, and not of early modern humans (Conard et al., 2004). The site is known for yielding numerous organic artifacts from the Aurignacian period, including lithics, organic tools as well as artifacts of symbolic significance including three-dimensional ivory figurines depicting mammoth, horse and cave lion as well as a relief and numerous personal ornaments. The site is also remarkable for the wealth of mammoth remains including bones, teeth and ivory, which in part served as raw material for artifact production (Conard, 2003; Conard and Malina, 2008; Riek, 1934).

The faunal assemblages from Vogelherd mostly consist of diagnostic pieces, and many of the unidentifiable specimens, including long bone shafts or burnt material, were not systematically recovered for analysis. Therefore, the material is not representative of all faunal material recovered at the site. U. Lehmann conducted an initial faunal study that involved a subsample of the faunal assemblage and described some of the identifiable pieces to taxa. Later, Niven studied the entire assemblage of faunal remains that had been recovered from the excavation, and not from waterscreening and sorting (2006).

Bockstein is a site complex that consists of several deposits including Bocksteingrotte, Bocksteintörle, Bocksteinhöhle, Westloch and Bocksteinloch/Bocksteinschmiede. Bockstein is located 500 m asl and around 12 m above the valley floor and is situated on the northwestern side of the Lone Valley. The deposit of Bocksteinhöhle was almost fully excavated in 1881 and 1883-4 by Ludwig Bürger and Friedrich Losch (Bürger, 1892). They identified a grave with remains from a female and child dating to 9 ka. Later, Robert Wetzel directed systematic excavations between 1932-6 and resumed the work after the Second World War from 1953-56 (Wetzel, 1961). He began with Bocksteingrotte and later excavated Bocksteinloch and Bockschmiede, which is the area in the mouth of Bocksteinloch. In the 1950s, he discovered another cave of Bocksteintörle, where Marie-Luis Wirsing directed excavations until 1956 (Krönneck, 2012).

The majority of the layers from Bockstein belong to the Middle Paleolithic. Wetzel initially attributed layer III in Bockstein to the Micoquian complex. In particular, he identified bifacially backed knives which others have called *Keilmesser* (Hahn et al., 1985). This is one of few lithic finds from the Middle Paleolithic of the Swabian Jura with a clear style attributed to a cultural industry. One of the first excavations from the Aurignacian layer was conducted at Bocksteinhöhle in the 1880s that led to recovery of perforated bear canines (Bürger, 1892). Bocksteintörle VII and Westloch are the components with Aurignacian layers, and Bocksteintörle also produced Gravettian layers (IV/ V/VI), which are rarely found in the Lone Valley. This may partially be due to the recovery methods of the 1930-50s. The faunal material, analyzed by P. Krönneck, comprised of material excavated by R. Wetzel in 1930 and in the 1950s (Krönneck, 2012; Krönneck et al., 2004). His result may be biased towards larger and identifiable remains due to the lack of systematic recovery of all faunal material regardless of the size and the absence of waterscreening. The faunal material mostly derives from Bocksteinschmiede and Bocksteintörle, both of which were occupied over the Middle and Upper Paleolithic period.

Geißenklösterle and Hohle Fels

Hohle Fels is one of the largest caves in the karst system of the Swabian Jura and is situated on the southeast side of the Ach Valley. It is found 7 m above the valley bottom and 564 m asl with the mouth of the cave facing north. It reaches in some areas to a height of 13 m with a length of 29 m, and the base of the cave covers 500 m^2 of the surface area. O. Fraas and J. Hartmann first excavated the deposit in 1870-71 uncovering cave bear remains as well as stone and organic artifacts (Fraas, 1871; Fraas, 1872). Following their investigation, R. R. Schmidt conducted a study on the excavated material (1912). Later, G. Matschak and G. Riek conducted an excavation focusing on the large niche in the passage leading to the main hall in the cave, and the artifacts recovered there were studied between 1958-1960 (Saier, 1994). The site was intensively investigated by J. Hahn between 1977-79 and 1987-1996, and later continuously excavated by N. Conard from 1997 to the present.

The Paleolithic layers consist of a Magdalenian archaeological horizon (AH I), which is dated to around 13,000 BP, followed by two Gravettian horizons (IIb, IIc) and a transitional layer between the Gravettian and Aurignacian (IId) dating between 30-25 ka. Relevant to this study, three layers of Aurignacian occupation (AH III/IV/ V) are dated between 38-32 ka. Further, there are several layers of the Middle Paleolithic (AH VI-IX) with the youngest layer dating to ~40 ka. The lower levels remain to be dated, but the artifact density is relatively low compared to the Aurignacian.

Some of the notable artifacts at this site involve ivory artifacts that include figurines, personal ornaments, musical instrument and debris of worked fragments. The oldest figurine is a carving of female with exaggerated body parts and a ring with polish suggestive of its use as a pendant. It was recovered from the basal layer of the Aurignacian occupation dating to 35 ka (Conard, 2009). This finding, among others, makes Hohle Fels one of the key sites in Paleolithic research in Europe. The studies of faunal remains from the Aurignacian and Middle Paleolithic have been studied by S. Münzel. The analysis is still in progress, but there are some clear signals allowing for preliminary comparisons. The Magdalenian material has been recently studied by Münzel and Napierala (in preparation). Most faunal material consists of specimens larger than 2 cm or identifiable fragments such as teeth, which were directly recovered *in situ* at the site. From 2 m^2, material found in waterscreened sediment was analyzed which would allow for a greater recovery small sized animals. Part of this result has been discussed in Conard et al. (2013).

Geißenklösterle is a rockshelter located 550 m asl and 60 m above the valley bottom. Oriented towards the west, it is roughly 2.5 km away from Hohle Fels. Large blocks of limestone indicate that there was a partial collapse of the roof during the Last Glacial Maximum, and an area of 16 m^2 is still sheltered and relatively small compared to Hohle Fels (Hahn, 1988). R. Blumentritt first discovered the archaeological artifacts during a systematic survey and G. Riek later excavated a 2 m^2 sondage in the entrance area in 1934. In 1973, E. Wagner excavated a test trench in an E-W orientation to extend the exposed Aurignacian horizon. J. Hahn and E. Wagner then started a systematic excavation that took place annually from 1974-1983, and again from 1986-1991. Deposits of up to 3 m in thickness were excavated in an area of 45 m^2 of the Upper Paleolithic layers, but a smaller area was excavated for the lower levels (Richter et al., 2000). From 2000-2002, N. Conard and his team excavated the Middle Paleolithic layers (Conard and Malina, 2006).

Geißenklösterle has a sterile layer dividing the Middle Paleolithic and Aurignacian, showing a discontinuity in hominin occupation at the site. At a microscopic scale, there is evidence of an erosional disconformity between the Aurignacian and Middle Paleolithic both at Geißenklösterle and Hohle Fels (Conard et al., 2006; Miller, 2009). It was one of the first excavated sites with stratified Aurignacian layers, with the horizon ranging from 43,000-33,500 cal BP (Hahn, 1988, Higham et al., 2012). The majority of faunal material, comprised of large mammalian remains, was analyzed by S. Münzel (in press) in addition to other animals including microfauna by B. Ziegler, birds by P. Krönneck and fish by M. Böhme and G. Böhme, respectively (Conard et al., 2013). The large proportion of the mammalian fauna includes measured pieces that are mostly >2 cm or identifiable pieces and minimal number of sieved remains. Preliminary results have been previously published (Münzel and Conard, 2004b) and all data are included in Münzel (in press). Miller, Goldberg and others investigated the geological matrix of the site. Miller concludes that the layers from the Middle Paleolithic at Geißenklösterle contain clay as well as coprolites and angular clast phosphates that likely derived from coprolites. The phosphatization that occurred in the sediment is an indication that the general climate was relatively warm and moist (Miller, 2009).

The site of Kogelstein is located on the valley floor of the Ach (Böttcher et al., 2000). First discovered in 1913, the site contained few artifacts and animal remains, which were recovered without exact documentation of the provenance. Successive excavations have been carried out in 1987 and 1996 by the Denkmalpflege, and the project resulted in 8 m^2 of exposed surface. The recent investigation has shown that the roof of the cave likely collapsed during the last glacial period or in the Holocene. The site is situated where the Ach and Schmiechen valleys cross, and the Schiechen valley leads to the higher plateau, which probably bore no water. Therefore, it is assumed that prey animals such as horses and reindeer used the valley as a pathway to come to the valley floor to obtain water. With regard to the positioning of the site between two main valleys, Kind (2000) discusses the possibility of its location as an ideal spot for sighting potential preys.

The undisturbed sediments measured roughly 50-70 cm in depth and yielded Middle Paleolithic assemblages. A total of 449 lithic artifacts represent a typical Middle Paleolithic industry. The assemblage consists mostly of debitage and tools such as side scrapers, points and bifacially worked scrapers produced with the Levallois technique. The bifacial tools including *Keilmesser* have been interpreted as representing the Micoquian industry (Bosinski, 1967; Kind, 2000). Burnt limestone debris and faunal remains with few anthropogenic modifications provide direct indication of hominin activities in the cave. The occurrence of two species of *Spermophilus sp.* indicates that the archaeological layer dates roughly to about 50 ka, during the interstadial period (Kind in Böttcher et al., 2000).

Summary

Hohlenstein-Stadel represents one of the major cave deposits in the Swabian Jura. R. Wetzel was one of the most active archaeologists who explored and excavated the majority of the deposits of the site. Known for the *Löwenmensch* ivory figurine, researchers visited the site with the aim of recovering missing fragments and of studying its depositional context and taphonomy. Recent excavations provide a greater understanding of the geology, stratigraphy and the chronology in addition to detailed documentation of Wetzel's excavation, which resulted in the mix of intact and disturbed sediments. The team from the Denkmalpflege recorded several cultural horizons assigned to the Middle Paleolithic and the Aurignacian. The Middle Paleolithic consists of the Black and Red Middle Paleolithic layers and the Aurignacian period represented by three horizons. The upper layers of the Middle Paleolithic are dated to 40 ka just before the emergence of the Aurignacian culture, and the dating of the lower layers is currently under way, while the Aurignacian spans between 40-35 ka.

Sites of the Swabian Jura share a similar chronology and artifact assemblages from the Middle Paleolithic to the Aurignacian. Data drawn from these archaeological records provide a basis with which we can assess inter-site variability and similarity in the faunal assemblages and study the regional patterns of animal exploitation and use of sheltered space.

4 Fauna and Methods

Most Pleistocene animals in this region represent a faunal community often found either in the open grassland or open forests/woodlands. The biogeographic distribution of mammals from grasslands reached their maximum around MIS 5-2 during the last two stages of the glacial period (Kahlke, 2013). The basic paleontological and biological background of mammalian taxon (excluding microfauna) present at the site is briefly given.

Hare

Hares are represented by two species in the late Pleistocene: *Lepus timidus* (varying hare) and *Lepus europaeus* (brown hare or European hare) starting from the Eemian interglacial. There are some morphological differences in the cranium and the mandible between the two species, with the postcranial skeleton exhibiting no clear distinction. However, *L. europaeus* is generally larger than *L. timidus* and body size will help identify the lagomorphs to species level. European hare prefer open grassland although they are highly adaptable (Smith and Johnston, 2008). They usually bred during winter and mid-summer with a gestation period lasting roughly one month, and with an average of 3-5 offspring (Macdonald, 1993). They are usually asocial, solitary animals except in the mating seasons and live up to 7-8 years. Today *Lepus timidus* inhabit taiga and tundra regions with a more northern distribution than *L. europaeus* (Smith and Johnston, 2008). The breeding season is comparable to *L. europaeus* but with a slightly longer gestation period and smaller litter size; they can live up to nine years (Macdonald and Barrett, 1993).

Wolf

Canis lupus derives from a Eurasian species *C. etruscus,* which existed from roughly between 2-1 Ma during the early Pleistocene. *C. lupus* emerged roughly around 1 Ma and later migrated into North America around 750 ka. The first fossils of wolves in Europe were recovered from the Middle Pleistocene (Kurtén, 1968). They are the earliest animals to be domesticated as early as 30-18 ka in Europe (Thalmann et al., 2013). The Pleistocene wolves are larger than the present ones (which weigh 18-55 kg for females and 20-80 kg for males) and their distribution was also wide spread in Eurasia (Niven, 2006; Ziegler, 1996).

They live currently in diverse environments except deserts above the latitude of 20 N° (Mech, 1974). Wolves are gregarious and live in packs consisting of 5-8 individuals and hunt together. Their prey consists of ungulates and some other small animals such as beaver in North America. They mate in April at higher latitudes and gestation usually lasts 63 days. They bear up to six pups in early summer in a sheltered space. A continual use of the same den year after year is observed, which may contribute to the accumulation of juvenile remains. Depending on their physical condition, young wolves stay with their mother throughout the winter or as early as October, when they join the adult pack. The deciduous teeth are replaced between the 16-26th week. Observations of modern wolves show their inclined tendency for hunting of young and old individuals (Fosse et al., 2004; Stiner, 2004a).

In addition to hyenas, wolves are taphonomic agents that hunt, transport and modify skeletal remains. While the discussion of middle-sized carnivores on archaeological deposits has mostly revolved around hyenas, wolves also exhibit similar behavior and produce scats with bone remains.

Fox

Two species of foxes are present in the Pleistocene faunal record of Europe that still exist today: Arctic fox and red fox. Artic foxes, or *Alopex lagopus*, first appear in the archaeological record in the Middle Pleistocene, descending from alopecoid foxes (Audet et al., 2002). They are found in the present arctic biotopes in the circumpolar region including the Arctic areas in Eurasia and North America and Arctic islands. Red fox first appear in Europe in the Middle Pleistocene and are found in many parts of Eurasia, North America and Australia. Both coexisted during the Late Pleistocene and their distribution overlapped (Sommer and Benecke, 2005). Thus, *A. lagopus* was not ecologically limited to a tundra/steppe landscape. At present, *Vulpes vulpes* (red fox) tend to dominate over *Alopex lagopus* due to their larger size when there is an overlap of their geographical distribution (Hersteinsson and Macdonald, 1992).

Arctic foxes mate between March and April. With a period of gestation that lasts roughly 52 days, they bear their young, numbering 6-10, in late spring and the young later abandon their dens by late summer. Dens are mostly formed during the breeding season. Deciduous teeth are replaced by permanent teeth by the end of the summer and are fully mature in 12-14 weeks. Longevity of the Arctic foxes in the wild is roughly 3-4 years (Audet et al., 2002). Arctic foxes today prey on small mammals that include lemmings and voles and scavenge prey hunted by larger carnivores and on food sources such as birds and fishes (Baryshnikov, 2006).

Red foxes (*Vulpes vulpes*) are one of the most widespread carnivores today, ranging in most of Eurasia, North America, and historically introduced to Australia (Larivière and Pasitschniak-Arts, 1996). They originated in the Old World from the Villafranchian fauna *V. alopecoides* like the Arctic fox around 400 ka and later colonized North America around 130 ka. At present they live in a variety of habitats and vegetation including the arid areas and tundra, and more generally have adapted to areas with heterogeneous landscapes. Their reproductive behavior and ontogeny are similar to that of the Arctic foxes but their breeding may occur earlier in temperate conditions or in lower latitudes. Their common prey includes small terrestrial mammals such as lagomorphs and squirrels and birds. They rarely live beyond 6 years in the wild (Larivière and Pasitschniak-Arts, 1996).

Red foxes are usually larger than arctic foxes, and few cranial features such as the occipital length and the interorbital region are distinct enough features to identify two species of foxes, but complete crania are rare in archaeological deposits. Further, some measurements of complete post-cranial skeletons can also help distinguish the species (Monchot and Gendron, 2010). Behaviorally, red foxes may be more aggressive than arctic foxes and occasionally prey on them (Larivière and Pasitschniak-Arts, 1996). Premolars in the *Alopex sp.* are higher crowned, m1 has a shorter talonid, and tubercular teeth are more reduced (Audet et al., 2002; Kurtén and Anderson, I980).

Cave bears

Cave bears (*Ursus spelaeus*) represent one of the common fauna found throughout Europe and part of Asia. Cave bears are often found in caves and rockshelters as they die during the winter hibernation, resulting in ideal preservation of their skeletal remains. Their common occurrences have led to interest in the animal from the advent of paleontology and have fostered research on the biology and evolution of their species. The type locality of cave bear is the Zoolithen Cave site near Gailenreuth in the Franconian Jura of southeastern Germany. The skull of a cave bear was discovered there initially by Esper in 1774 and was described by Rosenmüller in 1794 (Kurtén, 1958, 1968, 1976; Rosendahl and Kempe, 2004; Weinstock, 2000). The lowest level of Zoolithen Cave is dated to roughly 342 ±71.4 and its assemblage is composed mostly of cave bears (Rosendahl and Kempe, 2004).

The family of *Ursidae* descended from *Miacidae*, a family of carnivorous, tree-climbing mammals, which were distributed in Europe during the Miocene period and recognized from the development of flatter molars (Craighead and Mitchell, 1982; Kurtén, 1976) One of the primitive and earliest occurrences of *Ursus* is the Auvergne bear (*Ursus minimus*), which is relatively small and similar to modern Asiatic black bear dating to 6-4 Ma, and likely inhabited forest areas. Evolving from the Auvergne bears, *Ursus etruscus* of the Late Villafranchian (roughly around 2.5-1.7 Ma) appeared in Eurasia. It is the common ancestor to the extant *Ursus* including brown bears as well as cave bears and was larger than its ancestor. The direct ancestor of *U. spelaeus* is the Deniger's bear, *Ursus deningeri*, that existed in the Middle Pleistocene period. The earliest cave bears appear roughly in the Interglacial period around 250-128 ka (Pacher and Stuart, 2009). The two species are similar in morphology, and the identification of the species is mostly based on a temporal distinction (Pacher and Stuart, 2009), but recent osteometric analyses have suggested differences in limb proportions and metapodials and generally suggest that *Ursus spelaeus* was larger than *Ursus deningeri* (Athen, 2007).

Cave bears are one of the largest bears in the Quaternary period. The estimate of their weight is, at the maximum, around 1,000 kg for males. With pronounced sexual dimorphism, females are considerably smaller and roughly 4-600 kg (Pacher and Stuart, 2009). They are one of the largest animals in the Order of Carnivora in the Quaternary period of Eurasia and they became extinct roughly around 25-20 ka.

From the biology of extant bears, we can also infer the biology of cave bears. Mating of brown bears occurs in spring around May to July based on observations of grizzly bears in National Parks of North America and European brown bear populations (Craighead and Mitchell, 1982). The female bears have delayed implantation for 5 months until around October to November when they enter winter dormancy. After 6-8 weeks of a gestation period, 1-4 cubs are born around January to March when the females are usually in hibernation. Cubs usually spend the first year with the female bear and enter winter dormancy. Female bears and cubs stay together at least until the second year of spring, and the following winter is when one of the highest mortality rates for bears is recorded (Craighead and Mitchell, 1982).

Ursus spelaeus were initially known to exist only in Europe. However, a recent genetic study has positively confirmed the presence of European cave bear in the Altai Mountain region, the most eastern distribution of cave bears that has been identified to date (Knapp et al., 2009). Cave bears show a high level of variability in the morphology within the species, which has led to the confounding identification of subspecies or separate species. Genetic studies contribute to our understanding of species evolution and phylogeny.

The general consensus is that the divergence of cave bear and brown bear occurred around 1.2-1.6 million years ago (Knapp et al., 2009). Multiple mitochondrial DNA analyses indicate that three reproductively isolated clades of cave bear, including *U. spelaeus*, *U. ingressus* and *U. kudarensis*, existed as early as the Middle Pleistocene and until their extinction at 24 ka (27,800 cal BP), before the beginning of the Last Glacial Maximum (Dabney et al., 2013; Knapp et al., 2009; Stiller et al., in press). Recent studies suggest that *U. spelaeus* are more concentrated in Western Europe (Stiller et al., In press).

In contrast, *U. ingressus* are distributed in Eastern Europe including the Ural Mountains and overlap in Central Europe (Münzel et al., 2011; Stiller, in press). *U. kudarensis* are a group that currently has only been recovered in the Caucasus, Altai Mountains, and the region along the Yana River in eastern Siberia, extending their biogeographical distribution (Baryshnikov and Knapp, 2009). Other morphologically distinct types including *U. s. ladinicus*, *U. s. eremus* and *U. s. rossicus* occur infrequently and are older than *Ursus spelaeus*, indicating that they are possible archaic bear populations. Data suggest that *U. kudarensis'* genes differ significantly from that of the European cave bears and that it could be deemed as an independent species (Knapp et al., 2009; Stiller et al., 2009).

Stiller and colleagues (in press) further demonstrate that the greatest diversity was identified from 40-50 ka and 30-40 ka for *U. ingressus* and *U. spaleaus*, respectively. It appears that the genetic diversity steadily decreased from the east westwards (Stiller, in press). In another genetic study, Stiller et al. compared the mitochondrial DNA diversity of extinct cave bears and extant brown bears to understand the pattern in which cave bear populations diminished during the late Pleistocene and the underlying cause of their extinction. The authors estimate the population size of the European *Ursus spelaeus* and the extant brown bears, calculating the diversity within mtDNA of the two ursid populations. The pattern of cave bear indicates that there is a decrease in diversity, and thus the number of female cave bears, starting 50 ka until the population dwindled. The evidence points to the possible role of humans, who may have forced cave bears out of their preferred sheltered locations for hibernation, instead of climate change as a likely cause of their extinction.

The diet of the cave bears despite their size consisted of plant material. The first study of cave bears demonstrated that the tooth morphology, with molars developing broader Masticatory surface with low and rounded cups, points to a diet dominated by plant material (Kurtén, 1976; Rabeder and Hofreiter, 2004). Further, the stable isotopic signatures have supported previous statements about the diet (Bocherens et al., 1994). The stable isotopic signatures of cave bears are similar to herbivores than carnivores that existed on the landscape. The average values of ^{15}N for cave bear populations in Europe range between 2-6 ‰ and ^{13}C values range between 22.2-20 ‰ (Bocherens, 1994). Recent study on the microwear also confirms the herbivorous diet of the cave bear (Münzel et al., in press).

A few studies attempted to claim consumption of animal protein by cave bears based on microwear patterns on the cave bear teeth. Peigné et al. (2009) note that their diet may have consisted of a mixed diet with some hard material that includes invertebrates and meat in addition to plant matters. Richards et al. (2008) claim that the higher stable isotopic signature of ^{15}N, which is employed as a marker of trophic level, as evidence of a diet based on meat on specimens from Peştera cu Oase. Others have argued for different reasons for the elevated ^{15}N values, including the environmental condition that may affect enrichment of ^{15}N in soil, or inversely, a diet with poor protein intake or due to changing metabolism during hibernation (Grandal-d'Anglade et al., 2011; Pérez-Rama et al., 2011).

Study of live female grizzly bears and cubs demonstrate that the difference of ^{15}N values measured from red blood cells and plasma was only on the order of ~ 1 % and indicate no trophic level enrichment (Jenkins et al., 2001). The results, however, may not apply to studies of collagen in cave bears because there are different physiological processes that differentially affect the stable isotopic values of hard and soft tissues. Keeling and Nelson (2001) demonstrate, based on cave bear remains from Divje Babe, Slovenia, that the neonate and fetus had consistently higher ^{15}N values. According to the authors, collagen turnover of mature bears reflects their diet on a longer scale beyond the scale of months due to the slow turnover of collagen. On the other hand, the collagen of the cubs reflects the diet of the first winter. Increased protein intake and lack of nitrogen cycle are some of the possible explanations for the increased ^{15}N values of young bears. An alternative explanation is that bears, which do not survive hibernation, can produce urea and lose body mass, which also account for ^{15}N enrichment.

Stable isotopic data of cave bears and brown bears from the Paleolithic period indicate that there was a clear niche partitioning in diet between the two species. The brown bears maintained an omnivorous diet with higher ^{15}N values (Bocherens et al., 2011) and gradually shifted towards greater intake of plants after the extinction of cave bears (Münzel et al., 2011). Therefore, it is likely that ecological competition did not occur.

Münzel's work (2012, in press) in the Swabian Jura demonstrated two separate episodes of cave bear extinction for the *U. ingressus* and the *U. spelaeus sensu lato*. *U. Ingressus* are larger than *Ursus spelaeus* and outcompeted the cave bear population that inhabited the area before, surviving in the region at least until 25,000 years ago, outliving *U. spelaeus* by ~3000 years. The stable isotopic data show a relative small cluster of values that suggest strict plant-based diet without meat. If there was some consumption of meat as well as some forms of protein, it was not in significant amounts that would affect the stable isotope values.

Based on ethological work on extant ursid species, some factors that affect winter dormancy has been revealed. Hibernation is a unique adaptation to winter periods when the food sources are limited, with bears spending up to 6 months in dens. Their metabolism is usually reduced by 70 % (Watts and Jonkel, 1988), and they can lose roughly 20-40% of their body weight. Manchi and Swenson (2005) analyzed denning behavior of male brown bears and compared the result with data on female brown bears in present northern and central Sweden. Data suggest a prolonged hibernation practiced by females compared to males, especially when the females are pregnant. This pattern is likely due to the ability for larger bears to store more fat and also, due to the relatively small surface area to volume, they can remain active for a longer period during winter (Manchi and Swenson, 2005). More importantly, denning behavior is usually correlated with the timing of the snowfall, and there is a variation in the length of the hibernation period depending on the latitude. Adult bears usually stay within the general area where they denned in the past and their activity range is smaller than that of sub-adult males.

Brown Bear

Brown bear (*Ursus arctos*, also known as grizzly bear) today is found in diverse habitats. The brown bears, which initially evolved from Asian Etruscan bears, were first identified around 500 ka, possibly at the site of Zhoukoudian in China (Herrero, 1972). They migrated later to Europe and coexisted with cave bears around 250 ka and also spread to

North America by roughly 25 ka, initially in Alaska. Today, two subspecies, grizzly and brown bears, exist in North America. The distribution in Eurasia is fragmented, and pockets of brown bear populations exist in Scandinavia, the Cantabrian Mountains of Spain and the Pyrenees Mountains of France and parts of Russia (Pasitschniak-Arts, 1993).

Cave lion

The cave lion of the past represents a separate species or subspecies of modern African lions (Barnett et al., 2009). Cave lions are larger than the extant African lions, which are the second largest felids today, and the depiction of cave lions from Paleolithic cave paintings, such as Chauvet, show the absence of manes that may have developed in the last 320-190 ka (Clottes, 2003; Yamaguchi et al., 2004). The weight of extant male lions varies between 150-225 kg, with females weighing between 120-182 kg. Recent discoveries support the phylogenetic data, which have pointed to the highlands of Central Asia as the origin of large felids (Tseng et al., 2014). The fossil of a new species, *Panthera blytheae*, was dated to 4.1-5.95 Ma, found in the Zanda Basin of the southwestern Tibetan Himalayan Plateau, most closely resemble snow leopards (Tseng et al., 2014). Lions dispersed from Asia into Africa in the late Pliocene and appear in the fossil record at Laetoli, Tanzania, 3.5 Ma (Turner and Antón, 1997). Lions are present in Europe at least by 900 ka at the site of Vallonet. They spread to North America and northern South America (subspecies known as *Panthera l. atrox*) and persisted until the beginning of the Holocene around 10 ka when lions including sub/species of cave lions became extinct outside of Africa and southern Asia. They began to contract and became extinct roughly around 11 ka in Eurasia (Stuart and Lister, 2011).

In Africa today, lionesses give birth often between February-April and June-July (Haas et al., 2005). The gestation period is roughly 110 days and litter size is between 1 and 4. The cubs stay in the den with the mother for at least a month, and milk teeth erupts around 3 weeks and fully develop at 8 weeks while the permanent teeth begin around 9-12 months. They live in prides, which consist of 5-9 females, 2-6 males and their offspring. Their hunt includes large ungulates such as wildebeest and young African elephants, but if prey is abundant, they also often scavenge on other prey and practice active scavenging to scare off other animals for their hunt. Their mode of capture includes stalking and attacking and they mostly hunt in groups. Lions share prey preferences and dominate over hyenas unless hyenas are in groups of 20-40. Females have greater morality rates after 3-4 years while males have an average longevity of 12 years (Haas et al., 2005).

Eurasian lynx

Lynx (*Lynx lynx*) is a felid that is widely distributed in northern Eurasia and North America, which is a distinct subspecies of *Lynx canadensis*. While its present habitats include boreal forests, its past range extended into tundra and wooded steppe (Sunquist, 2002). *F. issodorensis* is the known ancestral species that originated in Africa during the early to middle Pliocene (3.5-3 Ma). It migrated north by the middle Villafranchian and later evolved into *Lynx lynx* in China and spread to Europe during the Pleistocene 1.5-1 Ma (Larivière and Walton, 1997). The lynxes later spread north and gave rise to *Lynx canadensis*. *Lynx pardina* is known to occur on the Iberian Peninsula both in the present and the past, but their range appears to be limited and they did not occur in Central Europe (Rodríguez and Delibes, 1992).

They breed around February to May and their gestation period ranges from 67-74 days, following the birthing that occurs around May-June. The litter size ranges between 2 to 4. Their deciduous dentition is fully developed after 30 days and they become replaced at 4 months of age. The young stay with their mothers until the next breeding season after 1 year or longer if the mothers breed in alternate years. The average lifespan is 5 years as the juvenile mortality rate is high.

Marten

European pine marten (*Martes martes*) and beech marten (*Martes foina*) occur in the Palearctic region of Eurasia and are commonly associated with forest habitats although they have adapted when needed to open areas (Carter, 2004). Two extinct species of mustelids in Pliocene China are identified and *Martes* species exist in Eurasia by 1.8 Ma (Powell, 1981). Mating occurs in July and August, but is followed by delayed implantation, which occurs in February-March. After implantation, the gestation period lasts 28-35 days and females give birth around March-April, with each litter producing 2-5 young. Their diet is mostly omnivorous, with a preference for small mammals, but is flexible, adapting to local abundant resources.

Cave hyena

Cave hyena (*Crocuta crocuta spelea*) belongs to the same species of spotted hyenas that exist in Africa today. The hyenas from the Quaternary period are larger, but genetic analysis revealed that spotted hyenas from Africa belong to the same genetic group (Rohland et al., 2005). The *Hyaenidae* family appears in the fossil record by 17-18 Ma and a number of hyenid species existed in Africa during the Miocene (Turner et al., 2008). The fossil record is patchy and it is not clear whether they first originated in India or Africa, with the earliest occurrence of the genus currently dated to 3.8-3.6 Ma in Laetoli, Africa. *Crocuta crocuta* later migrated out of Africa at least by 1.2 Ma into Asia and reached Europe by 0.8 Ma (Sardella and Petrucci, 2012). They persisted in Europe until the end of the Pleistocene when they became extinct by 30 ka (Stuart and Lister, in press).

Unlike many carnivores, sexual dimorphism is reversed and females are 12 % larger than males. The modern hyenas weigh 45-60 kg for males and 55-80 kg for females while the estimate of Pleistocene hyena’s weight is roughly 90-120 kg or heavier (Lister, 2001). Cave hyenas were adapted to both woodland and tundra-steppe environments known from its widespread distribution in Pleistocene Eurasia. The extremities of cave hyena are characterized by shorter but broader bones than modern African hyena, or *Crocuta crocuta*.

Spotted hyenas are social carnivores living in clans with multiple males and females that roughly number 3-80 individuals. The clans are matrilineal and females are dominant over males. Hierarchies among females exist and are also inherited by their offspring, enabling a stable hierarchical clan over time. Females stay within the natal clan while the males disperse after puberty and join another clan.

Spotted hyenas can breed year round with the gestation period lasting 4 months. They usually give birth to twins with a peak of births occurring in November in Africa today. Like bears, the cubs need shelter for long periods in dens or caves. Females first give birth in burrows and later bring their young to a communal den, which is shared by other females, although no communal care takes place. Young are not weaned until 12-16 months and have complete erupted adult teeth by this time. For carnivores of their size, they have high parental investment. This is thought to be the tradeoff between development of a massive skull and a long developmental period that is required for the ontogeny for skull development.

Competition among members for food resources is intense and partially affects their predation behavior. The level of competition among the members of the clan is high, and hunted preys are usually either cached elsewhere or consumed immediately (Kruuk, 1972). Provisioning is rare for spotted hyena with an exception of mothers that occasionally share with their cubs because food is often stolen in their large social group. Therefore, the total accumulation of bones is small among modern hyenas. Further, the study in the intensity of prey consumption shows that the intensity is higher among social animals (Wilmers and Stahler, 2002). Further, experiments have shown that the level of carnivore damage on the long bones remained constant regardless of the number of hyenas, but any increase led to less selective consumption of body proportions (Faith et al., 2007).

Hyenas and other animals that crack bones use their premolars to extract blood and marrow especially from limb bones. Their snouts are also shortened so that they produce greater bite force. They are distinct from other carnivores for their specialization in bone cracking. The bite force can leave pits as large as 7 cm in diameter to extract marrow (Van Valkenburgh, 2007).

Mammoth

Earliest mammoths in the paleontological record are found in Africa where the elephant family originated 6 Ma (Lister and Sher, 2001). *Mammuthus meridionalis* is one of the earliest mammoths from Europe (~2.5-1.5 Ma) and inhabited a woodland habitat. Later *Mammuthus meridionalis* was pushed towards Western Europe, with *M. trogontherii* in Eurasia and *M. columbi* in North America, being more adapted to a steppe environment, appearing around ~1.5-1 Ma. Around 500 -125 ka, *M. primigenius* spread from east Beringia to Eurasia, later migrating back into North America (Lister and Sher, 2001).

Adaptation towards a steppe habitat is observed in the increase in the height of crowns and enamel bands, accommodating for a more grazing diet. Their frozen remains from Siberia provide us insight into the physical appearance of the animals (Fisher et al., 2012; van Geel et al., 2008b; van Geel et al., 2011). They are similar to extant elephants, but had shorter tails and smaller ears, with fur in order to preserve body heat.

The extinction of mammoths was a gradual process that involved contraction of their distribution at first in most of Eurasia, with relic populations existing into the Holocene 11 ka in northeastern Siberia (Stuart et al., 2004). Further, few mammoths existed on Arctic islands until 6.5 ka and 4 ka on St. Paul’s Island and Wrangel Island, respectively (Guthrie, 2004; Vartanyan et al., 1993). While the cause of extinction is not clear, mammoths reached their maximum distribution during the Last Glacial Maximum after the expansion of modern humans in Eurasia. Their genetic data coupled with modeling data also confirm their population in the same period, with it likely that the abrupt warming in the Holocene being one of the major factors underlying their extinction.

Horse

Horses are one of the most abundant fauna in the Lone Valley region. One possible explanation for their common occurrence lies in the topography, which allowed the grassland to develop and persist in the area. Horses are, as such, mostly associated with open habitats. Horses have evolved in North America from *Hyracotherium* in the Eocene and *Dinohippus* in the late Miocene with gradual adaptation to a grazing diet and a reduced number of toes for prolonged running. Unlike the fossil record, which places the first appearance of *Equus* around 2 Ma, a recent genetic study indicates that the *Equus* lineage originated around 4-4.5 Myr BP, represented by *E. simplicidens* (Bennett and Hoffmann, 1999; Eisenmann, 1992; Orlando et al., 2013). *Equus* then dispersed through Beringia to Eurasia, Africa and South America around 2.5 Ma (MacFadden, 1992).

While the taxonomy and the question of species are often debated, the caballine horses represent *Equus ferus*, or the wild horse, which clearly are present in Europe, northern Asia and North America by the Middle Pleistocene, later becoming domesticated (*Equus caballus*). Caballine horses are differentiated from other *Equus* species such as the wild ass *E. hydruntinus* based on the morphology of mandibular teeth (Orlando et al., 2013) and its bigger size. While they dispersed and adapted into various biotopes, they preferred cooler habitats of steppe, tundra and open forest as opposed to the wild ass and hemiones. They later became extinct in North America and largely replaced by a domesticated counterpart in Eurasia. Przewalski‘s horses are the only extant wild horses that exist today, ranging from Siberia to Mongolia; domesticated horses diverged from the wild ones around 38-72 ka (Bennett and Hoffmann, 1999; Orlando et al., 2013).

Horses are known as a grazing animal with grass dominating their diet (MacFadden, 1992). They weigh between 300-450 kg. In the wild, they form either harem bands consisting of several mares led by a dominant stallion male with offspring or bachelor males forming a group of 2-4 that is maintained throughout the year (Berger, 1986). Observation of feral horses indicates that although males can breed any time of the year, horses tend to mate around spring to late summer. The gestation period is roughly 340 days and females birth usually one foal between April and July (MacFadden, 1992).

Woolly rhinoceros

Woolly rhinoceros (*Coelodonta antiquitatis*) is known to have originated in Asia by the middle Pliocene. One of the earliest ancestors, *Coelodonta thibetana*, has been recovered from the Tibetan Plateau dating to 3.7 Ma, and *C. tologoijensis* appear first in Europe around the early Middle Pleistocene at 460 ka (Deng et al., 2011; Kahlke and Lacombat, 2008; Stuart and Lister, 2012). Evolutionary changes are represented through an increasing adaptation to a grazing diet such as observed in the thickening of enamel and cementum on teeth and some cranial morphological changes. The fully evolved *C. antiquitatis* appears in the fossil record of Europe and Asia during the cold phases of the late Middle Pleistocene, during MIS 10 or 8. Now extinct, their numbers decreased from the west, and they survived until around 14 ka in northeastern Siberia (Stuart and Lister, 2012).

Several frozen rhinoceros were recovered from the Siberian permafrost (Boeskorov, 2012). The finds show thick skin with a coat of hair and under wool for insulation. They bore two horns; the frontal horn was most likely used to clear snow to access vegetation in winter. However, their distribution was likely affected by snow cover, inhibiting their expansion into the arctic zones, evidenced by their short legs and lack of hooves or pads to move around in deep snow (Kahlke, 1999). Their diet consisted mostly of herbaceous vegetation, *Artemisia*. Their teeth were high crowned with thick enamel, and adapted to highly abrasive food (Boeskorov, 2001). Their estimated body mass is 1500 kg. Frozen specimens show 2 nipples, suggesting birthing of one calf (Boeskorov, 2012). For extant Black and White Rhinoceros in Africa, the gestation period is 16 months with two peaks of birthing around Jan-Feb and June-August having been observed. It is likely that birthing for woolly rhinoceros peaked around the warmer period, in spring or summer, but the exact timing is not exactly reconstructed.

Red Deer

Red deer (*C. elaphus*) is first recognized in Europe during the Interglacial Period in Britain approximately 475-505 ka, but red deer evolved its crowns on the antler around 347-421 ka. Present distribution shows that red deer, which originated in Eurasia, migrated into North America (also known as North American elk) around the Illian glacial stage at 128 ka across Beringia, although differences in size exist (Steele, 2005).

Red deer have an ability to adapt to various climatic zones as they are generalists and forage opportunistically. They prefer woodlands that provide forest cover without much snow cover, and are rarely found in areas with reindeer. They are known to subsist on a variety of grasses and browse, and their dietary niche is relatively large and geographically variable. Red deer males and females live in separate herds except during the seasons of rut when there are harems with a single male and several females in groups. Males form their group during the rut and over the year or choose to live solitary. Herds with females and their calves and sub-adults form in spring. Limited seasonal migration may occur attitudinally depending on the local conditions for seeking better forage and for avoiding insects. (Straus, 1981).

Reindeer

Reindeer are known to have originated in Alaska roughly 1 Ma years ago (Geist, 1998). They are widespread across Eurasia and northern North America throughout the Pleistocene and exist at present in the northern latitudes, namely Scandinavia, Russia and northern North America and in few areas as managed by herders. The earliest documented fossil of reindeer in Europe was recovered from Süssen, Germany, approximately 500 ka (Kurtén, 1968). They are adapted to both steppe and conifer forest biomes in the northern latitudes as they are adversely affected by relatively warm climate and thus largely absent in interglacial periods (Kalhke, 1999). Reindeer also consume lichens, which is low in protein and high in carbohydrates, during the winter (Geist, 1998).

Reindeer weigh on average 50-85 kg (females) and 80-150 kg (males) (Spiess, 1979). Mating occurs in May and the birthing occurs in late May and early June (Bergerud, 1980). The juvenile mortality is high for the first six months, and mortality of male reindeer at around 3-4 years of age skews the sex ratio to 2 or 3:1. During the rut in fall, the herd includes all ages and sexes, and the males form herds separate from the females and the calves in other times of the year. Reindeer migrate annually and prefer to make use of mountainous terrain, using ridgelines or rivers (Speiss, 1979: 38). The predictability of their migration route must have influenced hunting strategies of reindeer by hunters during the period of migration. Hunting outside this period occurred occasionally, as the herds would have been harder to locate on the landscape. Calving occurs synchronously in late spring, usually around May-June.

Reindeer is the only extant species with both sexes growing antlers. Males and females also shed them at different times. The main beams are curved towards the back (Speiss, 1979). The females retain their antlers through the winter and shed the antlers at the time of calving from March to June during the calving season, while the pregnant females shed their antlers after calving around May. Young animals begin growing antlers one month after birth and shed their antlers between March and June. The males shed during or after the rut and new antlers begin to grow starting in March. The females and young reindeer grow smaller and simpler antlers, and the size of the base can be used for distinguishing the sex, as male antlers are larger than young and female antlers. Shed antlers are not precise indicators for the seasonality of site occupation or prey procurement as they could be collected for their use in manufacturing artifacts. Male antlers are larger than females, especially among males around 6-7 years old, although juvenile males cannot be readily distinguished from female antlers.

Their social group consists of female herds as well as males that are in groups or solitary. During the rut, they usually copulate in early fall, and herds of females are defended by a sole dominant male and other males in the periphery. Stags congregate for protection in male herds or become solitary during winter. In the spring, females produce one calf in May-June and calving herds consist of females, infants and juveniles, while adult males are absent. As they grow older, the life expectancy of bulls decreases more rapidly than of the cows due to rutting activities that require greater energy during winter (Speiss, 1979).

Aurochs/Bison

Two contemporaneous large bovids are relatively difficult to distinguish, although some differences in the tooth morphology and post cranial remains have been suggested (Olsen, 1960; Slott-Moller, 1990). Aurochs are the extinct progenitor of domesticated cattle.

Its origin remains unclear, but early remains of a *Bos/Bison* lineage, or *Leptobos*, occur in central and southern Asia in the Pliocene. *Bos* then evolved around 1.5-2 Ma and later migrated into Siberia, northern Africa and Europe. Found first in central Europe dating to the Holstein Interglacial, aurochs is associated with somewhat warmer conditions either during the interglacial period or in the southern region during the glacial period (Koenigswald, 1999). Aurochs in Europe persisted until around 300 years ago but are extinct today (Uerpmann, 1999; Van Vuure, 2002). They tended to live in open flat areas at low elevations and not in woodlands (Hall, 2008) and their diet mostly consisted of graze, grasses and sedges.

Bison priscus appear in the fossil record by the early Middle Pleistocene and their range extended from Europe to Siberia and spread to North America through Beringia between 300-130 ka (Meagher, 1986; Shapiro et al., 2004). They survived through the Pleistocene-Holocene climatic transition, but their numbers reduced significantly during the historical period due to habitat fragmentation and overhunting. Today, their distribution is limited in protected ranges and reserves in Central and Eastern Europe as well as North America.

Bison are known to inhabit a variety of habitats from open grasslands to forests, but are primarily grazers, subsisting on grasses and sedges (Julien, 2009). They are gregarious, forming mixed herds of females, calves and young males. Older males can join the herd during the rut season, but are otherwise solitary or form bull groups. The breeding season of extant bison is between July and September and gestation period is estimated to 285 days. Thus, birthing/calving occurs around April to June with one calf (Meagher, 1986).

Method

The analysis of faunal remains follows a method that is employed in most zooarchaeological studies, consisting of collecting primary data and forming the database necessary for tabulating data and study patterns (O'Connor, 2000; Peres, 2010; Reitz and Wing, 2008). For the primary data, taxonomic designation and skeletal elements constitute the basis of all identification. All the material was weighed and rounded to the nearest tenth of a gram. Specimens larger than 1 cm were closely examined using 10 x hand lens to study the surficial modifications, and other information such as the degree of weathering was recorded. Additional data including age/sex, measurements and any remarkable traits were collected when relevant. Fragmentary specimens within the same spit (*Hieb*) and meter (*Abbaumeter*) were refitted to increase the frequency of identified specimens. These procedures were followed by tallying the data and running basic statistical analysis.

Identification

Taxon is the designation of an organism to a certain level of classification in the Linnaean system, which ideally allows us to determine the specimens to the species level. However, when this is not possible, a higher level such as genus, family or order is designated. Specimens without diagnostic features are broadly categorized by the body size of the animal (Brian, 1981 with modification) (Table 4.1). As this analysis focused on mammals, other non-mammalian remains in the sampled assemblages are studied by P. Krönneck. Few non-mammalian bones were identified in the Middle to early Upper Paleolithic deposits, including birds and fish. Most of the analysis for taxonomic identification was aided by comparing specimens with extant animals from the reference collection housed in the Institute for Archaeological Sciences at the University of Tübingen.

	weight (kg)	fauna
body size 1	4-30	hare, fox, wolverine, badger, beaver
body size 2	30 - 100	small felid, wolf, small artiodactyl
body size 3	100 - 300	hyena, red deer, reindeer, musk ox
body size 4	300 - 1000	large bovids, horse, cave bear
body size 5	2000 - 3000	mammoth, rhinoceros

Table 4.1 Body size of the animal (Brian, 1981) with modification

The skeletal element and proportion (such as diaphysis of long bone or maxilla of crania) were also recorded for each specimen. When present, the landmark, such as the nutrient foramen, interior diagonal lattice of humerus and grooves on ungulate metapodial, was documented based on Stiner's faunal coding keys (Stiner, 2004b). The proportion and landmark are useful in studying the skeletal representation and quantifying the proportion of skeletal elements (see below for detail).

Cave Bears

Some faunal remains were identified based on the comparison with paleontological assemblages. Cave bears are larger and more robust compared to brown bears, which coexisted in the Paleolithic period, and other extant bears. Further, cave bears have more developed muscular and ligament attachments which are morphologically distinctive and identifiable. Thus, the paleontological material of cave bears from the *Paläontologische Sammlung* in the University of Tübingen served as a reference for comparison. Cave bear specimens derive from Bärenhöhle near Erpfingen in southwestern Germany, a paleontological site that spans a period of Lower Pleistocene from the Würm complex to Holocene (Rathgeber, 2003). Some of the specimens were dated to at least 30,000 years ago and represent a population of *Ursus spelaeus* in the late Pleistocene. In addition, bear remains from reference collections housed in the Institute for Archaeological Sciences in Tübingen include a fetus of a polar bear and a juvenile of brown bear between 1-2 years old (UR 5), allowing for adequate comparison and positive identification of bears from various stages of development.

Animals which are taxonomically close make for difficult identification. However, morphological differences in the skull, dentition and postcranial skeleton between cave bears and brown bears exist (Hidalgo, 1988; Weinstock, 1999). The crania show clear morphological differences (Kurtén, 1959, 1976; Hidalgo-Torres, 1988; Weinstock, 1999). Brown bears have a sloping forehead whereas the cave bears have a domed forehead that is related to the dietary habits and development of chewing muscles. Further, the mandible of the *U. spelaeus* has an alveolus for P_3 while *U. arctos* often lacks it (Bishop, 1982). Teeth also exhibit some distinguishing characteristics. P_4 of cave bears is sometimes not retained and brown bear P_4 lacks a paraconid. Also, the morphology of M^1 differs, with an angular and relatively narrow form and an anterior lobe broader than the posterior one for cave bears (Weinstock, 1999). Further, M_2 of cave bear is also narrow and shows a constriction between the anterior and the posterior lobe.

The postcranial skeletons are mostly distinguished by robusticity and general size. Female cave bear and male brown bear overlap in size, but cave bears are generally larger and with greater shaft thickness, width and pronounced muscular marks. Some exceptions include metapodials of cave bears, which are short but robust (Kurtén, 1959). Thus, cave bears can be distinguished from brown bears when they are fully developed.

Close study of the fetus remains from bears and other carnivores shows that some elements of the fetus are often not distinctive enough to permit identification to species, but most of the complete long bones as well as teeth remains can be distinguished when compared with lion, hyenas and wolves. Most juvenile remains and fragmented bones without clear landmarks and complete ends cannot be positively identified to one species of bears. These bones were assigned to *Ursus sp.* on a genus level to avoid inconsistency in the documenting of taxa (Driver et al., 2011).

In general, paleontological investigation in Pleistocene Europe has shown that cave bears dominate in most deposits that can be identified to *Ursus* (Pacher and Stuart, 2009) with occasional brown bears, which also made use of caves and rockshelters for shelter and denning. Thus, juvenile remains are recorded as *Ursus sp* based on the number of species identified to adult cave bears and brown bears, I assume that juvenile remains can be assigned to cave bears and can further be used to evaluate the demographic profile of cave bears at the site.

Carnivores and ungulates

The identification of the nondiagnostic long bone specimens is crucial in assemblages, which can potentially be affected by intentional or unintentional fragmentation of specimens. Some nondiagnostic shafts were identified to the Order of Carnivora or Artiodactyla/Perissodactyla. The diaphysis of long bones especially in metapodials from middle-sized ungulates, especially of cervids, shows a smooth inner surface inside. In contrast, shafts of mid- and large carnivores often contain cancellous bones within the shafts, making this a diagnostic feature to classify specimens according to the mammalian order. Further, common size 4 animals are cave bears as well as occasional horses. The differences among the two taxa are at times distinguished through the structure of the cancellous bones, with horses having a distinctive structure common among perissodactyls.

Quantification

All the data were quantified using several measures and units. Several quantification methods to calculate relative abundance of skeletal remains are employed by faunal analysts. Tallying counts, measuring abundance and quantifying faunal data hinge on bridging variables that we attempt to measure, and we actually can measure which approximates the target (Lyman, 2008). All units of measurement are met with advantages as well as drawbacks and thus the validity and assumptions of certain measures should be assessed before employing the measures. Here, the use of certain measures is discussed.

NISP (Number of identified specimens) is the most basic unit of analysis employed in zooarchaeology for quantifying animal remains. NISPs are counts of specimens assigned to a particular taxonomic unit such as species or genera. The unit provides the fundamental basis for comparing the abundance of each taxon in assemblages and across sites. The NISP, with some faults, is nonetheless the most common measure used by zooarchaeologists working in various geographic and temporal contexts and serves as a unit of comparison among diverse assemblages.

Its weakness mainly stems from the problem of ‘interdependence’ (Grayson, 1984; Lyman, 2008), which could lead to unequal representation of the specimen due to the varying degrees of fragmentation. Simply put, identifiable fragments originating from one specimen may be counted redundantly due to fragmentation. We assign ‘one’ to one identified specimen assuming that other identified specimens derive from other specimens and are separate. The association is obscured in archaeological assemblages due to differential breakage, disassociation through natural taphonomic processes and hominin behavior relating to butchering (Lyman, 2008).

Keeping these drawbacks in consideration, the NISP serves as one of the basic units of quantification in this study. While other measures are used, the NISP is employed in most faunal analyses, and as discussed below, makes relatively few assumptions compared to other quantitative units of faunal remains.

Bone weight was also recorded for each specimen. It is another method to quantify and estimate the biomass, specifically of meat, from animal remains (Uerpmann, 1973a; Uerpmann, 1973b). As bones make up 6-9 % of body weight, weighing the fauna will be proportional to meat that was potentially available for exploitation (Gündem, 2010). Some recent measurements of weight of the entire carcass and bone weight for specimens in a reference collection of Tübingen show a greater variation from 3.5-11% (Napierala, 2012), but it is reasonable to assume that bone weight mirrors abundance of fauna and the contribution of animals to the diet.

As Lyman notes (2008), the weight method was developed to measure the biomass or edible meat. It is based on allometry, which studies the relationship of the size of a particular part of the body with the rest of the body. Therefore, the weight method is based on the allometric relationship between the bone weight and the body weight (Lyman, 2008: 94). As Barrett (Barrett, 1993) notes, it can be employed with a ‘ratio approach’. Some approaches calculate approximate biomass by employing formulas while others have mostly used the bone weight as a mean of direct inter-taxonomic comparison. While the biomasses result in absolute values and are calculated based on the presumption that complete animal carcasses were present in sites, bone weights are mostly used for relative comparisons. For both approaches, bone weight can serve as a direct or relative proxy of usable meat and their relative contribution to hominin diet.

One of the advantages is that this measure allows assessment of abundance regardless of the degree of fragmentation, unlike NISP, which has clear limitations when skeletal and dental remains are heavily or differentially fragmented across comparative units (stratigraphic unit or site) and animals. In this study, weights can be used when the faunal material is assessed for taphonomic study. The degree of fragmentation can also be evaluated by employing weight and also useful in quantifying burnt material, which is not readily quantified by NISP. Cannon (2013) explores the relationship of NISP and fragmentation as well as measures to determine the degree of fragmentation. Besides specimen size, weight can relate directly to the fragmentation rate if other variables such as diagenesis and density-mediate attrition have not had a significant impact on the specimen assemblage. It is a way to quantify zooarchaeological material in manners that are not affected by fragmentation.

There are some shortcomings. Bone weight best applies to material from recent period where the bones are not heavily affected by taphonomic processes. When the taphonomic processes and preservation of the specimens are comparable, the bone weight can be used to quantify exploitation of animals from greater time depth, but precautions must be made so that assemblages are not solely compared on bone weight. Bone weight is more often applied on assemblages from recent history, as the condition of the animal remains most likely are comparable between archaeological horizons with relatively few differences in the taphonomic processes. Diagenesis of organic remains can alter significantly among comparative cultural units, especially in Paleolithic assemblages, many of which accrue over a longer period and are subjected to varying depositional contexts and processes.

Further, the estimation of weight and body mass cannot be easily calculated, which ranges from 8.5-13 %, but has a relatively large range (Casteel, 1978). The relationship between bone weight and body weight are curvilinear, which also means the use of the relationship for predicting the contribution of animal meat may not be tenable. Animals, even those that are closely related, show different allometric scaling, so the bone-body relationship is not constant among taxa (Lyman, 2008). Simply put, larger animals have greater body weight compared to bone weight than small animals. Further, conversion of actual bone weight to biomass must be based on an assumption that the relationship is constant, although it can clearly vary over time and among individuals depending on the sex, season, and general biology that can vary within and across populations. Lyman (2008) also notes that fragmentation can affect bone weight when the material is heavily fragmented, affecting the identifiability of specimens.

In addition, the relative weight proportion of complete skeletal elements from extant animals in the reference collection was used to compare with the relative proportion of body parts in the archaeological assemblage. Such methods enable us to evaluate which body parts may be over or underrepresented in assemblages (Münzel, in press).

One can avoid or circumvent certain issues by directly employing bone weight as a measure of taxonomic abundance, but the measure can only be used on an ordinal scale. Such measures cannot function on a rational scale as the relationship of bone and body weight can vary among taxa, and we cannot assume that bone weight equates to the amount of meat exploited by humans. Further, the biomass equation is based on complete skeletons, which are not always represented in assemblages due to selective transportation or other taphonomic processes.

As with other measures, the bone weight correlates significantly with NISP. Lyman (2008) finds that the correlation between NISP and bone weight for various collections is statistically significant, suggesting that while in most scenarios, the NISP and bone weight would point to similar tendencies in relative abundances of taxa in faunal assemblages. As most analysts agree, most methods have shortfalls and the use of different measures also depends on the questions that drive the zooarchaeological research.

Alternative measures include MNE (minimum number of element), MNI (minimum number of individual) and MAU (Minimal Animal Unit). MNE is calculated based on the frequency of skeletal proportions that account for the minimum number of skeletal elements in assemblages (Lyman 2008). The unit is thus always employed with reference to body parts. As noted before, documentation of proportion and landmark (such as nutrient foramen) is fundamental to the calculation of MNE values. MNE values here do not account for the side of the element (right/left). The correlation of NISP and MNE is significant and high at 90%, which suggests that they track similar patterns of abundance (Grayson and Frey, 2004). One can also estimate the degree of fragmentation using the ratio of NISP and MNE. MAU resembles MNE, but is standardized by the number of elements that occur in a complete individual (Binford, 1978). Standardized MAU values are also calculated by dividing the MAU values with the highest MAU values for body parts.

MNI represents the minimum number of individuals in an assemblage, usually taking age and side of elements into consideration (Grayson, 1984; Lyman, 2008). It is based on treating complete individuals as a basic unit of measurement. Thus, MNI indicates the minimum number of taxa, which is a conservative estimate, whereas NISP represents the maximum number of taxa within a given assemblage. MNI became an alternative measure of identified taxa as the quantification of NISP came under scrutiny. The intention for employing MNI is to avoid the overrepresentation of specimens that are potentially affected by differential fragmentation. One benefit lies in that the counts for faunal group/aggregates remain independent (Grayson, 1984).

However, we encounter a different set of issues with MNI. One assumption underlying this measure posits that entire carcasses were deposited at sites, which does not apply for many hunting scenarios. Optimal Foraging Theory predicts that body parts with greater caloric gains will be favored over other parts when hunting occurs far from the destination (Metcalfe and Barlow, 1992; Smith and Winterhalder, 1992). Butchering and partial transportation of animal carcasses are economic decisions made by hunters to maximize the return. Ethnographic examples also document manners in which whole carcasses are disarticulated and selectively transported (Binford, 1978). Thus, MNI does not necessarily reflect the amount and the part of carcasses that were brought to the site.

MNI values further suffer from an aggregation effect. Namely, this measure is heavily affected by how the cultural or sedimentary units are defined and samples within these units are grouped. When the cultural units alter, either subsumed by other units or subdivided, MNI values needs to be reassessed, which in turn reflects how analytical categories alter the MNI values (Grayson, 1984). The MNI values increase with finer division of samples, which has been termed as an aggregation effect by Grayson (1984). Similar to MNE values, the NISP and MNI values show significant correlations (Grayson,1984). Further, since MNI values represent estimates, no numerical analyses should be undertaken (Plug and Plug, 1990).

In this study, NISP and body weight will be the principle measure of quantifying the faunal remains. When possible, MNE and MNI are also employed. Further, the NISP values are utilized to conduct some basic statistical analysis including χ^2 values and residual values as well as linear correlation of variables.

In assessing species abundance, it is relevant to study the diversity of the assemblage. Diversity is an encompassing term used often in ecology, but can point to different variables that include taxonomic richness, which is equivalent to the number of taxonomic groups represented in an assemblage, or evenness, which is a measure of how specimens are distributed across taxa (Lyman, 2008; Smith and Wilson, 1996). The evenness increases as the number of specimens across each taxon reaches an equal value. In other words, evenness becomes low when there are dominant taxa (greater proportion of a few taxa over other taxa).

The diversity of species abundance can be assessed by calculating the Shannon index of evenness and the Simpson's index (Simpson, 1949), which are both employed often in paleontological and archaeological studies (Lyman, 2008; Magurran, 2004). The Simpson's index is heavily weighted towards the dominant taxa (and thus it is abbreviated as D) and is less sensitive to taxa richness or the number of taxonomic groups (Magurran, 2004). It is calculated using the following equation:

$$D = \sum \frac{n_i(n_i - 1)}{N(N - 1)}$$

Where the n_i equates to the number of specimens of the *i*th taxon and N is the total number of specimens. Simpson's index is often expressed as the reciprocal (1/D), but Magurran (2004 and references within) also discusses the utility of 1-D or –ln(D) to interpret the values. In all variations, higher values denote greater diversity. The evenness can then be determined by dividing the reciprocal of D by the number of species (S) as shown below (Magurran, 2004).

$$E_{1/D} = \frac{1/D}{S}$$

The Shannon index of evenness, another measure of diversity, is derived differently and weighs the rare taxa more heavily (Lepofsky and Lertzman, 2005). The evenness measure is calculated using the following equation:

$$H = \frac{-\Sigma p_i \ln(p_i)}{\ln(S)}$$

where p stands for the number of the proportion of specimens found in the *i*th taxon and S for the number of taxon. Simpson's index ranges from 0 and 1 (Simpson, 1949) and is not sensitive to species richness.

Two measures should be thus compared to determine if the temporal trend or the difference among sites is consistent in both indices. As with most measures of taxon richness and diversity, these measures need to be evaluated in terms of sample size (Baxter, 2001; Lepofsky and Lertzman, 2005).

The squared Euclidean distance (SED) values were also employed to assess differences among cultural units and sites in the distribution of taxonomic groups (Grayson and Delpech, 2008; Jackson and Williams, 2004) by comparing the proportion of faunal samples. The squared Euclidean distance is a way to analyze the spatial distance in geometric studies but is often employed to evaluate similarities among pollen assemblages (Jackson and Williams 2004). It is calculated by summing the squared differences of the proportion in a taxonomic group in two sample groups.

Ageing / Sexing

The determination of age and sex is based on the biological development and growth of individuals as well as the degree of sexual dimorphism. Such reconstruction can help determine the seasonality of site, modes of animal procurement and the depositional history of the carcasses. Ageing and sexing of animal populations hinge on the preservation and recovery of certain skeletal elements. The procedure and key sources are presented briefly in this section.

First, systematic measurement of animal remains, or osteometrics, helps determine the composition of a faunal population. In addition, measurements also enable us to study size variation among species (Athen, 2007) and within animal populations over evolutionary time or geographic areas (Leney and Foley, 1999). A manual by (Driesch, 1976) Von der Driesch (1976), initially developed for studying domesticated animals, serves as a standard that provides figures and specific landmarks on bones for measurement. Other sources specific to cave bear include Athen (2007) and (Tsoukala and Grandal D'Anglade, 2002). Further, stages of tooth eruption and patterns and extent of wear serve as useful indicators of age of the animals at the time of death (Bunn and Pickering, 2010; Levine, 1982). For each taxon, different sources with ethological studies enable us to estimate the age at death. The growth of fetal bone and the epiphyseal fusion of skeletal elements are also useful in estimating age for fetuses and juveniles.

When ages are determined, specimens are categorized in the age groups of juvenile, prime adult and old adult (Stiner, 1990) to reconstruct broad mortality patterns. Specimens are juvenile from birth to the replacement of deciduous teeth by permanent teeth, followed by prime adults showing slight wear on teeth and old adults with substantial wear either through greater exposure of dentine or shortening of crown height. Triangular plots were initially employed in Stiner's work (1990) to represent percentage of age groups (Figure 4.1). In this study, the program developed by Weaver and colleagues (Weaver et al., 2011) was used to calculate the age scheme in a ternary diagram with a confidence interval (95%).

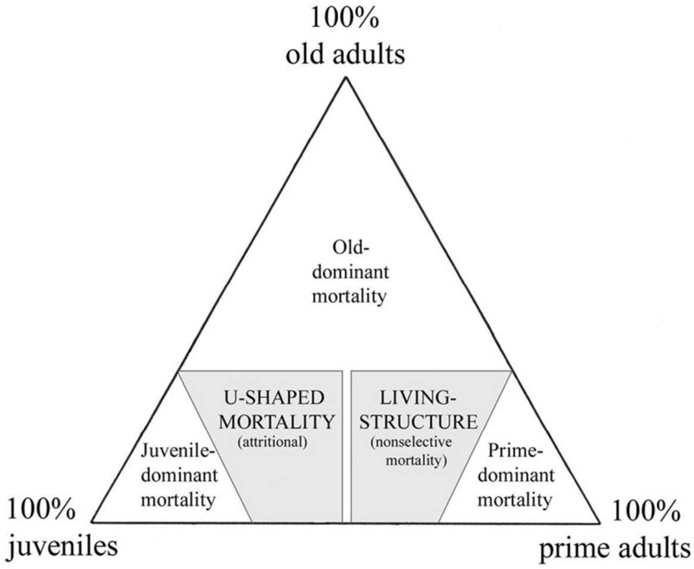


Figure 4.1 Triangular plot for age groups (Stiner, 1990, 2009)

The age groups are based on all teeth elements with age determination, NISP, as well as MNE for each tooth element. The use of MNE will better account for the number of individuals that are present and their ages; we therefore avoid exaggerating values in cases where individuals may be represented by more than one tooth element. At the same time, the sample size of an individual tooth is limited for some species and thus, teeth were also grouped to determine the broad pattern of the mortality profile. In all cases, complete or relatively complete teeth were employed for ageing the specimens.

The interpretation of mortality profiles is based upon the comparison of patterns with modern animal populations. In the ecological literature, attritional profile (U-shape) refers to populations represented by a higher proportion of juveniles and old adults while the living profile reflects animal populations with an overrepresentation of juveniles and a decreasing proportion of prime and old adults (Klein, 1984; Stiner, 1990). Stiner has also identified a third mortality pattern with prime adult dominated age profiles. This pattern appears to be consistent with the hunting behavior of hominins (with the possible exception of hyenas (Kruuk, 1972). Further, the abundance of juveniles may point to evidence of denning.

Münzel’s scheme for ageing cave bears (Table 4.1) is based on the stages of tooth development and general wear. Instead of a broad age category ‘juvenile’, fetus, infant, juvenile and subadult are separately categorized. The life history of extant bears follows that they are born in dens with infants becoming juveniles roughly after 3-4 months in spring. Juveniles are 4-10 months old while subadults, at 10-13 months, enter the second hibernation in winter. During this period, the deciduous teeth of subadults are replaced by permanent teeth with roots that gradually close by adulthood. Adults refer to individuals with worn teeth between 1-3 years of age, while individuals become old adults with heavily worn teeth.

Code: Age group	**Age and season**
100: fetus - infantile	1. Winter
200: infantile	< 3 mon old, 1. Winter
300: infantile –juvenile	~3-4 mon old, 1. Winter
400: juvenile	4-10 mon old, early summer- summer
500: juvenile- subadult	4-10 mon old, early summer- summer
600: subadult	10-13 mon old, 2nd Winter
700: subadult –adult	10-13 mon old, 2nd Winter
800: adult	1-3 yrs old
900: senile	> 3 yrs old

Table 4.2 Age group and corresponding ages by S. Münzel

Further, Stiner (1998) systematically categorized the degree of wear on cave bear teeth. The availability of plants consumed by cave bears in various environments and biomes most likely led to diverse patterns of wear. Thus, the use wear of bear appears slightly different from what is illustrated in Stiner (Münzel, pers. comm.) where the teeth surfaces around the cusps wear down and expose dentine first before the cusps.

The degree of tooth wear can be systematically measured for ungulate teeth to determine age (Grant, 1982a, b). For horses, Levine's method (1982) is employed for premolars and molars. Incisors are used to determine ages of live horses today (Habermehl, 1975). Guadelli (1998) points out the inconsistency in estimating the age for older individuals, but here, we are interested in the general age distribution and the ratio of juveniles, prime adults and old individuals. Isolated cheek teeth are at times hard to determine to one tooth element. In this case, they are identified to P3/P4 or M1/M2. The crown height is measured between where the root begins and the center of the occlusal surface. With paleontological assemblages, individuals are categorized as juveniles (0-4 years old), prime adults (5-12 years old), and then old adults (13+ years old). Further, identification of horse canines indicates male individuals.

The age determination of woolly rhinoceros is based on dentition of modern *Diceros bicornis* (Black Rhinoceros) and extinct *Dicerorhinus hemitoechus* (European Soft Nose Rhinoceros) mostly using the development of tooth and wear pattern (Goddard, 1970; Louguet, 2006). When the teeth are not present in a row, molars and premolars are at times difficult to distinguish, and therefore are put in broader element categories. The age groups are juveniles (0-11 years old), adults (12-19 years old) and old adults (20+ years old).

For reindeer, the eruption and wear of mandibular teeth have been studied by Miller (1972, 1974) on modern caribou populations in North America. For juveniles, precise ages can be determined with the exception of M3, which can vary up to a year based on eruption sequence (Enloe and Turner, 2006). Juveniles (0-4 years old), adults (5-8 years old) and old (9+ years old) are the major age groups.

Carnivores have low cusped dentition, with enamel wearing off over time. While variation in wear could exist among populations, the exposure of dentine becomes larger with age. For major carnivores that potentially occur in archaeological sites, wolfs and hyenas, Stiner's work (1994) schematized the stages of wear that correlate to general age groups. Many carnivore species grow permanent teeth earlier than ungulates after few months or up to a year.

The sex ratio is also informative of the demographic pattern in an animal population. Certain skeletal elements only occur among one sex, including baculum of carnivores and bears or horse canines for males. However, other methods need to augment these finds, as this factor alone will not provide a relative proportion of each sex in an assemblage. The assignation of sex is determined based on measurements of complete elements from animals that exhibit sexual dimorphism. Scatterplots with measurements of complete elements (i.e., length and breadth) can exhibit clusters of values that potentially represent male and female populations (Berger et al., 2001). Among most mammalian animals, males exhibit greater size and robusticity. However, precautions must be taken as size varies with age and sex. Determination of sex must be considered with data on age structure.

Sexual dimorphism has been long noticed in cave bears, and Kurtén (1969) analyzed the mortality profile of cave bear assemblages based on the age and sex. The degree of sexual dimorphism is comparable to that of modern bears such as brown bear (Reisinger and Hohenegger, 1998). Stiner and colleagues used the size of canine in order to determine the sex of cave bear, following (Gordon and Morejohn, 1975) to obtain simple measurements of the lower teeth applied on the North American black bears. Their method was modified by Stiner et al. (1998) who measured the teeth rather than alveolar length of the mandibular canine, which in comparison preserves poorly in depositional contexts.

Antlers are also an indication of male cervids. Reindeer are the only exception as both males and females bear antler and shed their antlers during different seasons: spring for females and late fall for males. The measurement of the antler base can help determine the sex and/or the age of the animal (Høymork and Reimers, 2010). Juvenile males and females overlap, but antlers from one year olds can be identified by the lack of tines.

Seasonality

With age determination, we can also estimate the season in which the animals were killed based on our current understanding of birthing season. Fetus and juvenile remains help constrain season in which the animals became incorporated in the assemblage. Epiphyseal fusion eruption stage and pattern also derive from modern equivalents of the Pleistocene mammals. Antlers attached to skull fragments also help us determine the season in which the animal died if the sex of the individual can be identified (for reindeer specifically).

Taphonomy

Physical and chemical mechanisms that alter deposited organic remains vary. Taphonomic analysis became a regular part of faunal inventory beginning in the 1980s with the work of Brain (1981) and (Binford, 1981). Archaeologists began to explore changes aside from anthropogenic modification that alter animal carcasses and to critically assess the premise that faunal remains associated with stone artifacts are equated to human causality. Taphonomic studies, however, face issues of equifinality, and attributing causes of modification at times seems questionable. Thus, several lines of evidence are considered in drawing conclusions on the depositional history of the faunal remains and human involvement in their accumulation.

Weathering is "the process by which the original microscopic organic and inorganic components of bone are separated from each other and destroyed by physical and chemical agents operating on the bone in situ, either on the surface or within the soil zone " (Behrensmeyer 1978: 153) or simply put, weathering is the process of degradation and consequent loss of integrity (O'Connor, 2000). In most assemblages, weathering affects the overall preservation of animal remains and serves as one way of assessing the degree of bone preservation in deposits. At times, it is often used to evaluate the time the specimens were exposed before burial.

Weathering results from the exposure of specimens to sunlight, wind, as well as to trampling by animals; it can also result from chemical weathering in sedimentary matrices. The different stages of weathering range from partial longitudinal cracking along the bone structure to flaking and complete deterioration. These in turn reflect the preservation of specimens (Behrensmeyer, 1978). Importantly, weathering can also obscure prior taphonomic processes particularly on bone surfaces. In this analysis, Behrensmeyer’s stage of weathering (1978) has been recorded for each bone specimen, excluding teeth, antler and ivory. Some bones show micro-flakage (Figure 4.2), which shows another form of weathering that may not occur so frequently in open-air contexts, and which therefore was used as the standard for Behrensmeyer’s study.

Figure 4.2 Specimen with heavy weathering and flaking

Density mediated attrition

It has been long acknowledged that bone elements and segments preserve differently. In his seminal work, (Lyman, 1984) quantified the differential bone mineral density. Other researchers, informed by his approach, aimed at understanding attritional processes and preservation bias (Lam et al., 1999; Lam and Pearson, 2005). The bone density of cancellous bones with a relatively thin bone wall and spongy bones differ from cortical bones at 1:2 or 1:3 (Lyman, 1984; Stiner, 2004b). All conditions being equal, the pressure of the sediment and other processes, such as trampling or chemical leaching, adversely affect cancellous bones due to its porosity and microstructure compared to cortical bones. Further, skulls are also prone to fragmentation as it takes much more sediment to bury crania, which are composed of cavities and thin bone plates.

Ravaging on animal remains by carnivores also has a similar effect. Carnivores prefer to feed directly on cancellous bones to extract fat while cortical bones are not heavily modified as they themselves have no nutritional value across many carnivore species in different environmental contexts (Blumenschine, 1988; Bunn and Kroll, 1986). Cleghorn and Marean (2007) refer to this type of destruction as nutritive attrition, which should be accounted for in the interpretation of faunal assemblages.

Assessing the destruction of fragile elements is one of many non-anthropogenic processes that affect the nature of faunal assemblages. These studies assess the degree to which density mediated destruction overrides observational patterns of skeletal abundances (Cleghorn and Marean, 2007; Lam et al., 1999; Lyman, 2008). In this study, the frequency of diaphysis and epiphysis is used as a coarser analytical method for evaluating the effect of density mediated attrition on the fauna, particularly regarding cave bear.

Anthropogenic modifications

Understanding patterns of alteration of animal remains by hominins is one of the fundamental objectives for many zooarchaeological researchers. Common anthropogenic modification observed in Paleolithic assemblages includes cutmarks, percussion marks, burning and artifact production.

Cutmarks are one of the most common anthropogenic modifications, and serve as direct evidence of exploitation of animals for dietary and non-dietary purposes (Abe, 2005; Binford, 1981). Although not universal (Costamagno and David, 2009), cutmarks on certain skeletal elements roughly correspond to particular butchering activity. For instance, cutmarks on articulating joints (epiphyses of long bones) signify disarticulation, meaty parts of limb bones (shaft with muscle attachment) indicate defleshing/filleting, and skin-covered bone surfaces and extremities point to skinning (Binford, 1981; Bunn and Kroll, 1986).

The morphology of cutmarks is also well documented with experiments (Blumenschine, 1988; Domínguez-Rodrigo and Yravedra, 2009; Fisher, 1995). Simple flakes often produce V-shaped cross sections when used for butchering on bone surfaces while the retouched flakes can produce open U-shaped cross sections. When bone surfaces are well preserved, straight, internal microstriations at the base and the wall within the striae, with flaking of the edges, are distinguishing traits of trampling marks. Most microstriations resulting from cutmarks do not preserve from archaeological remains, but the shape of the groove and the trajectory help distinguish trampling marks from cutmarks (Dominguez-Rodrigo et al., 2009).

Cutmarks can leave either deep incisions or superficial scratch marks on the surface of bones, which are harder to identify as other modifications can imitate such marks. Cutmarks are not easy to quantify, as frequency of cutmarks does not necessarily correlate with the level of intensity in butchering activities (Egeland, 2003). Here, the placement and orientation of cutmarks are noted.

Other manifestations of butchering activities on bones include percussion marks that leave impact fractures, notches, cones as well as flakes resulting from impact fractures, not unlike lithics (Blumenschine and Selvaggio, 1988), and chop marks with broad, wedge-shaped depressions from using an axe or cleaver (Fisher, 1995). They result from blows of hammer-like tools onto the bones either for the use of bones for raw material or to extract marrow from the limb bones (ibid.). Percussion can also result in green or fresh fractures with oblique and smooth break surfaces as well as helical fracture outlines (Niven, 2006). Some have also suggested possible features of human gnawing on bones, but no clear diagnostic features unique to humans have been evaluated systematically and defined (Saladié et al., 2013).

Burning is also a common modification of bones, which were cooked or served as a fuel source (Costamagno et al., 2005; Théry-Parisot et al., 2005; Villa et al., 2002). Alternatively, combustion features could also result in unintentional burning of faunal remains (Stiner et al., 1995). Exposure to varying temperatures can be put on a scale from carbonized (lower temperatures) to calcined (higher temperatures). Burnt faunal materials occur relatively frequently in Paleolithic habitation sites, but the criteria for identifying burned faunal remains are not standardized (Shahack-Gross et al., 1997). In these deposits, manganese staining, when observed, appears dotted on surfaces of bones and dentins of teeth (for instance, seen in figure 4.2). Burned material was identified in most cases through complete carbonization and calcination of fragmented remains. Some small fragments with lustrous texture were not considered as burning as the color resulted from staining.

Lastly, organic artifacts range from functional tools to personal ornaments that served non-economical purposes. Artifacts, as the end result, usually undergo processes of cutting, rounding, polishing, boring and other forms of mechanical alteration intended by hominins. Retouchers are common bone tools used for retouching lithics in the Middle Paleolithic, and percussion pits are diagnostic features of the use of bones as retouchers (Chase, 1990). They are, however, identified through unintentional modification of the bone for manufacturing other tool artifacts, which means they slightly differ from artifacts that were purposely altered to achieve certain forms by the makers. At some sites, debitage, resulting from the production of artifacts, has been recovered from the working of organic material such as ivory fragments. At our site, organic tools were recovered but were mainly studied by other researchers (Hahn et al., 1989; Wolf, 2013).

Trampling

Physical alterations caused by natural processes can mimic anthropogenic modification on animal remains. Trampling by large-bodied animals causes pressure on bones that leads to abrasion, rounding and fragmentation. Actualistic studies and experiments show that trampling results in linear and curved striations, which resemble cutmarks, dry breakage, pitting, polishing and rounding of edges (Behrensmeyer et al., 1986; Domínguez-Rodrigo et al., 2010; Gaudzinski-Windheuser et al., 2010).

Scratch marks occur as the bones come in contact with coarse sediment and can be confused with signatures of butchering and processing by hominins (Behrensmeyer et al., 1986). The cross section of striation is generally characterized by rounded U shapes with broader bases and microstriations that are spaced unevenly in contrast to V shapes in certain diagnostic cutmarks (see below). The exception to this distinction is the use of retouched tools, which could create broad bases and more U-shaped grooves (Dominguez-Rodrigo et al., 2009). Further, the curved trajectory of striae also signifies trampling action. Criteria for cutmark identification still remain at times questionable, especially with material of greater time depth, leading to discussion on the degree of human involvement and to attributing humans as causative agents. The contestation over the purported butchering marks from the Plio-Pleistocene period in Africa exemplifies the difficulty in distinguishing cutmarks from trampling marks (Domínguez-Rodrigo et al., 2010; McPherron et al., 2010).

The anatomical position and orientation of striations need to be observed in conjunction with the morphology of marks (Bunn, 1991; Domínguez-Rodrigo et al., 2010). Intense trampling action results in random distribution and orientation of striations, although parallel marks do not preclude the possibility of trampling (Behrensmeyer et al., 1986; Dominguez-Rodrigo et al., 2010). Further, (Stiner et al., 2011) identified a lack of directionality in the orientation of cutmarks on fauna that are dated to the Lower Paleolithic. Although the mechanism behind the lack of orientation in the direction of butchering marks remains a point of discussion, greater consistency in the orientation and occurrence of parallel cutmarks characterize the general trend in the butchering process found in the Middle and Upper Paleolithic.

Intensive trampling can also result in fragmentation through pressure as well as rounding and polishing through the same mechanism of sediment abrasion. The fragmentation will result in dry breakage patterns that show relatively smooth edges and in addition obscure morphology of break patterns that are fresh. Cave bears often are known to clear bone remains to make room for their den, resulting in *charriage-a-sec* (Koby, 1943). Thus, it is likely that many of the trampling marks could be attributed to denning animals such as cave bears at the site.

Carnivore modifications

In attempts to study effects of hominins on animal remains, the study of non-anthropogenic modifications has also developed. Carnivore modification and its effect on animal remains have been intensively studied in taphonomy, leading researchers to discuss the origin and cause of faunal accumulations in the Plio-Pleistocene from hominin sites (Binford, 1981; Bunn et al., 1986; Capaldo, 1997).

Carnivore modification manifests in a range of mechanical alteration of bones (Binford, 1981). Gnawing is what we typically refer to when carnivores interact with carcasses. Typical damage is often seen in forms of toothmark imprints on the bones as punctures or pits. Dragging teeth on bone surfaces results in broad linear grooves referred to as scores. Further, gnawed edges often show crenulated forms manifesting as the negative of the toothmarks, or rounding and polishing occur as a result from salivary acid. Gnawing marks could at time mimic fracture patterns that could result from anthropogenic impact pattern in bone flake removal (Villa and Bartram, 1996).

Mid-size carnivores, namely hyenas and wolves, with powerful jaws and gnawing power modify bones through regurgitation or digestion (Haynes, 1983; Haynes, 2002; Stiner, 2010). Regurgitation by hyenas results in hair and bone chips that are altered in its morphology of the bone. Features including fine striations on the surface, thinning of edges, polishing and acid etching occur commonly on specimens that went through digestion (Figure 4.3). Some note that digestive corrosion could lead to formation of pseudo-tools (Villa and D'Errico, 2001). Digestion of bones can lead to the presence of coprolites, a bone matrix usually in chalky forms, rounded for hyenas and elongated in the form of feces for wolves (Brugal, 2010; Horwitz and Goldberg, 1989; Larkin et al., 2000).

Figure 4.3 Specimens with digestive corrosion

Some have attempted to identify carnivores that modified archaeofaunal assemblages (Haynes, 1983). Selvaggio (1994) studied the sizes and shapes of tooth marks from extant carnivores as well as impressions of teeth from fossils in relation to the density of the bones (Selvaggio and Wilder, 2001). The variables accounted for include length, breadth and circularity of the pits. However, many studies indicate equifinality that lead to similar tooth marks from different taxa of carnivores and the condition of the carnivores (Dominguez-Rodrigo and Piqueras, 2003). Domínguez-Rodrigo and Pickering (2010) argue that higher occurrences of scoring often manifest from ravaging of large fields.

Other modifications

There are a few other taphonomic agents that occur in fauna (Lyman, 1994). Rodent gnawing is usually characterized by edges of bones smoothed out by parallel grooves, mirroring the form of the rodent incisors. Some specimens also exhibit evidence of root etching, which manifests as sinuous marks on the surface of bones due to acid produced from plants and other fungi, which can also produce localized etching on bones. In some depositional contexts, bones show alterations due to rounding or acid etching through natural mechanisms such as water. Furthermore, bones go through the process of fossilization whereby the chemical composition of bones is gradually replaced by mineral.

Summary

The faunal community in the Swabian Jura during the Pleistocene represents a characteristic environment with steppe-tundra and some woodlands. The abundance of each taxon at Hohlenstein-Stadel will be further discussed in the next chapter. The section on zooarchaeological methods touches on matters of identification to taxa and skeletal element, quantification, taphonomy and other relevant information. The methods, especially taphonomic analysis, will help assess the extent to which humans and other animals contributed to the accumulation of animals into the cave as well as help extract signals of hominin behaviors from the faunal assemblage.

5 Results from Hohlenstein-Stadel

The result section of the faunal material from Hohlenstein-Stadel consists of a reprise of Gamble's work in 1978, which focused on taxonomic identification, skeletal representation and morality profiles; the reanalysis of the material particularly from the excavation of 1939; the data from recent excavations with samples recovered in 2009-2011. Despite differences in the analysts, recovery method and the nature of the sample, the general tendency in these faunal assemblages remains consistent with some few notable differences. The results of faunal analysis indicate that animal remains were not brought into the cave by human activities alone and other predators actively used the site of Hohlenstein-Stadel. The direct evidence of human predation is not clearly documented at the site due to preservational bias and other taphonomic factors that affected the remains of prey animals.

Previous work on the fauna

Wetzel's report provides a list of animals present at Hohlenstein-Stadel including mammoth, woolly rhinoceros, hyena, cave bear, horse, aurochs/bison, red deer and giant deer (Wetzel, 1961). He noted the diverse array of animals representing the glacial period, animals which were crucial in understanding the age of the site and in reconstructing the general landscape of the past. However, his work did not involve quantitative evaluation of the material but instead noted the presence of animal taxa, a common approach in the paleontological and archaeological literature in 1970's.

The majority of the collection from Wetzel's excavations of Hohlenstein-Stadel was later studied by Clive Gamble (1979, 1999). His work primarily focused on understanding the regional settlement system and adaptation in the Paleolithic by considering the ecological contexts such as the environments, faunal communities and the relationship among prey and predators (Gamble, 1979). His interest lies in human adaptation to the environment through economic activities. Gamble reconstructs hunting strategies based on a different scale of analysis, from the site of Hohlenstein-Stadel to Central Europe. The main objective was to examine the “comparative structure for Paleolithic hunting strategies” (Gamble, 1979: 35), which were not solely based on understanding species abundance and diversity. The analysis was conducted in the *Prähistorische Sammlung* in Ulm in 1974. In total, 10,470 remains were identified to species while 40,202 specimens were not unidentifiable or included some microfauna that are not considered in this study.

Gamble’s data on the assemblages of Hohlenstein-Stadel consist of taxonomic identification, body parts and ages of animals. While Gamble did not undertake extensive taphonomic analysis of individual specimens, he considered the overall taphonomic process and recovery of animal remains to determine the agent responsible for the accumulation of the assemblage. For instance, the ratio of cranial and post-cranial elements and the size of the fragmented specimens among major taxonomic groups indicated consistency in the degree of destruction and preservation among animal species (1979). Most large carnivores and herbivores are better represented by teeth, while post-cranial material went through considerable modification and loss. He attributes this pattern to differential butchering and transportation of body parts.

Gamble (1979) notes that the young bear remains are accounted for by the use of the cave as a den and hibernation site. The age scheme based on tooth eruption wear shows that the carnivores are predominantly represented by adult specimens with little deciduous teeth. In contrast, there is a greater variation in the age groups of herbivores. Mammoths and woolly rhinoceros are better represented by juveniles whereas the horse and reindeer adults make up a greater proportion (1979).

In all, Gamble (1979) interprets the assemblage as a result of selective selection of animals for exploitation by hominins. Gamble notes that “winter mortality of the bear, and possibly some carnivore bone collecting activity have combined with human agency to form the deposit” (1979:43), but the general pattern points to humans as the major agent for the animal accumulation with “a consistency through time in the processing of the prey population” (1979:43).

Based on the faunal composition, Gamble correlates the cultural layers with climatic phases that best fit with the expected environment of that period. He concludes that the Black/Brown Mousterian (A) levels consist of a woodland faunal community such as red deer, giant deer, and beaver and thus can be placed at the end of the last Interglacial (MIS 5e) whereas the Red Mousterian (B) belongs to the period of the Brorup Interstadial dating to ~45 ka with a greater element of tundra-steppe fauna, dominated by megafauna, large bovids and hyenas. The composition of the final period (C) is represented by fauna that are relatively close to the previous phase (B), but direct dating of this layer indicates middle to the late Würm. The layers are characterized by the abundance of wolf and reindeer (Gamble, 1979).

During the earliest phase in the Black Mousterian, mobility and aggregation potentials of Neanderthals were low (Gamble, 1979). This pattern contrasts with the Red Middle Paleolithic, which is characterized by a focus on megafauna with higher mobility and known for aggregation. The choice of prey hunting creates a focus on smaller herbivores during the Aurignacian period, although the prey still represents animals with high mobility on a seasonal basis. Gamble (1979) also notes that hyenas are associated with larger herbivores, such as horses and bovids, and wolves are associated with reindeer, red deer and saiga antelope. In addition, Gamble interprets the incorporation of birds and hares in the diet during the Magdalenian in the framework of foraging models, noting that the density of settlements and a changing climate account for the increase in small-sized game.

Gamble (1979) further considers the settlement pattern in the region by studying the distribution of sites, which are concentrated on the southern part of the Swabian Jura, or Flachenalb, which is likely attributed to the density of resources. Humans occupied the Swabian Jura on a seasonal basis, particularly during summer when larger migrating herds exploited the abundance of forage for herbivores. There are some indications, although not a robust signal, that some of the hunting occurred during spring, summer or winter occupations, supported by a number of cast reindeer antlers (Gamble 1979).

Revisiting the material, Gamble (1999) still maintains that the assemblage tracks hominin hunting and butchering activities in the cave, when the cave bears are excluded from consideration. Additional data on the anatomical representation and age data were provided. Gamble argues that the relative NISP frequencies of carnivore and herbivore are a good measure for distinguishing faunal assemblages that are either paleontological (reflecting carnivore accumulation or other natural process) or archaeological in nature. He also observes that horses and hyenas are overrepresented by teeth compared to taxa. Evidence suggests that humans contributed less to the assemblage as Gamble has previously interpreted. Gamble (1999) posits that the site was mainly a living area shared by non-hominin predators and hominins, and carnivores influenced the deposits of different prey species at the site.

During the Red and Upper Middle Paleolithic, Gamble reconstructs the age structure of herbivores and carnivores based on %NISP on teeth. Carnivores are mostly dominated by adults and very few specimens of juveniles, contradicting the hypothesis that the site was used as a carnivore den. On the other hand, the age groups of the herbivores are more evenly represented in the assemblage. The rhinoceros consists of an equal proportion of young, adult and senile adults while adults mostly dominate the horse population. Reindeer are represented both by juveniles and adults. The rhinoceros and reindeer broadly fall under the attritional profile with a greater presence of older individuals and juveniles, while the horse represents a living population, reflecting non-selective predation.

Gamble concludes the following: carnivores and herbivores are differentially represented based on anatomical parts and NISP frequencies. The carnivores appear to have access to all the caves in the Swabian Jura as opposed to caves in Latium (Stiner, 1994) where the occupation of caves by hominins and animals did not overlap substantially.

Sampling

The material from the excavations of 1939 and 2009-2011 will be first evaluated separately, and the summation of the two datasets is assessed. For comparability, the material from the Middle Paleolithic (MP) is subsumed in two categories: one is the Red Middle Paleolithic layer (MP R), based on Wetzel's designation 'Red Mousterian', the other is the Upper Middle Paleolithic (MP U), which occurs between the MP R and the Aurignacian layer. This designation of the MP layers is a rough correlation of the supposed depth at which the material was excavated in 1939 and the stratigraphic profile produced by Völzing. The material from modern excavations was also grouped based on the Völzing's documentation of the Upper Middle Paleolithic and Red Middle Paleolithic. Further, fauna from Aurignacian/Magdalenian were grouped with Aurignacian, with an assumption that the most of the material represent fauna from the Aurignacian layer. However, it should be noted that some specimens may derive from disturbed context.

Total finds of 9,606 animal remains from the excavation in 1939 were considered in the analysis. Gamble's sample size is larger for several reasons. One, he undertook additional analysis from excavations of 1937-8 and the early Middle Paleolithic that was uncovered in the late 1950s and early 1960s. The stratigraphic assignment of Wetzel after WWII was solely based on geological layers and differed from the method of 1930. Further, this analysis did not include material with questionable *Hieb* assignment. No systematic refitting was conducted, but few instances of refits show that there was mixing or misplacement of animal remains relating to their original spatial context, with an example of ivory fragments separated over 80 cm differences being refitted. The lack of both labels on each specimen and inscriptions of each box with specimens that were transferred from cigar boxes in which they were originally placed could have led to mixing and misplacement of specimens.

Other material from the upper spit levels of 1-3 also reveals considerable mixing of material dating either to the Gravettian, Magdalenian, Mesolithic and Neolithic. Also, the remains could not be securely assigned to the cultural layers from which they belong. This has been established due to differential preservation and coloration of skeletal remains as well as identification of cave bear remains that became extinct by 23.5 ka in the region. Therefore, a clear disturbance and unclear stratigraphic assignment have led to mixing of organic remains in the earlier spits, which roughly equates to 60 cm of sediment deposits. In the end, the method of excavation and sampling made it reasonable to focus particularly on the material of late Middle Paleolithic to the Aurignacian period. This also fits the general research interest of the region that largely revolves around the transition from the late Middle Paleolithic to the early Upper Paleolithic.

The assemblage of 1939 was excavated from 2-15 spits from a locality of 12-19 m (only ivory fragments were quantified from 20 m). Intervals of ~20 cm define each spit, and the excavation reached roughly 2.6 m in most areas and 2.8-3 m in some areas. Each spit corresponding to a cultural layer are grouped together.

From recent excavation, a total of 6,658 specimens were included in the analysis. The sample originates from the excavation seasons of 2009-2011 and derives from several intact layers directly dated to 40 -50 ka and older layers that remain undated. The material was either recovered *in situ* at the site and through 0.2 mm waterscreening and sorting. The assemblage derives from roughly 6 m^2 of excavated area, which corresponds to a 19-20 m locality towards the rear end of the cave. Intact deposits lie to the south and remain untouched for future investigation. With some exceptions, specimens larger than 2 cm and other identifiable fragments were considered in the analysis. The sample consists of recovered large mammalian bone, tooth, antler and ivory specimens. Few avian fauna were sorted out by the author and analyzed to taxon by P. Krönneck. The microfauna will later be analyzed by R. Ziegler.

To better understand the dietary choices of humans and to distinguish this pattern from other uses for animal remains, tusks and antlers are separated and are not included in the NISP and weight. As will be described below, antlers and tusks may have served as raw material and may not have resulted from the transport of mammoth or cervid remains into the cave. The antlers and tusks are thus evaluated independently from species abundance.

Species abundance

Results from the excavation of 1939

A total of 9,606 specimens, weighing 103,736.8 g, were studied from the collection of the 1939 excavation at Hohlenstein-Stadel (Table 5.1 and 5.2). The largest sample size in terms of number of specimens (excluding antler and ivory fragments) derives from the upper Middle Paleolithic (MP U) (N = 4576), followed by the Aurignacian (A) (N=3258), Red Middle Paleolithic (MP R) (N=1255) and Aurignacian/Magdalenian (A/MAG) (N=517).

Taxon/Body Size	**MP R**				**MP U**			
	NISP	NISP%	WISP	WISP%	NISP	NISP%	WISP	WISP%
hare	0	0.0	0	0.0	5	0.1	16.4	0.0
Eurasian beaver	0	0.0	0	0.0	0	0.0	0	0.0
wolf	12	1.0	173.5	1.1	31	0.7	337.4	0.8
red fox	0	0.0	0	0.0	1	0.0	8.9	0.0
polar fox	0	0.0	0	0.0	0	0.0	0	0.0
fox	2	0.2	5.3	0.0	10	0.2	26.5	0.1
cave bear	205	17.0	3443.8	21.1	708	15.9	10474.6	25.6
brown bear	0	0.0	0	0.0	3	0.1	14.1	0.0
bear	80	6.6	922	5.6	218	4.9	1561.8	3.8
cave lion,	6	0.5	321.7	2.0	3	0.1	35.4	0.1
Eurasian lynx	0	0.0	0	0.0	1	0.0	10.6	0.0
marten	0	0.0	0	0.0	1	0.0	1.2	0.0
hyena	25	2.1	332.5	2.0	75	1.7	904.6	2.2
mammoth	27	2.2	1693.4	10.4	82	1.8	3259	8.0
(tusk)	22		392.9		17		39.3	
horse	56	4.6	1571.7	9.6	193	4.3	5497.6	13.4
woolly rhinoceros	14	1.2	1478.3	9.1	48	1.1	2055.7	5.0
red deer	1	0.1	19.8	0.1	1	0.0	11.1	0.0
reindeer	7	0.6	76.9	0.5	31	0.7	428.6	1.0
(antler)	8		1267.1		34		1391.4	
aurochs/bison	7	0.6	451.6	2.8	4	0.1	497.1	1.2
rodent	0	0.0	0	0.0	2	0.0	0.5	0.0
carnivore small	1	0.1	0.8	0.0	2	0.0	0.8	0.0
carnivore medium	33	2.7	136.8	0.8	62	1.4	190.2	0.5
carnivore large	38	3.2	354.8	2.2	106	2.4	777.5	1.9
cervids	4	0.3	37.3	0.2	4	0.1	32.4	0.1
(antler)	19		210.5		66		418.8	
bovids	0	0.0	0	0.0	2	0.0	3.2	0.0
perissodactyl	0	0.0	0	0.0	0	0.0	0	0.0
artiodactyl	0	0.0	0	0.0	0	0.0	0	0.0
ungulate small	1	0.1	2.2	0.0	22	0.5	87.5	0.2
ungulate medium	5	0.4	33.8	0.2	15	0.3	97	0.2
ungulate large	13	1.1	628.6	3.9	33	0.7	473	1.2
ungulate	4	0.3	12.7	0.1	20	0.4	57.4	0.1
Body size 1	0	0.0	0	0.0	6	0.1	3.2	0.0
Body size 2	32	2.7	41.4	0.3	90	2.0	85.1	0.2
Body size 3	286	23.7	958.7	5.9	1240	27.8	3062.7	7.5
Body size 4	335	27.8	2969.7	18.2	1360	30.5	10333.2	25.2
Body size 5	7	0.6	642.9	3.9	14	0.3	410.7	1.0
mammal	5	0.4	9.4	0.1	56	1.3	202.1	0.5
bird	0	0.0	0	0.0	10	0.2	8.4	0.0
fish	0	0.0	0	0.0	0	0.0	0	0.0
Total	1255	100	18190.1	100	4576	100	42815	100
Total without antler/tusk	1206		16319.6		4459		40965.5	

Table 5.1 NISP, NISP%, WISP (g), WISP% of taxa and body size from MP R, and MP U layers from the excavation of 1939.

Taxon/Body Size	**A**				**A/MAG**			
	NISP	NISP%	WISP	WISP%	NISP	NISP%	WISP	WISP%
hare	10	0.3	20.6	0.1	2	0.4	3.1	0.0
Eurasian beaver	0	0.0	0.0	0.0	1	0.2	1.4	0.0
wolf	42	1.4	486.5	1.5	6	1.2	151.8	2.4
red fox	0	0.0	0.0	0.0	0	0.0	0	0.0
polar fox	2	0.1	6.4	0.0	1	0.2	0.4	0.0
fox	6	0.2	17.5	0.1	7	1.4	19.4	0.3
cave bear	642	21.2	16034.6	48.5	97	20.1	3999.1	63.1
brown bear	2	0.1	13.8	0.0	0	0.0	0	0.0
bear	281	9.3	2594.9	7.8	49	10.1	360.6	5.7
cave lion,	9	0.3	289.8	0.9	3	0.6	209.9	3.3
Eurasian lynx	0	0.0	0.0	0.0	0	0.0	0	0.0
marten	0	0.0	0.0	0.0	0	0.0	0	0.0
hyena	3	0.1	53.6	0.2	0	0.0	0	0.0
mammoth	3	0.1	369.5	1.1	1	0.2	101.3	1.6
(tusk)	20		54.4		0		0	
horse	37	1.2	1240.9	3.8	5	1.0	135.4	2.1
woolly rhinoceros	11	0.4	1956.4	5.9	0	0.0	0	0.0
red deer	0	0.0	0.0	0.0	0	0.0	0	0.0
reindeer	27	0.9	430	1.3	6	1.2	119.3	1.9
(antler)	79		2095.9		9		318.3	
aurochs/bison	1	0.0	44.2	0.1	0	0.0	0	0.0
rodent	1	0.0	0.2	0.0	0	0.0	0	0.0
carnivore small	2	0.1	1.2	0.0	1	0.2	0.2	0.0
carnivore medium	96	3.2	435.2	1.3	26	5.4	129.2	2.0
carnivore large	107	3.5	838.7	2.5	26	5.4	159.7	2.5
cervids	10	0.3	72.0	0.2	1	0.2	3.5	0.1
(antler)	124		706.9		25		134.3	
bovids	0	0.0	0.0	0.0	1	0.2	1.1	0.0
perissodactyl	1	0.0	30.2	0.1	0	0.0	0	0.0
artiodactyl	1	0.0	1.2	0.0	0	0.0	0	0.0
ungulate small	11	0.4	64.8	0.2	0	0.0	0	0.0
ungulate medium	12	0.4	48.9	0.1	8	1.7	50.9	0.8
ungulate large	25	0.8	367.3	1.1	3	0.6	108	1.7
ungulate	9	0.3	30.8	0.1	0	0.0	0	0.0
Body size 1	2	0.1	0.6	0.0	0	0.0	0	0.0
Body size 2	59	1.9	89.1	0.3	6	1.2	3.8	0.1
Body size 3	795	26.2	2075.8	6.3	127	26.3	243.1	3.8
Body size 4	781	25.7	5124.0	15.5	100	20.7	533	8.4
Body size 5	10	0.3	292.7	0.9	0	0.0	0	0.0
mammal	31	1.0	43.4	0.1	3	0.6	5.3	0.1
bird	4	0.1	4.2	0.0	3	0.6	2.9	0.0
fish	2	0.1	0.5	0.0	0	0.0	0	0.0
Total	3258	100	35936.7	100	517	100	6795	100
Total without antler/tusk	3035		33079.46		483		6342.4	

Table 5.2 NISP, NISP%, WISP (g), WISP% of taxa and body size from the Magdalenian/Aurignacian and Aurignacian from the excavation of 1939.

Roughly 35.5 % of the material was identified to the level of genus and species while the rest (64.5%) was assigned to family, order and body size. Identifiability does not fluctuate greatly between cultural layers. The percentages of identifiable specimens were most frequent in the Red Middle Paleolithic assemblage (37.6%), followed by Aurignacian/Magdalenian (36.2%), Aurignacian (36%) and upper Middle Paleolithic (32%). Unidentifiable specimens classified to body size show that the majority could be identified as body 3 and 4, and are the two most common categories that the specimens are assigned to across all the cultural layers. This pattern reflects the abundance of identified animals of body size 3 and 4.

The sample size based on weight mirrors the NISP with the MP U (42,815 g) being the largest followed by the Aurignacian (35,936.7 g), MP R (18190.1 g) and A/MAG (6,795 g). Roughly half of the entire specimens ranging from 46.9-56% weighed under 5 g with only less than 4.5 % of the assemblage represented by specimens 50 g or heavier (Figure 5.1). The identifiability of specimens increases with an average of 70% in terms of weight (WISP). The A/MAG layer produced a larger number of identifiable material based on weight (79.8%) followed by Aurignacian (71.5%), MP R (66.8%) and MP U (62.1%).

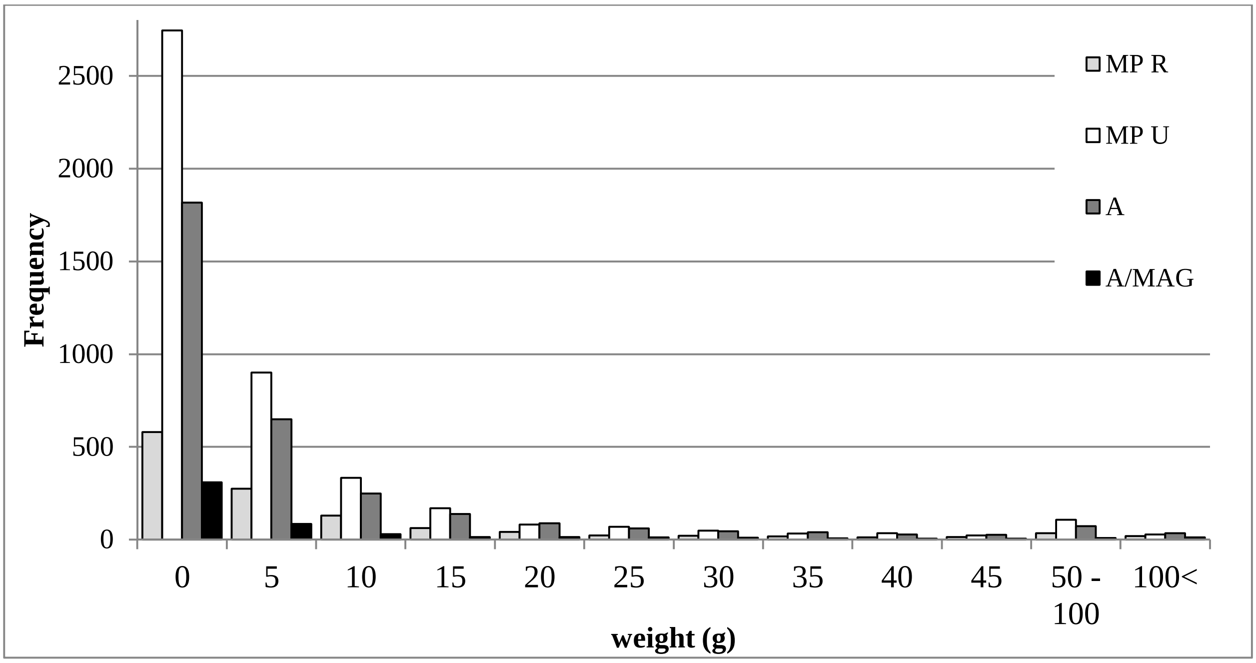


Figure 5.1 Frequency distribution of speciments in weight from the excavation in 1939.

The faunal assemblages of the Middle Paleolithic are dominated by cave bears and unidentified ursids, which mostly belong to cave bears. Unidentified large carnivores are also frequent and correlate with the general abundance of bear. From the Red to Upper Middle Paleolithic, the number of cave bear increases roughly three folds and the number of bears decrease, indicating that the relative proportion of fragmentary specimens that cannot be identified to the species level and/or the juvenile remains consistent during these two horizons. Brown bear occurs in the MP U, but is almost nonexistent compared to the cave bear. Relative NISP values of cave bear and unidentified bear do not fluctuate significantly. The proportion of weight among cave bear and unidentified bear delineates a similar pattern. The relative weight proportion of cave bear in the assemblage is attenuated, while the bear remains are comparable to NISP %.

The most common herbivore is horse in the Middle Paleolithic, and while the NISP increases considerably in the MP U, the relative frequency is consistent, making up ~4.3-4.6% of the assemblage. In weight proportion, horses make up a higher proportion at 9.5% and 13.5 %, respectively. The second most common herbivore is mammoth. The NISP value is small, but is better represented in weight. The amount of tusk also remains consistent in the MP including the worked ivory pieces. Woolly rhinoceros is also present in both layers in equal abundance of 1.1% in NISP and represented by 8.9% and 5% of total weight for MP R and MP U, respectively. The reindeer occur rarely, but a comparable number of reindeer antlers were recovered in both MP sequences. The red deer do not occur frequently, but some of the cervid specimens potentially belong to red deer. Cervids are mostly represented by antler fragments, which increase from the MP R to MP U. A greater abundance of reindeer points to a tundra-steppe vegetation in the local area. The aurochs and bison exist in low numbers and large bovids are not common in the Middle Paleolithic.

Except for bears, the dominant carnivore is hyena, represented by ~2% in both MP sequences for NISP and weight, although the absolute value of NISP is greater in MP U. In contrast, wolves are less frequent than hyenas in the MP. Felids such as cave lions and Eurasian lynx are infrequent in the assemblage. Small carnivores are not common in the assemblage, although this is likely due to the recovery method, but fox is the most common taxon. The relative frequency of herbivores including unidentified ungulates, perissodactyls, artiodactyls and proboscideans, compared to bear and carnivores maintain roughly at 1:4 ratio during the MP.

Rodents and lagomorphs are rare in both MP layers. Only a scarce number of non-mammalian animals including bird and fish were recovered. Scarcity of small animals may partially be due to excavation bias. In all, the sample size of the MP U is considerably larger than MP R, but the relative proportion of most animals remains the same and the weight roughly correlates with NISP values when proportions are considered.

The Aurignacian period is characterized by the decrease of species diversity. The cave bears are still the most represented taxon in the assemblage, although NISP values decrease slightly in the Aurignacian. Conversely, the NISP of bears increases in the Aurignacian, reflecting either the number of juveniles or increased fragmentation of specimens. The relative % of NISP increases in the Aurignacian and Aurignacian/Magdalenian to 21.2% and 20.1% for cave bears and 9.3% and 10.1% for bears, respectively. Two specimens of brown bear were identified. In terms of weight, the proportion of cave bears increases significantly, making up 48% and 63.1% of the entire assemblage. The bears are also better represented in weight compared to the Middle Paleolithic.

In general, the herbivores decrease significantly in contrast to the MP. The most common herbivore, the horse, is represented by 1.2% of the assemblage, comparable to the second common herbivore, reindeer (0.9%). However, antlers of reindeer increase significantly by two folds. This is also reflected by the increase in cervid antlers, which are not assigned to species. Compared to MP U, woolly rhinoceros are represented by fewer NISP values. The number of mammoth in NISP is also scarce in the Aurignacian period, and besides the known ivory artifacts from the Aurignacian, a number of ivory fragments also exist in the MP.

Carnivores show changes in relative abundances. Wolf becomes the most frequent taxon among middle-sized and large carnivores, showing gradual increase from the MP U to the Aurignacian period. The lions still remain low in frequency and hyenas disappear almost completely. Small carnivores are still sparse and do not change in relative abundance. Small animals such as hares are also infrequent, but there are a few specimens of birds and fish. The ratio of herbivores and carnivores decreases from 1:4 to 1:5 and the overall proportion of herbivores declines notably in the Aurignacian.

	MP			Aurignacian		
Taxon	Gamble NISP	AR	Kitagawa NISP	Gamble NISP	AR	Kitagawa NISP
cave bear	2674	**4,85**	1214	1935	**4,42**	1071
wolf	141	-1,71	43	157	**-3,29**	48
fox	78	**-3,12**	13	107	**-5,00**	16
hyena	476	**-6,46**	100	44	**-4,02**	3
cave lion	47	-2,14	9	15	1,15	12
mammoth	58	**10,46**	109	3	1,29	4
woolly rhinoceros	116	1,73	62	14	1,06	11
horse	735	-2,79	249	50	2,39	42
reindeer	95	-0,11	38	82	-1,36	32
aurochs/bison	112	**-4,95**	11	-	-	-
hare	1	2,93	5	22	0,16	12
∑	4533		1853	2429		1251
χ2		**212,92**			**65,40**	

Table 5.3 NISP and associated adjusted residuals (AR) of the NISP of Gamble and current analysis of 1939 material with composite χ2 values (p-value<0.001); Signs of AR refer to values of this current analysis; significant AR values at p<0.05 in bold.

Gamble's analysis of the material from the older excavations and this current analysis show significant differences in taxonomic abundances. Taxa with the minimum NISP values of 5 from both MP and Aurignacian combined were compared using χ^2 analysis. The MP U and MP R are subsumed under one unit, because the boundary between the two layers is not entirely clear and also differently defined. Cave bears, brown bears and unidentified bears are all grouped under cave bears for this current analysis, as Gamble did not make the taxonomic distinction. The χ^2 value and adjusted residuals (Table 5.3) show significant differences in the NISP values, with MP showing a greater χ^2 value (212.92) compared to the Aurignacian (65.40).

During the MP, bears, mammoths and hares are better represented in this current analysis while foxes, hyenas, horses and aurochs/bison are more abundant in Gamble's analysis. Similar to the MP, the cave bears are represented by greater proportions in the current analysis in the Aurignacian strata while wolf, fox and hyena occur more frequently in Gamble's sample. Other animals show considerable similarity. Relatively high χ^2 values are expected as Gamble's results also include excavations from the sector closer to the entrance of the cave.

In addition, the correlation of the two datasets can also be studied to understand overarching tendencies. Despite the differences in the χ^2 values, the correlation of the transformed taxa NISP is still significant. The R_s values are 0.68 for the MP and 0.75 for the Aurignacian at a significant level ($p<0.005$). Therefore, the overall trend is reflected both in the MP and Aurignacian, with the Aurignacian showing a greater correlation. Spearman's rank correlation coefficient is also high for the MP ($R_{s\,=}$ 0.77, $p<0.01$) and even greater for the Aurignacian ($R_{s\,=}$ 0.81, $p<0.01$). Bear is consistently overrepresented in the recent excavations compared to the excavation in 1939.

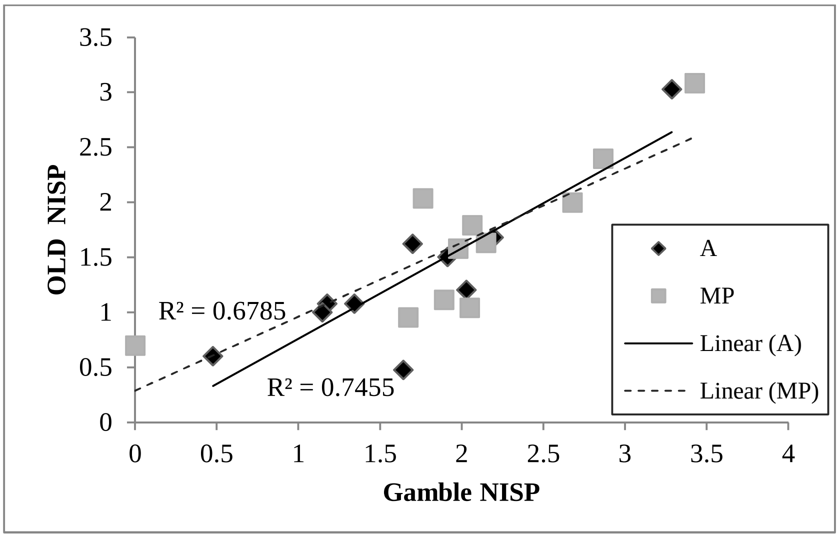


Figure 5.2 Correlation of NISP taxa from Gamble and the current analysis of material from 1939. The correlation is high and significant (p-value=.001).

Excavations 2009-2011

A total of 6658 specimens, weighing 19,914.02 g, comprised the assemblage from recent excavations. The material derives from roughly 6 m^2 of excavation surface, which corresponds to 19-20 *Abbaumeter* from Wetzel's excavation. First, data from the main horizons are given below.

Taxon/Body size	**G (XI)**				**F (X)**			
	NISP	%NISP	WISP	%WISP	NISP	%NISP	WISP	%WISP
European mole								
hare								
wolf					9	0.7	8	0.31
fox					5	0.4	1.2	0.05
cave bear	5	4.8	17.5	6.94	41	3.1	239.1	9.30
bear	6	5.7	3.6	1.43	207	15.8	440.2	17.12
cave lion					2	0.2	6.4	0.25
Eurasian lynx								
mustelids								
marten								
hyena					10	0.8	43	1.67
mammoth	1	1.0	0.8	0.32	23	1.8	49.4	1.92
(tusk)					8		0.7	
horse	1	1.0	2.2	0.87	21	1.6	36.1	1.40
woolly rhinoceros					6	0.5	7.7	0.30
reindeer					9	0.7	24.1	0.94
(antler)					3		284.1	
aurochs/bison	2	1.9	17.2	6.82				
human								
rodent								
carnivore small	2	1.9	0.5	0.20	10	0.8	1.6	0.06
carnivore medium	5	4.8	1.7	0.67	67	5.1	29.9	1.16
carnivore large	4	3.8	3.2	1.27	34	2.6	60.3	2.35
cervids					1	0.1	0.8	0.03
(antler)					32		99.3	
bovids					1	0.1	0.4	0.02
ungulate small						0.0		0.00
ungulate medium					6	0.5	15	0.58
ungulate large					8	0.6	5.8	0.23
ungulate	1	1.0	0.1	0.04	4	0.3	2.4	0.09
Body size 1	1	1.0	0.1	0.04	6	0.5	1.6	0.06
Body size 2	17	16.2	6.8	2.70	162	12.4	120.9	4.70
Body size 3	34	32.4	49	19.44	167	12.7	264.7	10.30
Body size 4	9	8.6	21.2	8.41	112	8.5	438.3	17.05
Body size 5	3	2.9	98.5	39.07	5	0.4	2	0.08
mammal	14	13.3	29.7	11.78	391	29.8	771.4	30.01
bird					1	0.1	0.1	0.00
fish					2	0.2	0.5	0.02
Total	105	100	252.1	100	1353	100	2955	100
Total without antler/tusk	105		252.1		1310		2570.9	

Table 5.4 NISP, NISP%, WISP (g), WISP% of taxa and body size F/X (MP R),G/XI (MP R) from the excavation of 2009-2011.

Taxon/Body size	**E (IX)**				**D-D4 (VII-VIII)**			
	NISP	%NISP	WISP	%WISP	NISP	%NISP	WISP	%WISP
European mole					1	0.1	0.4	0.01
hare					10	0.5	2	0.03
wolf	1	0.3	0.6	0.07	5	0.3	25.5	0.33
fox	2	0.6	0.3	0.04	20	1.1	5.7	0.07
cave bear	14	4.0	143.5	16.95	113	6.0	1046.2	13.45
bear	79	22.4	64.3	7.59	335	17.7	197.8	2.54
cave lion					1	0.1	0.3	0.00
Eurasian lynx								
mustelids								
marten								
hyena	4	1.1	7.2	0.85	23	1.2	108.2	1.39
mammoth	5	1.4	11.7	1.38	46	2.4	991.1	12.75
(tusk)	1		0.1		35		24.5	
horse	5	1.4	65.6	7.75	54	2.9	449.8	5.78
woolly rhinoceros					21	1.1	186.9	2.40
reindeer	1	0.3	1.6	0.19	11	0.6	25.6	0.33
(antler)								
aurochs/bison								
human								
rodent					4	0.2	0.3	0.00
carnivore small	1	0.3	0.1	0.01	10	0.5	2	0.03
carnivore medium	19	5.4	9.6	1.13	96	5.1	44.5	0.57
carnivore large	9	2.6	8.3	0.98	46	2.4	90.7	1.17
cervids					10	0.5	4.2	0.05
(antler)	2		10.8		26		71.8	
bovids								
ungulate small	1	0.3	0.3	0.04	4	0.2	3.1	0.04
ungulate medium	1	0.3	10.5	1.24	4	0.2	2.4	0.03
ungulate large	1	0.3	9.8	1.16	9	0.5	20.7	0.27
ungulate					9	0.5	3.5	0.05
Body size 1	4	1.1	1.3	0.15	21	1.1	3.1	0.04
Body size 2	33	9.4	32.2	3.80	113	6.0	87	1.12
Body size 3	40	11.4	85	10.04	180	9.5	317.3	4.08
Body size 4	24	6.8	81.1	9.58	190	10.0	1123.7	14.45
Body size 5	1	0.3	0.4	0.05	4	0.2	216.6	2.79
mammal	106	30.1	313.2	36.99	538	28.4	2815	36.20
bird	1	0.3	0.1	0.01	12	0.6	2.1	0.03
fish					2	0.1	0.3	0.00
Total	355	100	857.6	100	1953	100	7872.3	100
Total without antler/tusk	352		846.7		1892		7776	

Table 5.5 NISP, NISP%, WISP (g), WISP% of taxa and body size of D-D4/VII-VIII (MP R), E/IX (MP R) from the excavation of 2009-2011.

Taxon/Body size	**A2 (VIIa)**				**C (VI MP)**			
	NISP	%NISP	WISP	%WISP	NISP	%NISP	WISP	%WISP
European mole								
hare	4	0.5	0.6	0.03	3	0.6	0.3	0.03
wolf					2	0.4	1.9	0.17
fox	7	0.8	3.7	0.16	3	0.6	2.5	0.22
cave bear	44	5.2	402.4	16.94	19	3.7	86.2	7.55
bear	161	19.2	70.4	2.96	68	13.2	33.2	2.91
cave lion	1	0.1	1	0.04				
Eurasian lynx	1	0.1	0.6	0.03				
mustelids	1	0.1	0.4	0.02				
marten								
hyena	9	1.1	20.7	0.87	4	0.8	18.7	1.64
mammoth	19	2.3	24.3	1.02	8	1.6	10.1	0.88
(tusk)					10		2.1	
horse	16	1.9	42.7	1.80	9	1.7	96	8.41
woolly rhinoceros	6	0.7	27	1.14	3	0.6	3.3	0.29
reindeer	1	0.1	2.3	0.10	2	0.4	5.1	0.45
(antler)								
aurochs/bison	1	0.1	0.5	0.02				
human	1	0.1	0.4	0.02				
rodent					1	0.2	0.1	0.01
carnivore small	5	0.6	1.2	0.05				
carnivore medium	48	5.7	29.9	1.26	19	3.7	26.2	2.30
carnivore large	29	3.5	82.6	3.48	23	4.5	62.9	5.51
cervids	4	0.5	0.7	0.03	1	0.2	0.2	0.02
(antler)					4		2.7	
bovids								
ungulate small	5	0.6	0.9	0.04	2	0.4	0.4	0.04
ungulate medium	2	0.2	0.8	0.03	1	0.2	0.7	0.06
ungulate large	6	0.7	22.5	0.95				
ungulate	4	0.5	1.4	0.06	2	0.4	0.5	0.04
Body size 1	12	1.4	2	0.08	17	3.3	2.8	0.25
Body size 2	36	4.3	19	0.80	43	8.3	28.3	2.48
Body size 3	54	6.4	107.1	4.51	57	11.0	102.1	8.95
Body size 4	72	8.6	398.5	16.78	56	10.9	224.3	19.65
Body size 5	1	0.1	14.9	0.63				
mammal	284	33.8	1096.22	46.15	171	33.1	434.5	38.07
bird	5	0.6	0.4	0.02	1	0.2	0.4	0.04
fish	1	0.1	0.1	0.00	1	0.2	0.7	0.06
Total	840	100	2375.22	100	530	100	1146.2	100
Total without antler/tusk	840		2375.22		516		1141.4	

Table 5.6 NISP, NISP%, WISP (g), WISP% of taxa and body size of C /VI (MP U), A2/VIIa (MP U) from the excavation of 2009-2011.

Taxon/Body size	Ao-Au (IV-V A)			
	NISP	%NISP	WISP	%WISP
European mole				
hare	19	1.3	6.5	0.15
wolf	6	0.4	8.7	0.20
fox	20	1.3	9.5	0.22
cave bear	59	4.0	368.3	8.57
bear	241	16.2	308.9	7.19
cave lion				
Eurasian lynx				
mustelids				
marten	1	0.1	0.8	0.02
hyena	3	0.2	9.3	0.22
mammoth	4	0.3	6.5	0.15
(tusk)	7		2.3	
horse	3	0.2	10.6	0.25
woolly rhinoceros	2	0.1	1072.3	24.95
reindeer	11	0.7	41.9	0.97
(antler)	4		116.6	
aurochs/bison				
human	1	0.1	0.1	0.00
rodent	6	0.4	0.6	0.01
carnivore small	9	0.6	2.4	0.06
carnivore medium	69	4.6	77.9	1.81
carnivore large	48	3.2	233.2	5.43
cervids	3	0.2	13.3	0.31
(antler)	26		38.6	
bovids				
ungulate small	5	0.3	11.7	0.27
ungulate medium				
ungulate large				
ungulate	4	0.3	5.2	0.12
Body size 1	41	2.8	9.3	0.22
Body size 2	192	12.9	127.7	2.97
Body size 3	190	12.8	373.1	8.68
Body size 4	111	7.5	495.4	11.53
Body size 5				
mammal	436	29.3	1104.3	25.69
bird	3	0.2	0.4	0.01
fish	2	0.1	0.2	0.00
Total	1526	100	4455.6	100
Total without antler/tusk	1489		4298.1	

Table 5.7 NISP, NISP%, WISP (g), WISP% of taxa and body size of Ao-Au /IV-V (A) from the excavation of 2009-2011.

Taxon/Body size	**MP R**				**MP U**			
	NISP	%NISP	WISP	%WISP	NISP	%NISP	WISP	%WISP
European mole	1	0,03	0,4	0,00	0	0,00	0,0	0,00
hare	10	0,27	2,0	0,02	7	0,52	0,9	0,03
wolf	15	0,41	34,1	0,30	2	0,15	1,9	0,05
fox	27	0,74	7,2	0,06	10	0,74	6,2	0,18
cave bear	173	4,73	1446,3	12,64	63	4,65	488,6	13,89
bear	627	17,14	705,9	6,17	229	16,89	103,6	2,95
cave lion	3	0,08	6,7	0,06	1	0,07	1,0	0,03
Eurasian lynx	0	0,00	0,0	0,00	1	0,07	0,6	0,02
mustelids	0	0,00	0,0	0,00	1	0,07	0,4	0,01
marten	0	0,00	0,0	0,00	0	0,00	0,0	0,00
hyena	37	1,01	158,4	1,38	13	0,96	39,4	1,12
mammoth	75	2,05	1053,0	9,20	27	1,99	34,4	0,98
(tusk)	44		25,3		10		2,1	
horse	81	2,21	553,7	4,84	25	1,84	138,7	3,94
woolly rhinoceros	27	0,74	194,6	1,70	9	0,66	30,3	0,86
reindeer	21	0,57	51,3	0,45	3	0,22	7,4	0,21
(antler)	3		284,1				0,0	
aurochs/bison	2	0,05	17,2	0,15	1	0,07	0,5	0,01
human		0,00	0,0	0,00	1	0,07	0,4	0,01
rodent	4	0,11	0,3	0,00	1	0,07	0,1	0,00
carnivore small	23	0,63	4,2	0,04	5	0,37	1,2	0,03
carnivore medium	187	5,11	85,7	0,75	67	4,94	56,1	1,60
carnivore large	93	2,54	162,5	1,42	52	3,83	145,5	4,14
cervids	11	0,30	5,0	0,04	5	0,37	0,9	0,03
(antler)	60		181,9		4		2,7	
bovids	1	0,03	0,4	0,00	0	0,00	0,0	0,00
ungulate small	5	0,14	3,4	0,03	7	0,52	1,3	0,04
ungulate medium	11	0,30	27,9	0,24	3	0,22	1,5	0,04
ungulate large	18	0,49	36,3	0,32	6	0,44	22,5	0,64
ungulate	14	0,38	6,0	0,05	6	0,44	1,9	0,05
Body size 1	32	0,87	6,1	0,05	29	2,14	4,8	0,14
Body size 2	325	8,88	246,9	2,16	79	5,83	47,3	1,35
Body size 3	421	11,51	716,0	6,26	111	8,19	209,2	5,95
Body size 4	335	9,16	1664,3	14,54	128	9,44	622,8	17,71
Body size 5	13	0,36	317,5	2,77	1	0,07	14,9	0,42
mammal	1049	28,67	3929,3	34,33	455	33,55	1530,7	43,53
bird	14	0,38	2,3	0,02	6	0,44	0,8	0,02
fish	4	0,11	0,8	0,01	2	0,15	0,8	0,02
Total	3766	100,00	11937,0	100,00	1370	100,00	3521,4	100,00
Total without antler/tusk	3659		11445,7		1356		3516,62	

Table 5.8 NISP, NISP%, WISP (g), WISP% of taxa and body size from the MP R and MP U from the excavation of 2009-2011

Taxon/Body size	**A**			
	NISP	%NISP	WISP	%WISP
European mole	0	0,00	0,0	0,00
hare	19	1,28	6,5	0,15
wolf	6	0,40	8,7	0,20
fox	20	1,35	9,5	0,22
cave bear	59	3,97	368,3	8,57
bear	241	16,23	308,9	7,19
cave lion	0	0,00	0,0	0,00
Eurasian lynx	0	0,00	0,0	0,00
mustelids	0	0,00	0,0	0,00
marten	1	0,07	0,8	0,02
hyena	3	0,20	9,3	0,22
mammoth	4	0,27	6,5	0,15
(tusk)	7		2,3	
horse	3	0,20	10,6	0,25
woolly rhinoceros	2	0,13	1072,3	24,95
reindeer	7	0,47	41,9	0,97
(antler)	4		116,6	
aurochs/bison	0	0,00	0,0	0,00
human	1	0,07	0,1	0,00
rodent	6	0,40	0,6	0,01
carnivore small	9	0,61	2,4	0,06
carnivore medium	69	4,65	77,9	1,81
carnivore large	48	3,23	233,2	5,43
cervids	3	0,20	13,3	0,31
(antler)	26		38,6	
bovids	0	0,00	0,0	0,00
ungulate small	5	0,34	11,7	0,27
ungulate medium	0	0,00	0,0	0,00
ungulate large	0	0,00	0,0	0,00
ungulate	4	0,27	5,2	0,12
Body size 1	41	2,76	9,3	0,22
Body size 2	192	12,93	127,7	2,97
Body size 3	190	12,79	373,1	8,68
Body size 4	111	7,47	495,4	11,53
Body size 5	0	0,00	0,0	0,00
mammal	436	29,36	1104,3	25,69
bird	3	0,20	0,4	0,01
fish	2	0,13	0,2	0,00
Total	1522	100,00	4455,6	100,00
Total without antler/tusk	1485		4298,1	

Table 5.9 NISP, NISP%, WISP (g), WISP% of taxa and body size from the Aurignacian from the excavation of 2009-2011.

Despite the differences in the sample size throughout each horizon (Table 5.3-5.7), the fauna mostly consist of bears and cave bears. Juvenile and fragmented unidentifiable bear remains ranging between 13-22% outnumber cave bear remains, which represent 3-6% in terms of NISP. Cave bear is better represented than bears in weight. Following cave bears, mammoths and horses are the abundant taxa in terms of NISP in layer F(X), D-D4 (VII-VIII) and A2 (VIIa). NISP values are comparable, but weight proportion varies. Ivory fragments are most abundant in D-D4/VII-VIII layers. Further, fauna such as woolly rhinoceros and hyena also occur occasionally.

Several stratigraphic layers were grouped together to augment the sample size. As noted before, the MP R consists of D, D4, E, F, and G, and the MP U consists of A2 and C. The Aurignacian horizons consist of three layers, Ao-Au. When grouped together, the MP R (N=3766) comprises the greatest proportion of the assemblage, followed by the Aurignacian (N=1522) and MP U (N=1370) (Table 5.8+5.9). On average, 28.2% of the material was assigned to a genus or species level while the rest was identified to family, order or body size. The percent of identified specimens is lower than the excavation of 1939. The identified specimens occur most frequently in the MP R (30.4%), which is comparable to MP U (29.4%) and identifiability decreases in the Aurignacian (24.9%). This does not correlate with the sample size of each assemblage. Unidentified specimens, which were grouped into size class, show that the fragments of body size 2 are more abundant than size 3 and 4 (Figure5. 3).

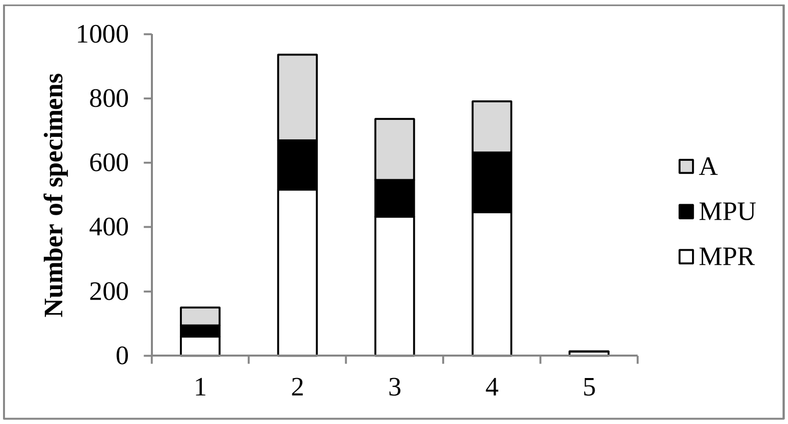


Figure 5.3 Number of specimens with for each body size class 1-5 from the excavation 2009-2011.

The weight of the specimens per cultural layer reflects the relative proportion of NISP, weighing 11,937 g (MP R), 3521.4 g (MP U) and 4455.6 g (Aurignacian), respectively. When quantified by weight, the proportion of identified specimens is greater than the %NISP for MP R and Aurignacian. The weight distribution of specimens shows that more than 87.2% of the assemblage weighs less than 5 g, showing that the average size was small in comparison to the material from the 1939 excavation. Identified specimens are differentially distributed among the cultural units. Altogether, 44% of the weight specimens are identified in the Aurignacian period, followed by 38% of MP R and reduced relative proportion of identified specimens (24.3%) compared to the NISP (29.2%). The difference in the proportion of identified material between NISP and weight possibly reflects the difference in the degree of fragmentation.

Both Middle Paleolithic assemblages are dominated by cave bears and unidentified ursids. Bears occur more frequently than cave bears represented by 17.1% and 16.9% for MP R and MP U as opposed to 4.7% for cave bears in both layers. The %NISP of both cave bears and unidentified ursids also remains the same in both MP R and MP U. No brown bear has been positively identified in the assemblage. The cave bears and unidentified ursids decrease from MP R to MP U, but correlates with the sample size. However, the summed weight of cave bears is still larger than bears. Cave bears represent 12.6 and 13.9% of MP R and MP U, respectively, and in comparison, bears make up 6.2% and 3%.

Herbivores make up a small proportion of the assemblage. The most abundant taxon in terms of NISP is horse (N=81) followed by mammoth (N=75) in the MP R. The woolly rhinoceros and reindeer are roughly comparable in number, and aurochs/bison are scarce but present. The weight of the herbivores is better represented compared to the NISP, with 9.2% represented by mammoth and 4.8% by horses. In the MP U, herbivores decrease in number considerably. The mammoth and horse are both present, but make up less than 2% of NISP, ranging between 1-4% of weight.

In the MP R, the most common middle to large carnivore is hyena, followed by wolf. As with the previous sample, cave lions are rare in the caves. The foxes appear relatively frequently, in part due to the recovery method. During the MP U, all carnivores including hyena, wolf, cave lion, lynx and fox decline in NISP, but this is partially due to the smaller sample size as the proportion of NISP does not alter significantly. The overall proportion of all herbivores and carnivores/bears including unidentified specimens shows that the herbivores account for 18% and carnivores account for 81-82% of specimens identified to the mammalian order.

Both the MP U and Aurignacian appear similar in terms of taxonomic composition. Bears are the most abundant taxon, followed by cave bears. The proportion of bears and cave bears remains consistent, representing 16.2% and 4%, respectively. The weight of bears and cave bears are comparable, making up 7-8.5% of the assemblage.

The number of herbivores including horse, mammoth, reindeer and woolly rhinoceros is low, adding up to merely 1.3% NISP. Unidentified cervids also decrease although the amount of cervid antlers increases from MP U. However, woolly rhinoceros is represented significantly in weight, accounting for 25% of the assemblages. This relative abundance in weight is higher than carnivores and ursids combined. The amount of ivory fragments from the recent excavation does not increase in the Aurignacian as one would presume with the presence of ivory artifacts. Hares increase slightly in NISP and weight compared to the MP combined.

Carnivores are scarce as well. The number of wolves increases slightly, and relative NISP of hyenas decreases progressively from the MP R to Aurignacian. Fox is the only carnivorous taxon that increases in the Aurignacian. Microfauna will be analyzed by R. Ziegler and other smaller mammals including foxes and hares may be identified. Some fish and avian remains are identified.

Like herbivores, carnivores are scarce in the assemblages and ursids dominate. The herbivores including those identified to the order and family decline in abundance considerably by the Aurignacian while within the MP, their proportions remain comparable.

Comparison of the excavations of 1939 and 2009-2011

Recovered faunal remains from the old and recent excavations at Hohlenstein-Stadel show little variance, and the general trends are mirrored in both assemblages. When differences exist, few possible explanations exist. One, the excavation method, especially the systematic incorporation of waterscreening and sorting during the excavations of 2009-2011 resulted in the recovery and identification of smaller remains. Further, heterogeneous spatial distribution of fauna in the cave can affect species abundance, which needs to be considered for any excavation work that includes sampling. Lastly, the definition of the cultural layers and stratigraphy may slightly alter in the future due to sedimentological analyses and spatial data of the deposits.

Sample size from each cultural phase differs, but the number of specimens in the MP R assemblage is larger for recent excavations, while the rest, the MP U and Aurignacian, are better represented in terms of the quantity of specimens. The older assemblages yielded greater weight across the cultural phases. Therefore, the material from the older excavation determines the general pattern of abundances and relative frequencies.

Identifiability is slightly higher from the earlier excavation, ranging between 32-37% than from the recent excavations (25-30%). The identified specimens form 62-80% of the weight of the older assemblage while they merely comprise 24-44% of the weight of the recent assemblage. With regard to NISP, specimens identified to medium and large body size 3-4 are more frequent, making up 92.3% in the excavation of 1939, while specimens identified to large body size 3-4 are less abundant at 52% in the excavations of 2009-11. Difference in size of fragments and the identified animals is also reflected in the weight distribution of bones. Altogether, 47-60% of specimens from the previous excavation weigh 0-5 g in contrast to 82-90% of specimens from the recent excavation (Figure 5.4). The assemblages from two excavations are comparable, and some differences derive from changes in the recovery method and sampling. Further, the frequency of material identified to body size shows that the fauna from the recent excavations are represented by animals of smaller body size, including size 1 and 2, while the excavation from 1939 is dominated by fauna identified to body size class 3 and 4 (Figure 5.5).

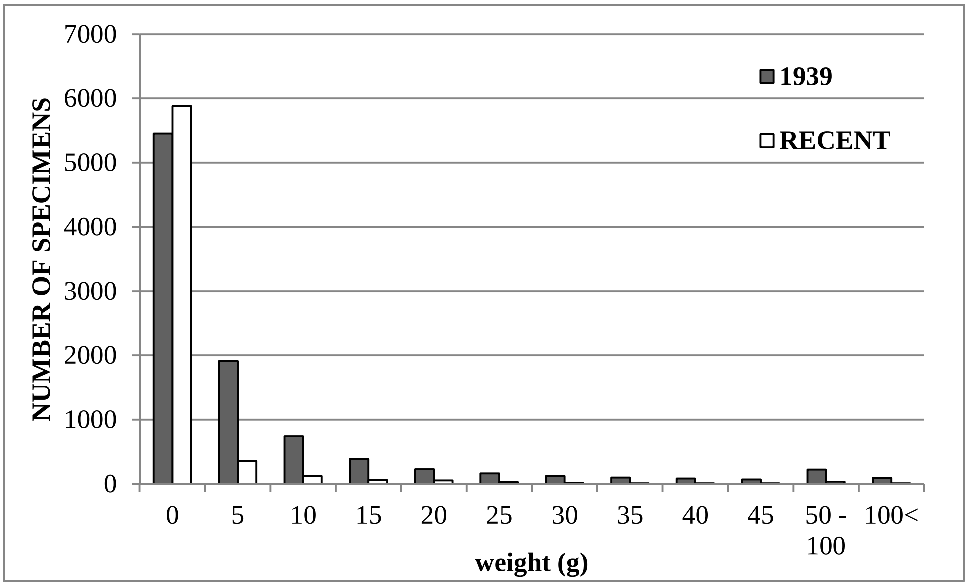


Figure 5.4 Frequency of specimens per weight from the excavation of 1939 and 2009-2011

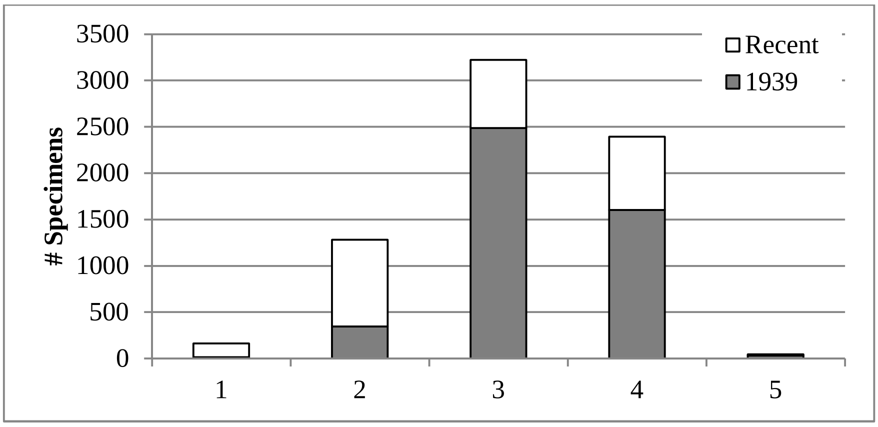


Figure 5.5 Number of specimens identified to body size class from the excavation of 1939 and 2009-2011

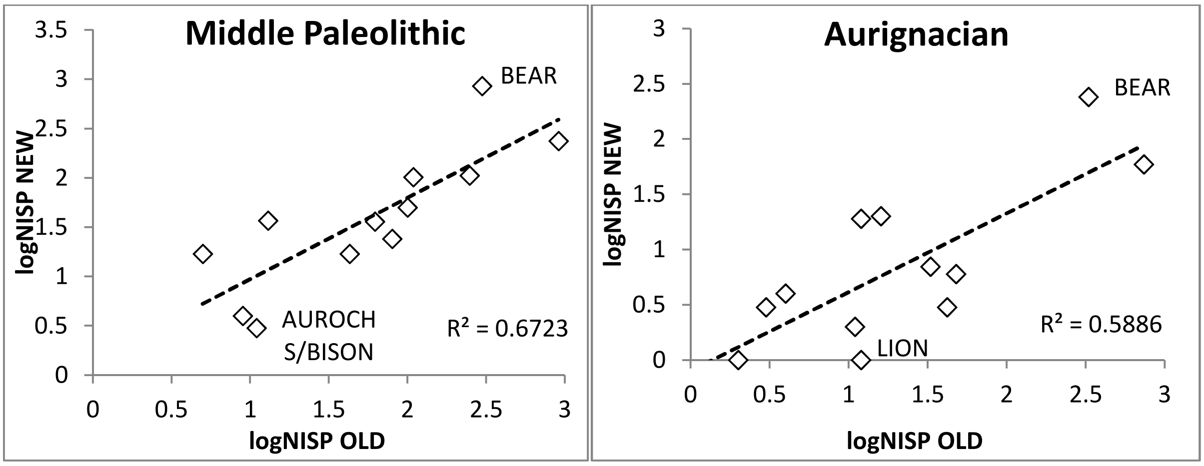


Figure 5.6 Correlation of logNISP taxa of old and new excavations. All the correlation are also significant (p-value = <0.01). Values with high residuals were labeled.

Simple linear correlation indicates that roughly 60% of variance based on taxa from the new assemblage is accounted for in the old assemblage (Figure 5.6). The correlation of transformed NISP values between the two assemblages is high and significant, both for the Middle Paleolithic (R_s= 0.67, p<.005) and the Aurignacian (R_s =0.59, p<.005). The outliers with relatively high standardized residual values include aurochs/bison (1.87) and unidentified juvenile bears (-1.33) for the MP. Aurochs/bison were overrepresented in the old excavation, and the bears were overrepresented in the recent excavations. Two outliers in the Aurignacian include cave lions (-1.47), which are underrepresented in the recent excavations and juvenile bears (1.49), which are overrepresented in the recent excavations. When MP is subdivided, the correlation is higher for MP U (R_s=0.71) than for MP R (R_s =0.55), showing greater disparity in the assemblages between the old and recent excavation. Bears are overrepresented consistently in all the layers, making this the prominent difference between the two assemblages.

With Spearman's rho test, the correlation becomes higher for the MP (R_s=0.81, p<.0001) but lower for the Aurignacian (R_s=0.39, p<.05). This is expected in the Aurignacian assemblage as the average NISP values from the recent excavation are small, which affects the ranking order of taxa. When the MP R and U are considered separately, the coefficient for MP R is R_s=0.67 (p<.001) and even higher for MP U (R_s=0.78, p<.0001). The overall trend tends towards greater correlation between the assemblage from 1939 and recent excavations during the MP and slightly lower correlations in the A, but the general patterns of taxonomic abundances are comparable.

Taxon/Body Size	MP R				MP U			
	NISP	NISP%	WISP	WISP %	NISP	NISP%	WISP	WISP %
European mole	1	0.02	0.4	0.00	0	0.00	0.0	0.00
hare	10	0.21	2	0.01	12	0.21	17.3	0.04
Eurasian beaver	0	0.00	0	0.00	0	0.00	0.0	0.00
wolf	27	0.56	207.6	0.75	33	0.57	339.3	0.76
red fox	0	0.00	0	0.00	1	0.02	8.9	0.02
polar fox	0	0.00	0	0.00	0	0.00	0.0	0.00
fox	29	0.60	12.5	0.05	20	0.34	32.7	0.07
cave bear	378	7.77	4890.1	17.61	771	13.26	10963.2	24.65
brown bear	0	0.00	0	0.00	3	0.05	14.1	0.03
bear	707	14.54	1627.9	5.86	447	7.69	1665.4	3.74
cave lion	9	0.19	328.4	1.18	4	0.07	36.4	0.08
Eurasian lynx	0	0.00	0	0.00	2	0.03	11.2	0.03
mustelids	0	0.00	0	0.00	1	0.02	0.4	0.00
marten	0	0.00	0	0.00	1	0.02	1.2	0.00
hyena	62	1.28	490.9	1.77	88	1.51	944.0	2.12
mammoth	102	2.10	2746.4	9.89	109	1.87	3293.4	7.40
(tusk)	66		418.2		36		41.4	
horse	137	2.82	2125.4	7.65	218	3.75	5636.3	12.67
woolly rhinoceros	41	0.84	1672.9	6.03	57	0.98	2086.0	4.69
red deer	1	0.02	19.8	0.07	1	0.02	11.1	0.02
reindeer	25	0.51	128.2	0.46	34	0.58	436.0	0.98
(antler)	11		1551.2		34		1391.4	
aurochs/bison	9	0.19	468.8	1.69	5	0.09	497.6	1.12
human	0	0.00	0	0.0	1	0.02	0.4	0.0
rodent	4	0.08	0.3	0.00	3	0.05	0.6	0.00
carnivore small	24	0.49	5	0.02	7	0.12	2.0	0.00
carnivore medium	220	4.52	222.5	0.80	129	2.22	246.3	0.55
carnivore large	131	2.69	517.3	1.86	158	2.72	923.0	2.07
cervids	15	0.31	42.3	0.15	9	0.15	33.3	0.07
(antler)	79		392.4		70		421.5	
bovids	1	0.02	0.4	0.00	2	0.03	3.2	0.01
perissodactyl	0	0.00	0	0.00	0	0.00	0.0	0.00
artiodactyl	0	0.00	0	0.00	0	0.00	0.0	0.00
ungulate small	6	0.12	5.6	0.02	29	0.50	88.8	0.20
ungulate medium	16	0.33	61.7	0.22	18	0.31	98.5	0.22
ungulate large	31	0.64	664.9	2.39	39	0.67	495.5	1.11
ungulate	18	0.37	18.7	0.07	26	0.45	59.3	0.13
Body size 1	32	0.66	6.1	0.02	35	0.60	8.0	0.02
Body size 2	357	7.34	288.3	1.04	169	2.91	132.4	0.30
Body size 3	707	14.54	1674.7	6.03	1351	23.23	3271.9	7.36
Body size 4	670	13.78	4634	16.69	1488	25.59	10956.0	24.63
Body size 5	20	0.41	960.4	3.46	15	0.26	425.6	0.96
mammal	1054	21.68	3938.7	14.19	511	8.79	1732.8	3.90
bird	14	0.29	2.3	0.01	16	0.28	9.2	0.02
fish	4	0.08	0.8	0.00	2	0.03	0.8	0.00
Total	5018	100	30127.1	100	5955	100	46336.4	100
total w/o ivory/antler	4862		27765.3		5815		44482.1	

Tab 5.10+5.11 NISP, NISP %, WISP (weight), WISP %, for combined assemblage per cultural layer

Taxon/Body Size	A			
	NISP	NISP%	WISP	WISP %
European mole	0	0,00	0,0	0,00
hare	31	0,62	30,2	0,07
Eurasian beaver	1	0,02	1,4	0,00
wolf	54	1,08	647,0	1,48
red fox	0	0,00	0,0	0,00
polar fox	3	0,06	6,8	0,02
fox	33	0,66	46,4	0,11
cave bear	798	15,95	20402,0	46,67
brown bear	2	0,04	13,8	0,03
bear	571	11,41	3264,4	7,47
cave lion	12	0,24	499,7	1,14
Eurasian lynx	0	0,00	0,0	0,00
mustelids	0	0,00	0,0	0,00
marten	1	0,02	0,8	0,00
hyena	6	0,12	62,9	0,14
mammoth	8	0,16	477,3	1,09
(tusk)	26		56,7	
horse	45	0,90	1386,9	3,17
woolly rhinoceros	13	0,26	3028,70	6,93
red deer	0	0,00	0,0	0,00
reindeer	40	0,80	591,2	1,35
(antler)	92		2605,2	
aurochs/bison	1	0,02	44,2	0,10
human*	1	0,02	0,1	0,0
rodent	7	0,14	0,8	0,00
carnivore small	12	0,24	3,8	0,01
carnivore medium	191	3,82	642,3	1,47
carnivore large	181	3,62	1231,6	2,82
cervids	14	0,28	88,8	0,20
(antler)	175		879,8	
bovids	1	0,02	1,1	0,00
perissodactyl	1	0,02	30,2	0,07
artiodactyl	1	0,02	1,2	0,00
ungulate small	16	0,32	76,5	0,17
ungulate medium	20	0,40	99,8	0,23
ungulate large	28	0,56	475,30	1,09
ungulate	13	0,26	36,0	0,08
Body size 1	43	0,86	9,9	0,02
Body size 2	257	5,14	220,6	0,50
Body size 3	1112	22,23	2692,0	6,16
Body size 4	992	19,83	6152,4	14,07
Body size 5	10	0,20	292,7	0,67
mammal	470	9,39	1153,0	2,64
bird	10	0,20	7,5	0,02
fish	4	0,08	0,7	0,00
Total	5296	100	47261,7	100
Total without ivory/antler	5003		43720,0	

Combined Assemblage

In total, 16,180 specimens, weighing 123,650.8 g, comprise the entire dataset for this study (Table 5.10+5.11). The sample size is also comparable throughout the MP and A, MP U (N=5815), followed by the Aurignacian (N=5003) and lastly MP R (N=4862). Weight also mirrors the number of specimens: 46,341.1 g for MP U, 47,373.6 g for the Aurignacian, and 30,314 g for the MP R. The identified specimens roughly make up 32.2% of the number of specimens, which remains consistent across cultural units, while the weight of identified material ranges between 55.7-70.2%. The unidentified specimens assigned to body size 3 are most common in the Middle Paleolithic, while specimens in body size 4 are more abundant in the Aurignacian.

The faunal assemblage is represented by 16 different mammalian taxa, which inhabited tundra-steppe and woodland environments in the Pleistocene. Overall, the general temporal trend does not alter when the data from two assemblages are combined. The most common taxon is cave bear/bear making up at least 20% of NISP and WISP, respectively. Brown bears are scarce throughout the assemblage, so we can subsume bears under cave bears; they will be considered as one taxonomic group when they are compared with other sites. The highest NISP and WISP values of cave bears and unidentified ursids are represented in the Aurignacian (NISP=1369, WISP=23,666.4 g), followed by the MP U (NISP=1218, WISP=12,628.6 g) and MP R (NISP=1085, WISP=6518 g). The %NISP and %WISP of cave bears are also the highest in the Aurignacian.

Horse is the second common taxon, after cave bears, in the MP. The NISP and relative proportion increases from the MP R (NISP=137, NISP%=2.8) to MP U (NISP=218, NISP%=3.8). In the Aurignacian, horse is the third most common taxon and still the most abundant herbivore in the cultural phase, but decreases substantially from the MP. With regard to weight, horses dominate among other herbivore or prey animals during the MP U, but their contribution is smaller in the MP R and they become rare in the Aurignacian.

Mammoths are the second most common herbivore in NISP and weight during the MP, and the weight proportion is greater than the horses. Mammoths become scarce during the Aurignacian. Ivory fragments are also more frequent in the MP than the Aurignacian. The number of two tusk fragments does not include pieces of ivory fragments recovered from the MP. Another megafauna, the woolly rhinoceros, exists in all the cultural units. The NISP value remains comparable in the MP and then decreases in the Aurignacian, although the weight increases continually from the MP R to the Aurignacian.

Reindeer exist in small quantities in both the NISP and WISP with no significant changes in their abundance over time. The notable increase, however, is observed in the number of antlers identified to the reindeer. Antlers that are confidently assigned to reindeer become more abundant in the Aurignacian period. Such a trend is also reflected in unidentified antler fragments, both for the number of fragments and their weight. Aurochs/bison as well as red deer are rare in all the cultural sequences.

Aside from cave bears, there are diverse carnivores represented in the assemblage. Hyenas and wolves are the most commonly represented middle-sized carnivores. On the one hand, the abundance of hyena remains increases slightly from the MP R to MP U in terms of %NISP and %WISP, which is followed by a clear decline in the Aurignacian. On the other hand, wolf inversely increases from the MP to the Aurignacian both in absolute numbers and %NISP as well as weight and %WISP.

Cave lions are small in number but exist in all cultural units. Among small carnivores, foxes are the most frequent taxon and their abundance does not vary over time. Eurasia lynx is hardly present in the assemblage, and the number of other small carnivores including mustelids and martens are few in number. Small carnivores may potentially also be included in the microfaunal assemblages and may be better represented.

The hares, although small in number, increase more in the Aurignacian period than the previous MP. Abundances of insectivores and rodents will be reevaluated when the analysis of microfauna is completed. There are a small number of birds and fish in the assemblage.

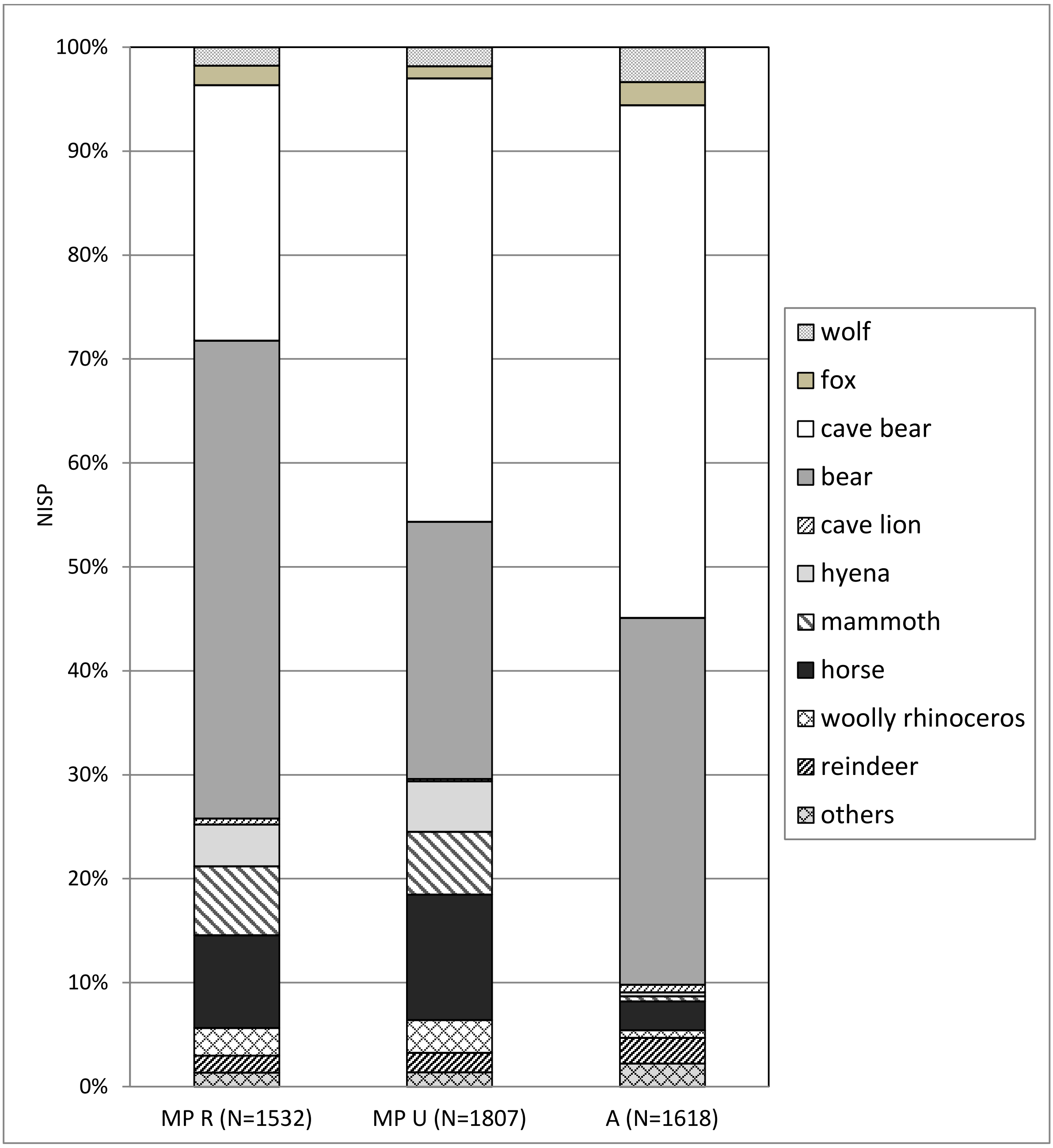


Figure 5.7 NISP of mammalian taxa for combined assemblage.

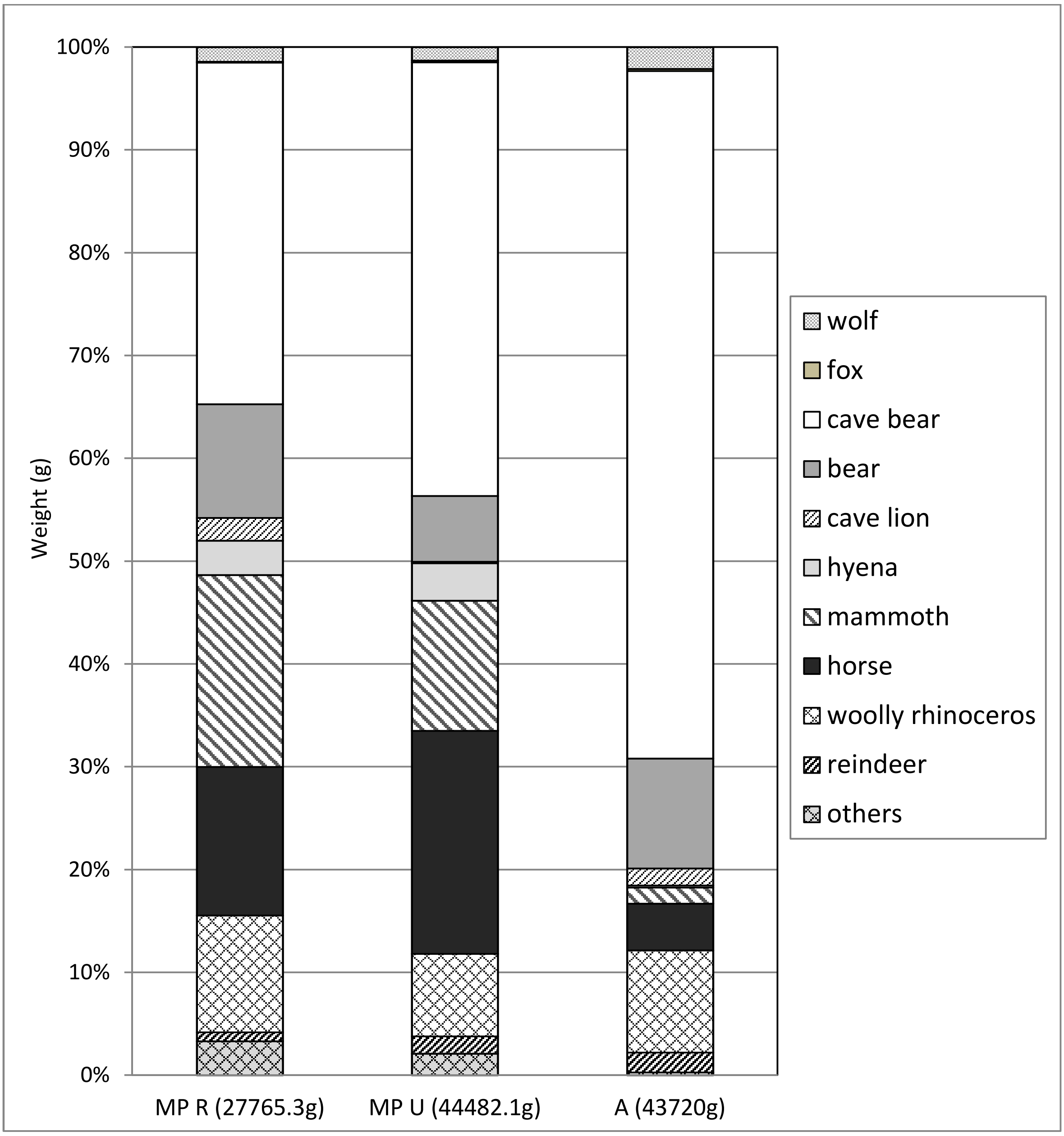
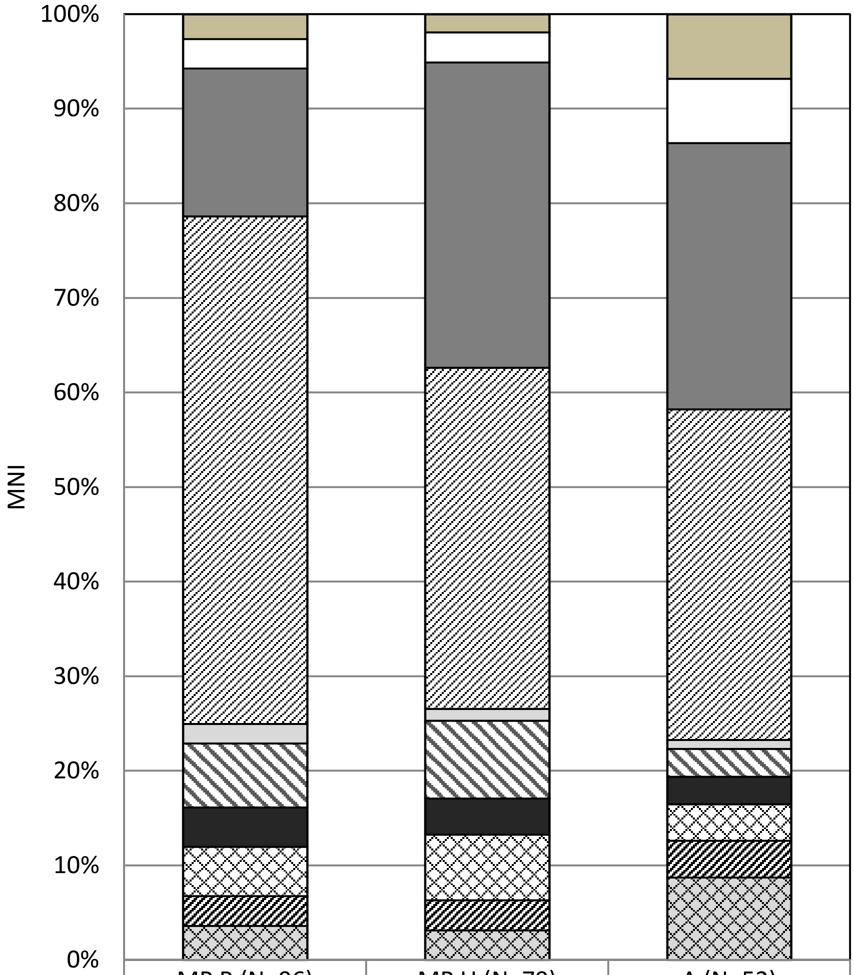


Figure 5.8 %WISP of mammalian taxa for combined assemblage.



	MP R (N=96)	MP U (N=79)	A (N=52)
■ wolf	3	2	4
□ fox	3	3	4
■ cave bear	15	26	15
▨ bear	52	29	18
□ cave lion	2	1	1
▧ hyena	7	7	2
■ mammoth	4	3	2
⊠ horse	5	6	2
▨ woolly rhinoceros	3	3	2
▩ reindeer	4	3	5

Figure 5.9 MNI of mammalian taxa for combined assemblage**.**

The relative NISP, weight and MNI of identified taxa are shown in Figures 5.7-5.9. The difference between NISP and the weight is clearly driven by the size and the overall contribution of larger mammals. Mammoths, woolly rhinoceroses and horses are better represented in the Middle Paleolithic, and herbivores make up roughly half of the assemblage.

Nonetheless, the relative weight proportion still shows decrease of herbivores in the Aurignacian. MNI values derived from MNE values closely resemble the NISP values. However, the MNI decreases for cave bears and unidentified ursids in the Aurignacian, which indicate that NISP and weight values exaggerate the abundance of cave bears.

NISP values and weight of taxon indicate positive correlations in the combined assemblage as well. The R_s values of transformed NISP and WISP per cultural phase are over 60%. During the MP R (R_s=0.60, p<.005), hare and fox have higher standardized residual values, both underrepresented in weight. During the MP U, Aurochs and bison are overrepresented in weight, but otherwise show high correlations (R_s=0.82, p<.0001). Woolly rhinoceros are overrepresented and hares are underrepresented in weight during the Aurignacian phase (R_s=0.67, p<.0001).

	MP			Aurignacian		
Taxon	Gamble NISP	AR	Kitagawa NISP	Gamble NISP	AR	Kitagawa NISP
cave bear	2674	**9,35**	2306	1935	**3,73**	1369
wolf	141	**-3,63**	60	157	**-4,41**	54
fox	78	-0,76	50	107	**-3,70**	36
hyena	476	**-9,70**	150	44	**-4,08**	6
cave lion	47	**-3,25**	13	15	0,47	12
mammoth	58	**12,19**	211	3	2,21	8
woolly rhinoceros	116	1,04	98	14	0,86	13
horse	735	**-7,41**	346	50	2,50	54
reindeer	95	-1,02	59	82	-1,67	40
aurochs/bison	112	**-7,15**	14	-	-	-
hare	1	**5,18**	22	22	2,90	32
∑	4533		3329	2429		1624
χ2		**412,62**			**73,49**	

5.12 NISP and adjusted residuals (AR) Gamble and combined assemblages with composite χ2 values (p-value<0.001); Signs of AR refer to values to this current analysis; significant values at p<0.05 in bold.

The comparison of the NISP from the combined assemblage and Gamble's analysis exhibits greater dissimilarity. This is also confirmed by the χ^2 values, 412.62 for the MP and

73.49 for the Aurignacian and adjusted residuals (Table 5.12). These χ^2 values are greater than χ^2 values based on the reanalysis of the material from 1939 and Gamble alone. The difference is particularly large in the MP in which wolf, hyena, cave lion, horse and aurochs are represented by fewer NISP while the cave bears, mammoths and hares are better represented in the combined assemblage. During the Aurignacian, the difference between Gamble and the current analysis is roughly comparable, but wolf, hyena and fox are better represented in Gamble's analysis while cave bear is better represented in the current analysis.

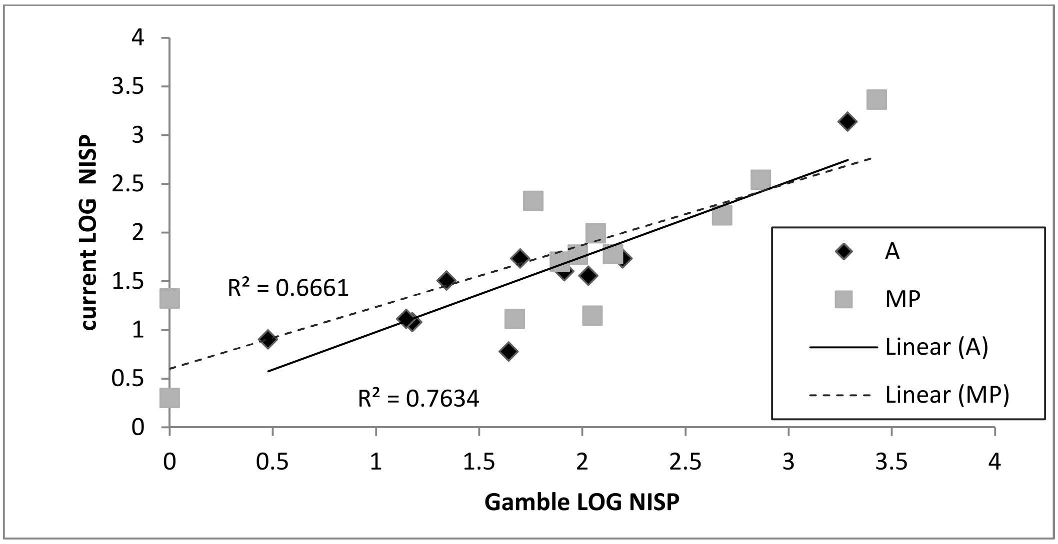


Figure 5.10 Correlation of NISP taxa from Gamble and the current analysis of material from 1939. The correlation is high and significant (p-value=.001).

However, the correlation between species abundance for this current analysis and Gamble's work is still high, with the R_s value of 0.67 for the MP and R_s value of 0.77 for the Aurignacian at the significance level of <.001 (Figure 5.10). These values of correlation coefficient are lower than when the material from the old excavation alone was compared, but still high and significant. Spearman's rho test points to a relatively high correlation (0.77 for MP and 0.78 for the Aurignacian) at a lower significance level of 0.05. These values suggest that the material from the old excavation sampled in this study is a good representation of

Gamble's work. Contrasting recovery methods and varying spatial distribution of animal remains may account for a greater degree of difference in the taxonomic abundances.

Taxon	MP R		MP U		A
	NISP	AR	NISP	AR	NISP
hare	10	0,06	12	**3,28**	31
wolf	27	0,17	33	2,80	54
fox	29	-1,71	21	2,42	36
cave bear	378	**11,05**	771	**3,85**	798
bear	707	**-12,81**	447	**6,71**	571
cave lion	9	-1,68	4	2,23	12
hyena	62	1,19	88	**-8,06**	6
mammoth	102	-0,69	109	**-8,92**	8
horse	137	**2,99**	218	**-10,20**	45
woolly rhinoceros	41	0,85	57	**-4,86**	13
red deer	1	-0,11	1	-0,95	0
reindeer	25	0,57	34	1,18	40
aurochs/bison	9	-1,37	5	-1,50	1
∑	1537		1800		1615
$\chi 2$		205,88		332,26	

Table 5.13 NISP and adjusted residuals (AR) for MP R, MP U and the Aurignacian assemblages with composite $\chi 2$ values (p-value<0.001); Signs of AR refer to values of cultural layer to the right; significant values at $p<0.05$ in bold.

Kitagawa Taxon	MP		A
	NISP	AR	NISP
hare	22	**4,04**	31
wolf	60	**3,40**	54
fox	50	1,85	36
cave bear	1149	**10,12**	798
bear	1154	0,54	571
cave lion	13	1,65	12
hyena	150	**-7,79**	6
mammoth	211	**-9,35**	8
horse	355	**-9,51**	45
woolly rhinoceros	98	**-4,75**	13
red deer	2	-0,98	0
reindeer	59	1,67	40
aurochs/bison	14	-2,15	1
∑	3337		1615
$\chi 2$		351,52	

Tab5.14 NISP and associated adjusted residuals (AR) between MP and the Aurignacian with composite $\chi 2$ values (p-value<0.001); Signs of AR refer to values of cultural layer to the right; significant AR values at $p<0.05$ in bold.

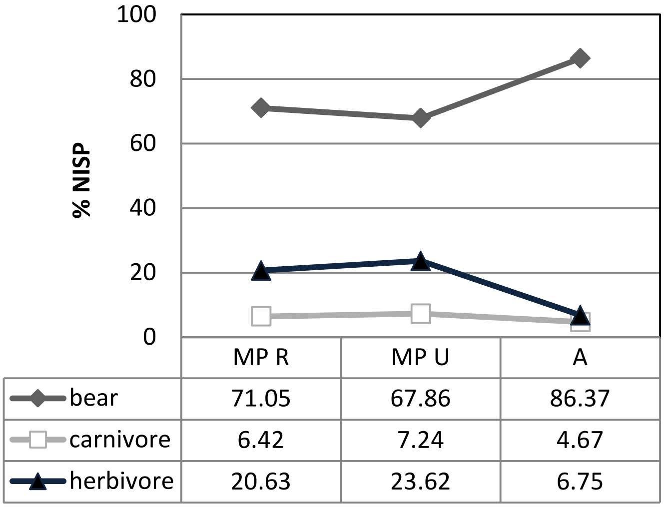
The comparison of each cultural sequence and adjusted residuals between the layers show that there is a significant difference between MP layers and the Aurignacian in species abundance (Table 5.13). The χ^2 values indicate that the difference is most significant between the MP R and the Aurignacian, but the number of taxon with significant adjusted residual values ($p<.05$) indicates a difference between the MP U and Aurignacian.

Between the MP U and MP R, cave bears and unidentified ursids result in higher adjusted residual values with significance at the level of $p<.0001$ and horses at the level of $p<.05$. The cave bears and horses increase from the MP R to MP U while the number of bears declines. The difference between MP R and MP U become even slighter when the cave bear and unidentified ursids are collapsed together. Besides these taxa, the relative NISP values of other animals reflect continuity. Between the MP U to the Aurignacian, χ^2 values are greater than between MP R and U. We observe a significant decrease in hyena, mammoths, horses and woolly rhinoceros, and overall increase in cave bear, bears and hare according to the adjusted residual values. When the NISP of the MP R and U are combined, the patterns of species abundance are similar to that of MP U/A. There is an increase in hare, wolf and cave bears, but decrease in hyena and prey animals including mammoth, horse, woolly rhinoceros and aurochs/bison.

With some exceptions, the trend of species abundance is similar when the adjusted residual values are analyzed based on Gamble’s data. In contrast to this current analysis, foxes and reindeer increase while aurochs/bison decrease from the MP combined to the Aurignacian. Therefore, the patterns of species abundance for the Middle Paleolithic and the Aurignacian are comparable for the current analysis as well as Gamble’s analysis, which makes up a larger sample pool. The patterns are characterized by the decrease of a number of prey animals and hyenas and a clear increase in cave bears and hares comprising the Aurignacian assemblage.

Cave bears, herbivores and carnivores

Herbivores decrease substantially from the MP to the Aurignacian (Figure 5.11). This is partially due to the increase of bears in the Aurignacian period. The abundance of herbivores expressed as herbivore index shows a gradual increase from the MP R to MP U and a clear decline in the Aurignacian. The herbivore indices, which include herbivore and carnivore remains identified to the order of Carnivora, Artiodactyla, Perrisodactyla , Proboscidea are 0.21, 0.25 and 0.10 for the MP R, MP U and Aurignacian, respectively. The lower values signify the decrease in the proportion of herbivores in the assemblage. Further, there is an insignificant but a positive correlation between the NISP of carnivores and herbivores. These values confirm the temporal trend in the decrease of herbivore input in the deposit during the Aurignacian relative to the Middle Paleolithic.



	MP R	MP U	A
◆ bear	71.05	67.86	86.37
□ carnivore	6.42	7.24	4.67
▲ herbivore	20.63	23.62	6.75

Figure 5.11 % NISP of carnivores, bears and herbivores per cultural layer

	MP R	AR	MP U	AR	A	MP	AR	A
bear	1085	-1,96	1218	**11,66**	1369	2303	**11,83**	6,418
mid/large carnivore	98	0,941	130	**-3,24**	74	228	**-3,1**	1548
herbivore	315	2,073	424	**-13,6**	107	739	**-13,6**	0
small carnivore	29	-1,43	23	2,256	37	52	1,819	71,05
lagomorph/rodent	11	-0,18	12	**3,406**	32	23	**4,067**	1498
χ^2		7,4		216,1			218,5	

Table 5.15 NISP and adjusted residuals (AR) of taxonomic group and $\chi 2$ values (p-value<0.001) for across cultural layer as well as MP combined compared to the Aurignacian; Signs of AR refer to values of cultural layer to the right; significant values at p<0.05 in bold.

The adjusted residual and χ^2 values for assemblages based on broad faunal groups (carnivore, herbivore, small carnivore, middle/large carnivore and lagomorph/rodents) also confirm this pattern (Table 5.15). The difference between MP R and MP U is insignificant with low χ^2 values and low adjusted residual values. There are significant differences between the MP U and the Aurignacian, with increases in bears and lagomorphs/rodents and decreases in middle/large carnivores and herbivores. The only animal group which remains consistent is the small carnivores. All these measures point to the increasing presence of cave bears and lagomorphs/rodents in the Aurignacian and a decreasing presence of the large predators and prey animals. This is an indication that there is relatively little contribution of animal carcasses transported into the cave, while the endogenous animals, mostly bears, become more abundant. Predators also show a decrease in presence in the faunal assemblages.

Diversity

Different measures of taxonomic diversity show lower evenness value for the Aurignacian in comparison to MP R and MP U (Table 5.16). The Shannon index of evenness is the highest in MP R, decreasing in the MP U and the Aurignacian. Such patterns reflect the dominance of certain taxa, namely cave bears, in the assemblage. Such patterns are also not driven by the sample size per se. The reciprocal of Simpson's Index (1/D) displays comparable measures of evenness for the MP R and MP U. In contrast, the Aurignacian period is characterized by reduced evenness with a lower Simpson's index value. Some evaluate evenness by dividing the Simpson's index with the number of taxa (NTAXA). The relative evenness among the strata alters slightly, with MP R showing the highest evenness value, though the Aurignacian is still the least diverse assemblage. Measures of taxonomic diversity all highlight the low diversity measure in the Aurignacian assemblage.

	All			Without bear		
	MP R	MP U	A	MP R	MP U	A
NTAXA	13	**16**	14	12	**14**	12
Shannon index of evenness	**0,46**	0,45	0,28	0,34	0,30	**0,36**
Simpson's index (D)	0,51	**0,48**	0,72	0,18	0,21	**0,15**
1/D	1,95	**2,10**	1,39	5,58	4,72	**6,80**
Simpsons index of evenness	**0,15**	0,13	0,10	0,46	0,34	**0,57**

Table 5.16 Diversity values for across different horizons with all taxa considered and cave bear/bear excluded.

When the cave bears are excluded from the analysis, the measure of diversity increases for all the cultural layers. The Aurignacian assemblage shows a greater value of evenness relative to the Middle Paleolithic. Despite the fact that the presence of carnivores and cave bears obscures signatures of hominin activity, it is possible that greater evenness of large game in the Aurignacian is a partial reflection of diversification in the prey choice of humans. There is a weak and positive correlation between sample size and the measures of diversity (Rs =0.96 for both Shannon and Simpson’s index of evenness), so this interpretation should be taken with caution. Nonetheless, it appears the diversity indices track the dominance of cave bears, while the exclusion of cave bears from the indices highlights the diversity in the herbivorous taxa at the site.

Taphonomy

Preservation of faunal remains

Based on the weathering stages, roughly 35-50% of specimens show some weathering (Figure 5.12). Among weathered specimens, most exhibited surface cracking or light flaking (stage 1 and 2). Heavier weathering between stages 3-5 affects the surface of the bone to the degree that it could obscure other modifications such as butchering marks from humans as well as scoring and trampling. From the lower to the upper horizons, there is a gradual increase in the number of weathering specimens. This could be attributed to the duration of specimens exposed on the surface prior to burial as well as mechanical weathering that can result from biological forces such as trampling.

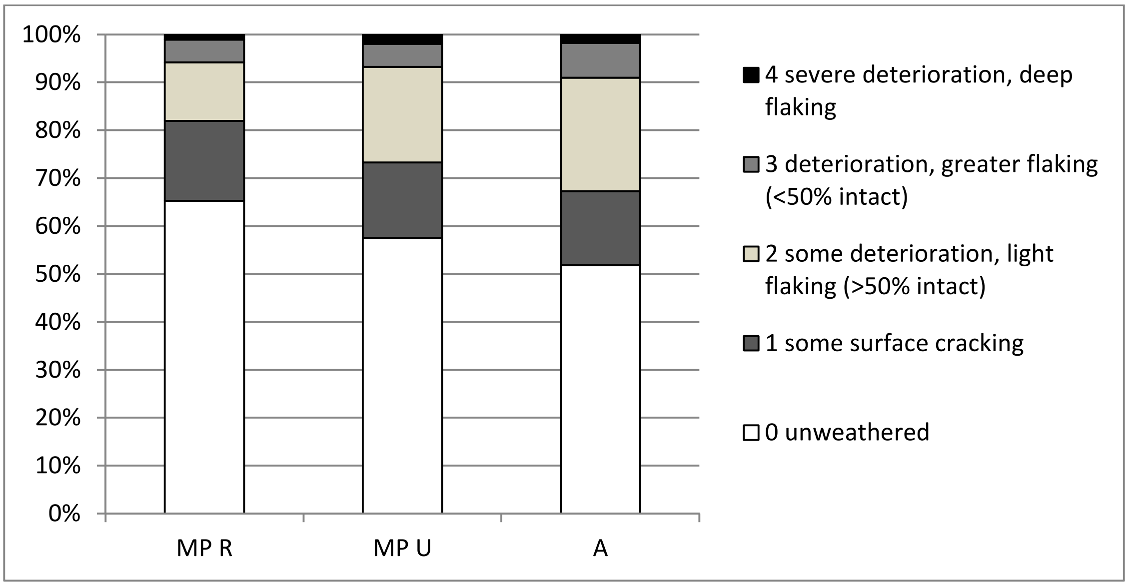


Figure 5.12 Weathering stages for each horizon

	rounded	%	heavily rounded	%	not rounded	rounded+ heavily rounded	AR	total
A	312	5,89	93	1,76	4891	405	**-35,45**	5296
MP U	1590	26,70	351	5,89	4014	1941	**17,09**	5955
MP R	1365	27,20	350	6,97	3303	1715	**18,14**	5018

Table 5.17 Frequency and % of specimens with rounding/heavy rounding. Adjusted residual (AR) values for rounded and heavily rounded specimens combined. χ^2 value: 1260.36 and significant AR values in bold ($p<.001$)

At the same time, the frequency of specimens affected by mechanical and chemical rounding is high in both layers of the MP, which affects the preservation of bone surface (Table 5.17). It appears that the faunal material from the Middle Paleolithic shows a greater a frequency of rounding or abrasion, which could result from several causes such as chemical weathering, trampling or carnivore gnawing. This is confirmed by adjusted residual values, which indicate that rounded specimens occur more frequently than expected in the MP R and MP U assemblages and occur less than expected in the Aurignacian. Thus, while the assemblage from the MP is characterized by, in part, a greater frequency of rounding in the assemblage, the Aurignacian assemblage shows a greater proportion of specimens with weathering. Since rounding could mask weathering that occurred prior to other abrasion, it is possible that the degree of weathering on faunal material did not differ significantly in all the horizons, but that a greater proportion of the MP assemblage is affected by rounding.

While rounding could be attributed to several causes, high frequency and the size of specimens cannot solely be attributed to carnivore gnawing. When specimens with carnivore digestive corrosion and rounding were excluded, there is a greater rounding without visible carnivore traces in the Aurignacian than in the MP. Trampling, another physical force that can account for rounding, has not been recorded as frequently as expected, considering that cave bears actively alter the spatial distribution of remains when they prepare for denning (Camarós et al., 2013). It is possible that unoriented scratches, which are a key trait in identifying trampling, do not always co-occur with specimens that undergo rounding, or that rounding itself masks other diagnostic features of trampling action.

Another possibility is that the rounding occurred due to chemical dissolution. This could account for the lack of other features that relate to biological agent and the range in the size of specimens affected by rounding, which could be at times relatively large. Water may have permeated the sediment or may have been substantial enough to cause a flow, which could cause rounding. The preliminary analysis based on micromorphology appears to disprove this possibility, noting that there is no clear evidence of water flow (Jahnke, 2013). This, however, needs to be confirmed with additional studies within the inner part of the cave. Also, Riek (1934) noted loamy sediment with water in the MP horizon of Vogelherd, which caused rounded edges and polished surface of bones (Niven, 2006). The phosphate enrichment of sediment will be analyzed to consider chemical corrosion of bones of MP R (Smith et al., 2007). Although at different sites, high phosphate levels in the micromorphological samples from Geißenklösterle and Hohle Fels in the Middle Paleolithic level do in part leave this possibility for future studies.

Anthropogenic modification

The signature of human activities linked to subsistence activities and habitual use of a site is not well represented in the faunal assemblages. Anthropogenic modification includes cutmarks, impact fractures and burning. Other forms of anthropogenic modification such as organic artifacts are not considered in this analysis.

ID #	Cultural layer	Taxa	Element	Anthropogenic modification
409	MP R	*Body size 3*	long bone shaft	impact fractures
193/173. 1322	MP R	*Rangifer tarandus*	Metatartus III	impact fractures
193/173. 852	MP R	*Body size 4*	Rib	cutmarks, possible
4209	MP U	*Body size 4*	long bone shaft	artifact, possible retoucher
866	MP U	*Body size 4*	long bone shaft	cutmarks
5848	MP U	*mid Carnivora*	Thoracic Vertebrae	cutmarks
4031	MP U	*Equus sp.*	metapodial	cutmarks
577	MP U	*Equus sp.*	long bone shaft	impact fractures
782	MP U	*Ursus spelaeus*	long bone shaft	impact fractures
1226	MP U	*Body size 3*	long bone shaft	impact fractures
7040	MP U	*Rangifer tarandus*	antler	impact fractures
1488	A	*Ursus spelaeus*	Rib	cutmarks
1416	A	*Equus sp.*	Humerus	cutmarks
1984	A	*Ursus sp.*	Rib	cutmarks
2158	A	*Body size 4*	Femur	cutmarks
3590	A	*Body size 3*	Rib	cutmarks
3814	A	*Body size 3*	Rib	cutmarks
5885	A	*Body size 4*	Rib	cutmarks
5995	A	*Ursus sp.*	Femur	cutmarks
1807	A	*Ungulata*	Rib	cutmarks
1539	A	*Body size 3*	Rib	impact fractures
1986	A	*Body size 4*	long bone shaft	impact fractures
3828	A	*Cervidae*	Radius	impact fractures
9184	A/MAG	*Body size 3*	ind. Long bone	Cutmarks
9376	A/MAG	*Ursus spelaeus*	Baculum	Cutmarks
9358	A/MAG	*Rangifer tarandus*	Femur	impact fractures
9345	A/MAG	*Rangifer tarandus*	Tibia	impact fractures

Table 5.18 Specimens with cutmark and impact fractures.

Cutmarks are sparse and warrant closer examination. Some of the cutmarks are deeply incised. Butchering marks with greater depth are likely to withstand surficial weathering and other forms of modification. Due to the common prevalence of rounding, we conclude that abrasive force adversely affected the identifiable anthropogenic marks that may have been left on the assemblage. Therefore, the interpretation of shallow striations remains elusive, which can result from human scarring, carnivore scoring or sediment abrasion on the surface.

In the MP, the number of specimens with impact fractures is greater than that with cutmarks. The impact factures of MP R are found on reindeer metatarsals and on an unidentified shaft fragment. There is also a specimen with possible cutmarks. Metapodials of reindeer contain larger amounts of marrow and is a possible indication of marrow extraction. During the MP U, there is one specimen that is an artifact, possibly a retoucher with percussion pits exhibited on the long bone shaft of body size 4 (cave bear and horse). Cutmarks are on one equid metapodial, one vertebra of a middle-sized carnivore, and one unidentified shaft fragment. Impact fractures are observed on four specimens including horse and cave bear as well as on the antler of a reindeer. We can only infer, however, that the last specimen is related to artifact production, since the morphology of the breakage patterns also differs from bones.

During the Aurignacian, there are a greater number of specimens bearing butchering marks than percussion marks. The cutmarks on the cave bear rib occur on two specimens (Figure 5.13). Butchery of ribs usually point to defleshing/filleting of the meat, which has not been documented often in the Paleolithic record. The evidence of cutmarks suggests the opportunistic exploitation of cave bear for subsistence. Impact fractures are again observed on cervids/reindeer, which could indicate marrow extraction. The number of impact fractures and cutmarks speaks to a relatively small role for humans in the modification of faunal assemblages, which also is an indication that other predators transported the material into the cave.

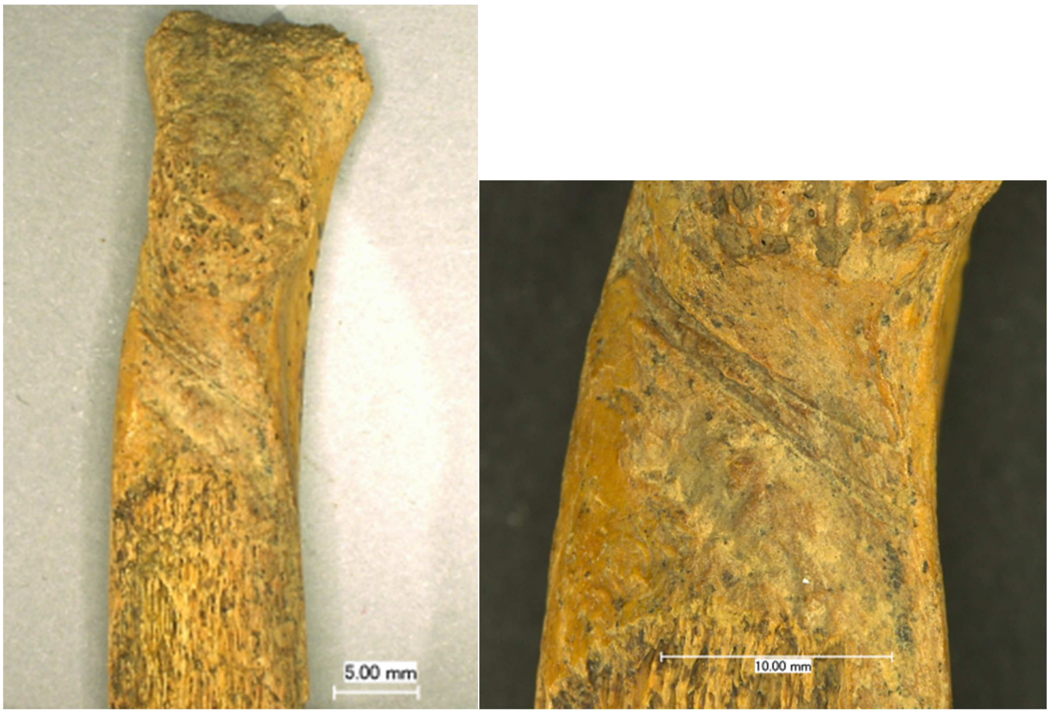


Figure 5.13 Cut marks on a bear rib with a close-up

Burning is the most common form of anthropogenic modification across all horizons. Many of the specimens were charred and highly fragmented, which point to the possible use of bone as fuel, although the direct exposure to heat could have been related to other activities such as cooking or due to unintentional subsurface burning of animal remains below combustion feature (Costamagno et al., 2005; Stiner et al., 1995; Théry-Parisot et al., 2005). During the MP, the relative frequency of burnt specimens remains consistent at 2%, but there is a decrease in the number of burnt specimens from the MP to the Aurignacian, which comprises 1% of bone specimens. This is also reflected in the weight of the burnt specimens, which tracks the pattern in the frequency of specimens.

	burnt bone	%	weight (g)	unburned bone	%	AR
A	48	1,04	52,3	4551	98,96	**-4,42**
MP U	94	2,17	131,7	4228	97,83	2,91
MP R	69	2,03	122,3	3332	97,97	1,67

Table 5.19 Frequency and weight of burnt bone specimens. Adjusted residual (AR) values for burned specimen. χ^2 value: 19,74 and significant AR values in bold (p<.001)

The adjusted residual values show that the burning of specimens occurring in MP R and MP U is within the expected range compared to rest of the strata, while the amount of burnt material in the Aurignacian is significantly less than expected (AR=-4.42) (Table 5.19). The decrease of burnt material in the Aurignacian is also significant (χ^2 =18.20, p<.0001) when the frequency in MP U and the Aurignacian is compared. Therefore, the most frequent form of anthropogenic modification, burning, decreases from the MP to the Aurignacian in a significant proportion and testifies to decreasing use of hearths and possible decline in human occupation of the cave.

	anthropogenic modification	%	unmodified	AR
A	64	1,21	5229	**-6,55**
MP U	102	1,71	5853	**-3,93**
MP R	212	4,22	4806	**10,75**

Table 5.20 Frequency of modified and unmodified specimens

anthropogenic modification	MP R	MP U	A
cutmark	1	3	11
impact fracture	2	5	5
burning	209	94	48
∑	212	102	64

Table 5.21 Frequency of specimens with cutmark, impact fracture and burning

Overall, the proportion of the specimens with anthropogenic modification is relatively low throughout the sequence (Table 5.20 + 5.21). In the MP R, the modified specimens make up 4.2% of the entire assemblage, while signatures of human activity related to hearth making and subsistence come to a mere 1.7% and 1.2% in the MP U and Aurignacian, respectively. Based on the AR values, anthropogenic modification occurs at a greater proportion in the MP R, but at a lower proportion in the MP R and Aurignacian as expected. The difference in proportions between MP U and Aurignacian is not as significant as the decline from the MP R to MP U. (χ^2=42.7, <.001).

Carnivore modification

Carnivore modification, as described in the methods, encompasses a range of mechanical alterations to animal remains. When all forms of carnivore modification are tallied, it is most frequent during the MP U (Table 5.22). Altogether, 11% of the specimens were affected by carnivore damage in the MP U in contrast to the MP R (6.1%) and Aurignacian (5.1%). The χ^2 value for specimens with and without carnivore modification is significant (157.47, p <.001).

	carnivore modification	undamaged	AR	% carnivore modification
A	269	5024	**-8,20**	5,08
MP U	649	5306	**12,40**	10,90
MP R	306	4712	**-4,61**	6,10

Table 5.22 Number of specimens with carnivore modification and adjusted residuals by horizon with $\chi 2$ value= 157.47. Signs of AR refer to values for specimens with carnivore modification. Significant values at p<0.001 in bold.

The proportion of carnivore modification from the MP R to MP U increases significantly (χ^2=78.98), and carnivore damaged specimens become infrequent at a significant level (χ^2=126.57) in the Aurignacian compared to the MP U. When the MP is combined, there is still a decline in the frequency in the Aurignacian (χ^2=67.4, <.0001). The adjusted residual values of carnivore damaged and undamaged specimens across the horizon are all significant, which, based on the sign of AR suggests that the carnivore damaged specimens occur more frequently in the MP U, while there appears to be less carnivore modification in the MP R and the Aurignacian than expected. The relative infrequency of carnivore modification is in part affected by rounding, which occurs commonly in the MP R assemblage, eliminating traces prior alterations.

Different forms of carnivore modification do not occur consistently across the horizons. The occurrence of gnawing, scoring, pits, punctures and digestive corrosion is tallied to observe the frequency over time (Table 5.23 and Figure 5.14). Specimens with multiple patterns of carnivore damage have been calculated twice. The most common form of modification is digestive corrosion in the MP R and MP U, and carnivore pits in the Aurignacian. The frequency of gnawing and scoring decreases from the MP R and MP U at a significant level while the specimens with digestive corrosion are better represented in the MP U according to the AR values (Table 5.24). Compared to the MP U, the Aurignacian is characterized by a high frequency of gnawing, scoring, pits, punctures, but a low frequency of digestive corrosion.

	MP R	%	MP U	%	A	%
carnivore gnawing	43	0,86	30	0,50	34	0,64
carnivore scoring	22	0,44	19	0,32	30	0,57
carnivore pit	75	1,49	145	2,43	154	2,91
carnivore punctures	14	0,28	31	0,52	41	0,77
carnivore digestive corrosion	169	3,37	448	7,52	40	0,76
total specimens with carnivore damage	306		649		269	
total specimens	5018		5955		5296	

Table 5.23 Number of specimens with different types of carnivore modification and %

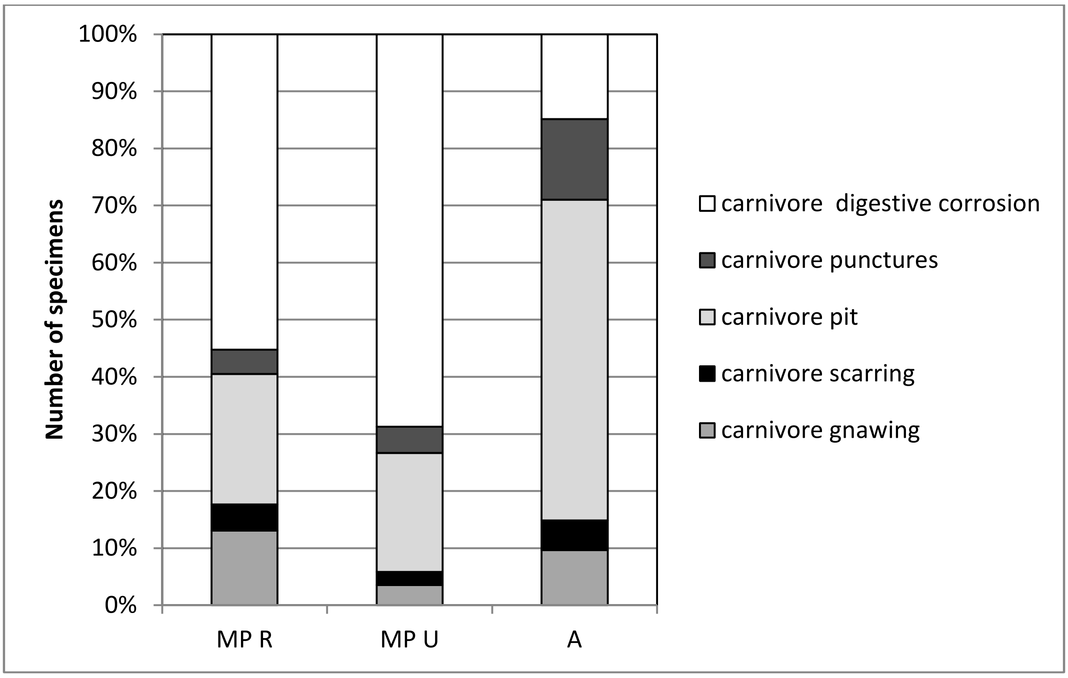


Figure 5.14 Number of specimens with different types of carnivore modification per horizon

	MP R/U	MP U/A	MP/A
carnivore gnawing	**-5,02**	**4,01**	2,23
carnivore scoring	**-2,97**	**4,74**	**3,94**
carnivore pit	-0,60	**9,34**	**9,84**
carnivore punctures	0,19	**5,00**	**5,60**
carnivore digestive corrosion	**4,33**	**-15,31**	**-14,73**

Table 5.24 Adjusted residual (AR) values for different types of carnivore modification

Thus, a change in the type of carnivore damage is documented from the MP U to the Aurignacian. The decrease of digestively corroded specimens is still significant when the combined MP assemblage is compared with the Aurignacian. Further, the infrequent occurrence of fauna damaged through digestion by predators in MP assemblages can in part explain the increase in the frequency of other forms of carnivore damage.

Corrosion through salivary acid alter the morphology of specimens in a form of heavy rounding, which then obscures other damage patterns, especially that of surficial modifications (scoring and pits when the depression is not so deep below the surface of bones). Therefore, it is probable that other forms of carnivore modification occurred more frequently than observed, and later obliterated. However, the decline in digestively corroded specimens is an independent trend that is not affected by other physical modification of specimens.

The decrease of digested specimens may relate to changing predators responsible for the modification of the animal remains on site. The general abundance of wolves, which also damage bones with salivary acid, is consistent from the MP to the Aurignacian, and carnivores appear to be present during the Aurignacian period. Instead, there is a clear decrease of hyenas from the MP to the Aurignacian. Further, the dentition of hyenids is adapted to crushing bones, and hyenas have greater bite force than other middle and large size predators such as wolves (Werdelin, 1989). They are therefore more inclined to consume and digest bone fragments and produce regurgitated scats or digested bone remains. Thus, specimens with digestive corrosion are associated with hyenas scavenging and consumption patterns.

The number of pits suggestive of small carnivore modification suggests foxes, martens, mustelids, wild cat, and their frequency increases significantly from the MP to Aurignacian (χ^2=7.91, p<.005). However, the frequency of middle and large carnivores does not indicate significant difference between the MP and the Aurignacian and thus, the number of specimens affected by carnivore pitting is similar in frequency. Carnivore puncture, on the other hand, increases slightly over time with some significance (χ^2=7.65, p <.006). Further, there is a significant decline in the number of specimens showing corrosion through carnivore digestion (χ^2=217.4, p <.0001).

Carnivores exploited a diverse range of taxa including herbivores, carnivores and ursids. %NISP of identifiable taxa with carnivore damage shows that herbivores are most heavily modified by predators, followed by carnivores and cave bears except for the MP U, where 26% of wolf and hyena remains were exploited by other predators (Table 5.25). The percent of ungulate and proboscidean remains with carnivore damage increases from the MP U to the Aurignacian from 12% to 29%, pointing to the greater importance of herbivores over carnivores in the early Upper Paleolithic. The modification on cave bears is at 1.8% in the MP R, but increases in the MP U and the Aurignacian to 5.6 and 6.5%, respectively.

	MP R			MP U			A		
	specimen	%	AR	specimen	%	AR	specimen	%	AR
bear	20	1,84	**-6,97**	68	5,58	**-5,61**	89	6,50	**-6,96**
carnivore	4	7,14	1,27	15	26,32	**5,25**	11	11,96	1,29
herbivore	33	10,48	**6,78**	51	12,03	**3,65**	31	28,97	**7,98**

Table 5.25 Frequency, % and adjusted residual (AR) values of specimen with carnivore modification on bear, carnivore and herbivore.

The adjusted residual values demonstrate that herbivores are inflicted by carnivore damage more frequently than expected and cave bears with carnivore modification occur infrequently in contrast to the other two faunal groups in the MP R assemblage (Table 5.25). During the MP U, carnivores consisting mostly of wolves and hyenas are modified extensively by other carnivores compared to other taxonomic groups. Nonetheless, herbivore remains with carnivore damage are also higher in number than cave bears. During the Aurignacian, the occurrence of herbivore specimens with carnivore modification is high while cave bears are not affected by carnivores as expected.

Carnivore damage can render the specimens unidentifiable due to attrition and fragmentation, and we need to evaluate whether the trend described above is still applicable to other carnivore-damaged specimens. When unidentified carnivore/bear remains (as they are cannot be distinguished on the level of Order) and unidentified herbivore remains are tallied, the number of carnivore/bear with predator damage still remains low in the MP R at 2%, increasing to 6% in the MP U and Aurignacian (Table 5.26). In contrast, herbivore remains with carnivore damage increase in the Aurignacian to 18% relative to the MP R and MP U (10.3 and 11.9%), respectively. The adjusted residual values show that carnivore/bear remains damaged by predators are not so well represented in the MP R as expected, and relative to other strata (-5.56), while herbivore remains, despite the proportional increase in the Aurignacian, is not significantly more common based on the AR values (on the level of $p<0.05$).

	Bear/Carnivore				herbivore			
	damaged	undamaged	%	AR	damaged	undamaged	%	AR
A	111	1734	6,02	2,67	38	164	18,81	2,94
MP U	96	1473	6,12	2,58	65	482	11,88	-0,70
MP R	30	1335	2,20	**-5,56**	39	339	10,32	-1,64

Table 5.26 Frequency, % and adjusted residual (AR) values of specimen with carnivore modification on unidentified bear, carnivore and herbivore.

The differential distribution of carnivore modification on faunal groups points to hunting and transport of herbivorous taxa by carnivores. Further, the damage on carnivore remains does not suggest a predator-prey relationship; intraspecific competition among hyenas is well documented in modern communities in the savannah, which can partially account for the intensive damage by carnivores. Contrary to some arguments that carnivores actively hunt and consume cave bears during winter hibernation (Diedrich, 2012), carnivores did not heavily prey on cave bears but turned to herbivores as their prey. However, the preference of prey and the behavior of predators vary in different ecological communities and the geographical settings of the caves (specifically with regard to accessibility and visibility), which does not lend itself to a broad generalization about carnivore and cave bear interaction in the Paleolithic landscape.

Other modifications

Certain alteration is due to the depositional context, the mineral and clay composition, which affected the faunal material. Some specimens show clear staining from manganese oxides. This appears in the form of black spots on the surface of the bones. This form of modification is most commonly observed in the MP U. (As a side note, this form of staining occurs in the lower level known as the Black MP on a more frequent and extensive degree, which accounts for the term ‘Black Mousterian’ to describe the horizon.) Other forms of modification such as root etching and rodent gnawing are rare in the assemblage.

Several lines of evidence point to greater contributions of exogenous faunal remains by non-human predators. Carnivore modification occurs more frequently than anthropogenic modification. Further, ungulate and proboscidean remains indicate carnivore modification at a higher proportion than anthropogenic modification throughout all cultural sequences. It is likely that many of the animal carcasses, except for the cave bears, were transported by non-human predators. However, the decrease of carnivore and anthropogenic modification from the MP U to Aurignacian is an independent phenomenon, pointing to a greater overlap of carnivore and human activity in the cave during the MP and subsequent decrease of human and carnivore presence. There is no clear sign of modification on fauna by cave bears. Determining the predators/scavengers responsible for carnivore modification always poses challenges and limitations. Patterns of carnivore damage and the interaction with animal remains are not determined solely by biological differences between animal species but also by the condition of the animal (such as the presence of competition, appetite) (Faith et al., 2007). Further, cave bears are known to consume plant material only based on the isotopic studies. This point requires further investigation in the future.

Skeletal representation and Ageing

Cave Bears

Cave bears often are recovered from caves as a result of natural mortality during winter. To test rather if this is the case at this site, we study the skeletal representation and ages of the cave bears. We expect that the cave bears will be represented by all body parts if animals entered the cave during hibernation. Several measures are used to assess if this is a reasonable assumption.

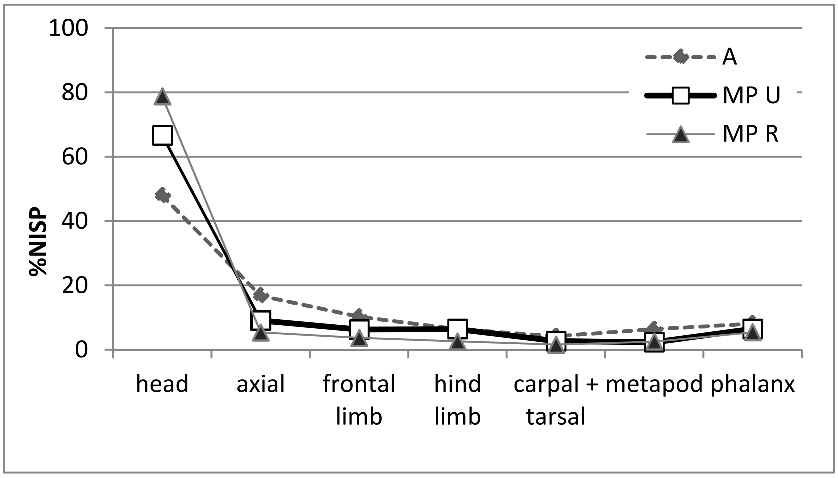


Figure 5.15 NISP abundance of skeletal elements for cave bear

The relative NISP abundance of skeletal elements is divided into head, axial, frontal limbs, hind limbs, carpals/tarsals, metapodials and phalanges (Figure 5.15). The cave bears and unidentified ursids are heavily biased towards the cranial elements or teeth and against other skeletal parts in MP R and MP U. When the NISP of cave bear and unidentified ursids, according to body parts, are combined, following a reasonable assumption that most bear remains are cave bears (due to the scarcity of brown bears in this deposit), there are significant differences in the skeletal element. The χ^2 values and AR values of MP R and MP U point to a significant decrease in the cranial parts and increase of axial elements, hind limbs and phalanges. The cranial part is less represented, but the axial element, frontal limbs and metapodials occur more frequently in the Aurignacian.

Further, the weight proportion of the complete skeleton of the brown bear (UR 7 in zooarchaeological reference collection of University of Tübingen) was compared to relative weight of the cave bears by skeletal elements (Table 5.27 and Figure 5.16). The difference in the weight proportion between the modern brown bear and Paleolithic cave bear is shown under % difference. For modern brown bear, crania as well as the upper frontal, hind limb (humerus and femur) and vertebra are heavier compared to other elements, but each skeletal part does not exceed 15% in the entire weight of the skeleton.

Cave bears from the MP R are represented by an excess weight of crania and mandible fragments, at 20.6% and 14%. In contrast, many of the limb proportions including humerus, femur and tibia and the axial elements, are underrepresented. The MP U is also represented by a similar pattern. The cranial and mandibular parts are overrepresented by 12 and 18.3%, respectively and the axial element, pelvis, vertebra and forelimbs are underrepresented by -4.5 to -9.6%. The Pearson correlation coefficient of the relative weight distribution for modern brown bears and the cave bears from the Middle Paleolithic (MP R and MP U) is low and indicates that the weight representation varies with little resemblance to the reference collection. Therefore, the skeletal representation of cave bears from the Middle Paleolithic contradicts the assumption that entire individuals are represented.

	Comparative skeleton		MP R		MP U		A	
Skeletal Element	g	%	g	% difference	g	% difference	g	% difference
Cranium + Maxillary teeth	833.0	11.6	2012.6	20.6	20.7	12.0	8.4	-2.4
Mandible + Mandibular teeth	374.0	5.2	1263.0	15.0	38.0	18.3	18.8	8.9
Hyoid	6.0	0.1	15.9	0.2	0.2	0.1	0.3	0.1
Scapula	353.0	4.9	7.4	-4.8	0.0	-4.7	0.0	-0.9
Humerus	711.0	9.9	254.2	-5.8	3.5	-4.5	4.7	-5.2
Radius + Ulna	594.0	8.3	585.1	1.1	3.4	-3.1	2.7	-4.9
Carpus	99.0	1.4	118.4	0.5	1.8	0.9	3.1	1.0
Metacarpus I-V	129.0	1.8	267.6	2.5	3.3	1.7	6.8	4.2
Baculum	0.0	0.0	99.2	1.6	0.4	0.4	0.6	0.7
Pelvis + Sacrum	575.0	8.0	6.2	-7.9	0.4	-7.5	2.6	-5.3
Femur	828.0	11.5	208.3	-8.2	5.2	-4.8	10.3	-2.8
Patella	40.0	0.6	124.0	1.4	1.4	1.0	1.9	1.0
Tibia + Fibula	555.0	7.7	166.9	-5.0	3.7	-2.2	2.9	-2.1
Tarsus	186.0	2.6	245.2	1.3	3.0	0.6	6.8	2.2
Metatarsus I-V	124.0	1.7	170.6	1.0	2.6	1.1	5.9	2.8
Phalanx + Sesamoid	208.9	2.9	234.2	0.8	4.2	1.9	4.3	0.5
Vertebra	963.0	13.4	133.1	-11.3	3.3	-9.6	12.3	2.6
Ribs + Sternum	618.0	8.6	344.3	-3.1	4.8	-1.6	7.8	-0.5
Total	7196.9		6256.2		12260.8		23304	

Table 5.27 Weight of skeletal element from cave bears and relative % difference with the comparative skeleton of brown bear.

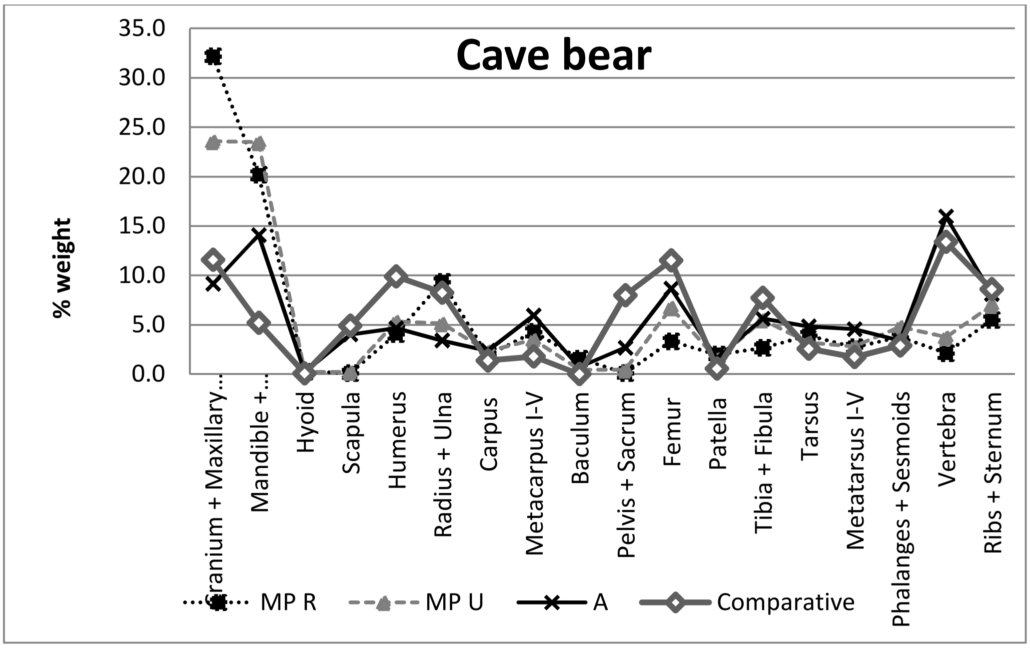


Figure 5.16 % Weight of skeletal element for cave bear from comparative reference skeleton and combined assemblage.

On the other hand, the weight proportions of Aurignacian and the comparative skeleton show a better fit with a higher Pearson's correlation coefficient, with the exception of the mandible. Further, forelimbs and pelvis are slightly underrepresented in the Aurignacian assemblage in comparison to the modern brown bear. Overall, the Pearson's correlation efficient is .66 at a level of $p<0.005$. Therefore, the skeleton is relatively equally represented without a substantial bias towards the dental elements. The Aurignacian assemblage fits the prediction that that bears died naturally in the cave, which resulted in more equal representation of skeletal elements.

The bulk density measurement, which is a measure of the compactness of bones for microstructure (Lam et al., 1999; Lyman, 1984; Stiner, 2004), predicts the degree of fragmentation that elements and element portions will undergo under natural *in situ* attrition. This usually results in the overrepresentation of the middle shaft that is most compact, and underrepresentation of epiphyses and other elements with cancellous bone structure. Ideally, one should measure the bulk density on the specific taxon, as the density may vary according to the anatomy. The general results show that the shafts preserve better than the epiphyses due to spongy bones, which are finer in structure, and the thin cortical bones of the end bones.

With fully developed cave bear remains, epiphyses of long bones including fore and hind limbs are nonexistent in the MP R and scarce in the MP U. In the Aurignacian, epiphyses occur more frequently, but still at 3.8:1 ratio. Further, we expect that the MNE of tooth and cranium/mandible would be comparable if there was no preservational bias against fragile parts (Table 5.28). However, the comparison of these values shows that the teeth make up the majority of the MNE cranium element for cave bears, especially for the MP R and the Aurignacian and less so in the MP U.

	MP R	MP U	A
NISP			
cranium	30	48	65
maxillary teeth	106	188	79
mandible	6	12	27
mandibular teeth	116	250	101
MNE			
cranium	8	7	7
maxillary teeth	23	44	21
mandible	1	3	3
mandibular teeth	26	47	27

Table 5.28 NISP and MNE value of cave bear

The skeletal representation does not at first sight confirm the assumption that cave bears died naturally in the cave, especially in the MP. However, biases against epiphyses and high occurrences of shaft fragments are evidence of *in situ* attrition, which likely affected the lower horizons more than the Aurignacian. Therefore, it is possible that the animal remains, including cave bears, were affected by *in situ* destruction of animal parts, which resulted from natural processes such as mechanical pressure from sediment or trampling. The data do not contradict the hypothesis that cave bear remains in the cave resulted from natural hibernation deaths when we consider that post depositional process affected the abundance of body parts and skeletal elements.

The mortality profile reveals the proportion of juveniles, adults and old adults in the cave bear population. As a general comparison, the post-cranial elements as well as the teeth are studied. We expect that the juvenile remains will be the most common age group represented in the cave bear assemblage if they died naturally during their hibernation.

The proportions of adult and juvenile post-cranial elements, mostly of limb bones, are simply tallied for adult and juvenile bones and show that the number of juveniles is comparable to or exceeds adults. The ratio of the adult and juvenile specimens consistently indicates that there is a greater abundance of juveniles, increasing in proportion from the MP

R to the MP U and Aurignacian. The ratio of the summed limb and scapula elements indicates that the juveniles are most abundant in the MP U, followed by the Aurignacian and MP R (Table 5.29). On the one hand, attrition is usually biased against juveniles due to its greater porosity and the lack of thick cortical structures. On the other hand, it is likely that heavy fragmentation of adult remains can lead to reduced identifiability of specimens in contrast to juvenile remains which will be buried more readily due to their size. We cannot assess which of these taphonomic forces had a greater role in this deposit, but the juveniles appear to be better represented than adults.

ADU	MP R	MP U	A	JUV	MP R	MP U	A	ADU:JUV	MP R	MP U	A
Scapula	0	3	17	Scapula	2	1	5	Scapula	0,00	3,00	3,40
Humerus	3	4	12	Humerus	18	24	36	Humerus	0,17	0,17	0,33
Radius	3	5	7	Radius	3	3	12	Radius	1,00	1,67	0,58
Ulna	4	7	7	Ulna	5	10	18	Ulna	0,80	0,70	0,39
Femur	2	9	12	Femur	7	7	15	Femur	0,29	1,29	0,80
Tibia	1	6	5	Tibia	6	11	11	Tibia	0,17	0,55	0,45
Fibula	2	20	15	Fibula	6	8	9	Fibula	0,33	2,50	1,67
Σ	15	54	75	Σ	47	64	106	Σ	0,32	0,84	0,71

Table 5.29 NISP of adult and juvenile cave bear based on scapula and long bone

To study the proportion of old adults and assess the representation among all the age classes, we turn to teeth. As mentioned before, Münzel’s scheme (in press) is based on a finer division of the development of teeth during the juvenile stage and can be applied to specimens that are slightly more fragmented than Stiner’s scheme (1998). Permanent teeth were only considered in the study as to avoid counting individuals twice by including both deciduous and permanent teeth. More importantly, the occurrence of deciduous teeth does not equate to the mortality of the individual.

Münzel		MP R	MP U	A	Stiner*		MP R	MP U	A
P^4	J	9	6	4	P^4	J	8	10	4
	A	4	3	1		A	0	1	0
	O	0	5	2		O	0	4	2
M^1	J	6	21	15	M^1	J	5	25	14
	A	3	3	1		A	1	2	2
	O	2	3	1		O	0	4	1
M^2	J	11	25	12	M^2	J	11	28	12
	A	4	5	0		A	2	2	0
	O	2	2	1		O	1	3	1
P_4	J	3	4	0	P_4	J	0	3	2
	A	2	4	2		A	1	2	0
	O	0	0	0		O	0	0	0
M_1	J	12	30	6	M_1	J	10	28	8
	A	5	9	6		A	3	12	6
	O	2	6	4		O	1	3	2
M_2	J	9	26	14	M_2	J	7	36	18
	A	5	9	7		A	4	3	1
	O	2	6	0		O	0	4	0
M_3	J	7	9	4	M_3	J	7	10	4
	A	3	2	1		A	2	6	1
	O	2	6	0		O	0	3	0
total		94	184	82	total		63	189	78

Table 5.30 Ages of cave bear for each premolar/molar according to Münzel and Stiner

Table 5.31 Ages of cave bear for each premolar/molar according to Stiner (1998) *ages correspond to the following cohorts: juvenile (I-III), adult (IV-VII), old adult (VII-IX).

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Most of the assemblages are characterized by a greater abundance of juveniles (Table 5.30). There are a large number of subadult/adults in the MP R and MP U. This corresponds to the second winter for cubs, which is a vulnerable period associated with high mortality. Such patterns show that many of the cave bears represent natural mortality that occurred during the second winter for subadult/adults. This, however, is biased against the erupting permanent teeth since they are not mineralized and are prone to fragmentation. After subadults, adults and old adults are more common. However, when all the juveniles from fetus to subadult are grouped together, juveniles dominate the assemblage in the MP R and MP U, comprising 63 and 67% of the aged individuals.

During the Aurignacian, subadult/adults become less common while the adults and old adults are more frequent. Among juvenile, prime adult and old adult groups, the juveniles and adults are equally represented, each comprising 38% of the assemblage. In all strata, old individuals are the least represented age group in the assemblage. Based on the program by Weaver et al. (2011), the M_1 indicates the assemblage reflects a juvenile dominated pattern for the MP. The sample size of the Aurignacian is relatively small and represents an assemblage with equal representation of all age groups (Table 5.30).

In Stiner's scheme, the mortality profile is heavily dominated by groups II-III (Table 5.30), which is equivalent to the subadult phase in Münzel's scheme, characterized by a complete eruption of the tooth with no wear and open root. Therefore, both ageing systems clearly demonstrate the abundance of juveniles at the site and relative scarcity of old adults in all the horizons. The abundance of juveniles points to the mortality of cubs either accompanied by the females or in their first winter alone in hibernation. Despite the bias against fragile remains in faunal assemblages, the abundance of juveniles in the earlier strata, MP R and MP U, indicates the dominance of individuals aged up to 2 years. The dominance of juveniles of cranial and post-cranial elements supports the assumption that cave bears occupied the site for hibernation and that the ursid assemblage represent natural mortality of the animals.

The cave bear assemblage in a deposit nearby can be compared to evaluate inter-site differences in the mortality profile. Cave bear remains from Bärenhöhle studied by Weinstock (2000) show that juveniles also dominate the site. Based on Stiner's system, there is a peak in age group I, represented in the assemblage by unerupted M_1 (Weinstock, 2000). This reflects infants/neonates that died in their first winter, 3-5 months after their birth. In general, 75% of the individuals derive from juveniles. There is a slight divergence in the proportion of adult and old adult. While old adults are abundant after juveniles, making up 15-18%, prime aged individuals are relatively small (6.5%). In the literature on demographics, such patterns reflect a classic U-shape profile in which more vulnerable individuals, the young and the old, die off more commonly than prime adults. This mortality profile differs from Stadel, which produced a relatively large proportion of adults and few old adults. Such patterns reflect living populations (L shape), which are characterized by the abundance of young, followed by prime adults and the old adults.

The determination of sex is based on few elements that are known to be sexually dimorphic, including canines (Gordon and Morejohn, 1975). Biologists have used measurement of canine alveoli to determine sex on modern brown bears. Since mandibles are more fragmentary, I follow Stiner's example (1998) with a slight modification. Stiner measures the crown of the canine whereas I measured the anterior-posterior diameter (DAP) and the transversal diameter (DT) of the canine root. There are not enough canines in the Aurignacian period, so canines from the MP are compared. Based on lower canines, the measurement values form two clusters, representing females and males (Figure 5.17). The lower canines (N=17) are equally represented by both sexes. In contrast, the upper canines (N=9) show that males dominate the assemblage.

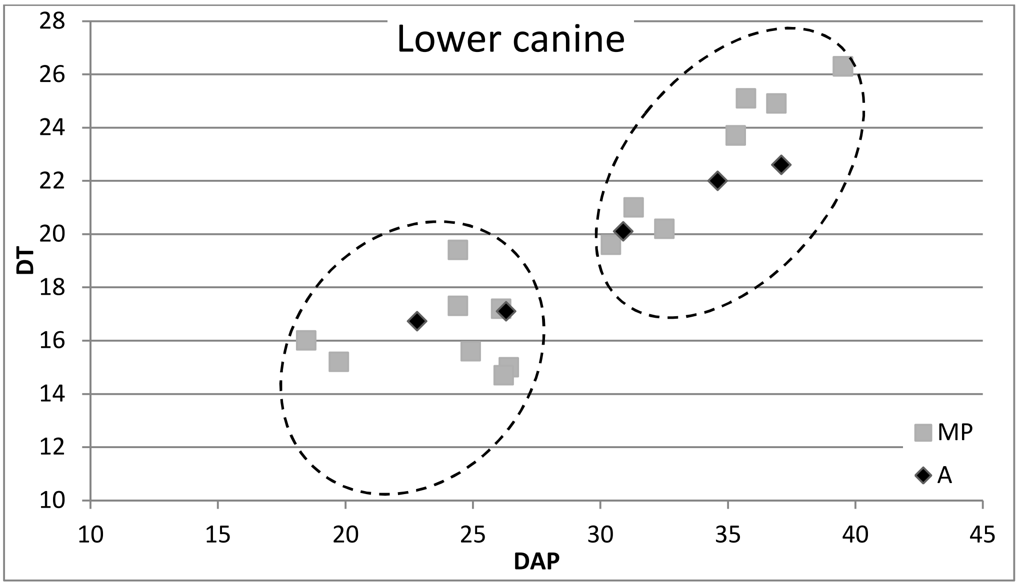

Figure 5.17 Scatterplot of measurement of cave bear canine

The sex ratio of the adult bears at Bärenhöhle shows that the males are overrepresented, making up 69% for the lower canine (Weinstock, 2000). Other elements also show that there was a greater representation of males. This bias towards males could occur in cave bear assemblages, although ethological studies indicate that females are likely to hibernate longer than the males as long as the food source availability remains adequate (Stiner et al., 1998 and reference therein).

The discrepancy between Stadel and Bärenhöhle does not lend itself to a simple interpretation, since the sites are close and we assume that they will be represented by a similar demographic pattern. However, Stadel shows no strong bias towards one sex and this may partially be due to smaller sample size. It is probable that there is a variation in the demographic profile as an artifact of sampling, but alternatively, the differences also may lie in the disparity in the duration of the site occupation. The chronological context of the material from the museum collection is not clear, and strata are not accurately dated. Therefore, this is not necessarily a spatial variation but a temporal difference. Weinstock (2000) notes an inverse correlation between the females and old adults. In assemblages with a lower percentage of older individuals, there tends to be a higher number of females. The sample of Hohlenstein-Stadel does not contradict this pattern, although a greater number of canines should be measured to assess the pattern.

Prey Animals

Prey animals in caves often result from hunting and scavenging activities of hominins and non-hominin predators. The study of skeletal abundance and age profile helps us assess the agent responsible for the transport of animal carcasses and the dietary choices of the predators. The common prey animals at this cave site include horses, woolly rhinoceros, reindeer and mammoths as well as aurochs/bison and red deer.

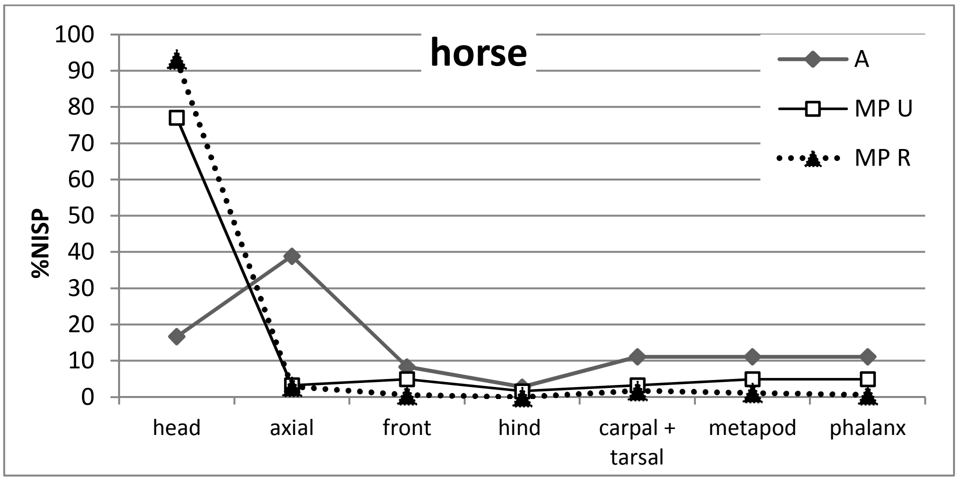

Figure 5.18 %NISP of body part for horse

The skeletal abundance of horses is heavily represented by cranial elements or teeth in the Middle Paleolithic assemblages, comprising more than 90% and 77% of all skeletal elements (Figure 5.18). Therefore, there is little to assess in terms of elemental abundance except that the cranial remains dominate. It is only during the Aurignacian period that axial elements become more common than the rest of the body parts. This is an indication that *in situ* attrition occurred less intensively during the Aurignacian, which is a pattern similar to that of cave bears. However, we should also note that the sample size is relatively small, especially for the Aurignacian period, and other factors affected the preservation of skeletal elements. The mammoths and woolly rhinoceroses show an even more extreme bias towards the teeth, and other skeletal elements are scarce or nonexistent. For these two large mammals, this is consistent from the MP to the Aurignacian period.

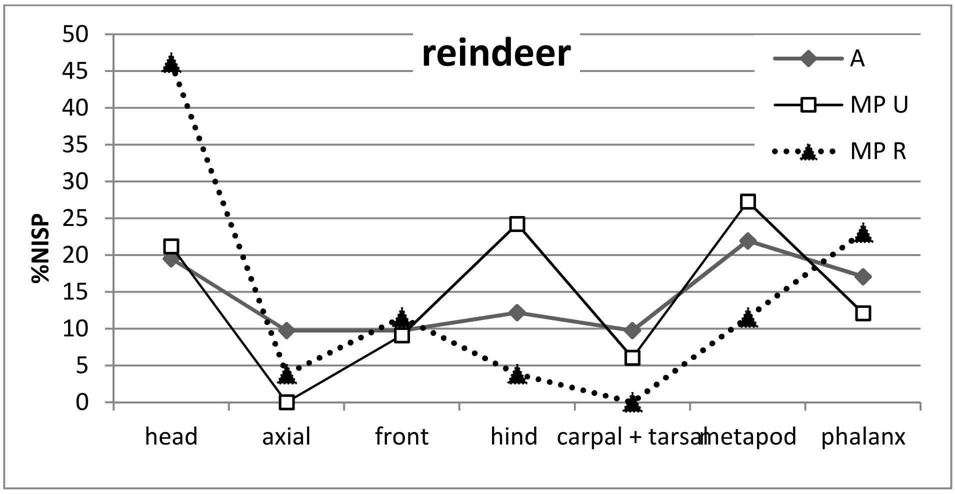

Figure 5.19 %NISP of body part for reindeer

Reindeer shows a slightly different pattern. The reindeer remains are represented by a greater abundance of head parts in the MP R while the hind limbs and the metapodials are relatively well represented in the assemblage in the MP U and the Aurignacian (Figure 5.19). Reindeer appear to be influenced by different attritional processes as other prey animals, calling into question why the skeletal representation differs from other prey animals.

First, the perrisodactyl and proboscidean teeth are robust and easy to identify (Hillson, 2005). Enamels are relatively thick and preserve better. Further, the teeth fragments are also readily identified due to their unique morphology and enamel structure. It is thus possible that the dental fragments are more likely to preserve and be identified in comparison to teeth from other taxa.

It is possible that other factors also contributed to the obliteration of post-cranial elements among the prey remains. The taphonomic modification indicates that carnivore modification occurs at a higher frequency in the MP compared to the Aurignacian. This suggests that carnivore activities in addition to post-depositional processes altered the faunal remains. As others have noted in the literature, the nutritive attrition by predators is likely the cause of this bias. Cruz-Uribe (1991) noted that the cranial parts are usually better represented for small size herbivores, but this does not apply to larger game. However, as Fosse (1997) and Niven (2006) rightly demonstrate, this pattern may be applicable to larger herbivores as well. According to modern hyena bone accumulations, limb parts and skulls frequently appear at dens than other portions (Lansing et al., 2009). Therefore, the disproportional representation of teeth can be an indication that carnivores actively used the cave either to deposit animal carcasses to avoid theft and competition, or as a den.

The complete obliteration of long bones is not commonly documented in paleontological and archaeological faunal remains mostly due to the high bone density of and because limbs are preferably transported to den sites (Lansing et al., 2009). However, the animal remains in the earlier sequence of the Middle Paleolithic were exposed to other attritional processes including chemical corrosion and mechanical destruction (trampling), evidenced by high occurrences of rounding, leading to erosion and destruction regardless of the relative survivorship of body portions. The deletion of non-dental skeletal elements points to the fact that attrition worked on the carcasses at a greater rate.

Further, selective transport of ungulate remains was likely practiced by hominins and other predators, but low frequency of non-dental elements does not permit a clear identification of agents and the nature of transportation. In all, biotic and abiotic factors affected the skeletal representation of the carcasses and possibly erased clear signatures of selective transport of prey remains into the site by hominins. The exception to this pattern is reindeer, in which post-cranial elements outnumber teeth in the MP U and MP R. The degree of attrition differs among mammalian taxa, which shows that instead of mechanical and chemical processes at work, carnivores targeted specific taxa such as horse, woolly rhinoceros, and mammoth, and that reindeer may have been transported by other predators: Neanderthals and modern humans.

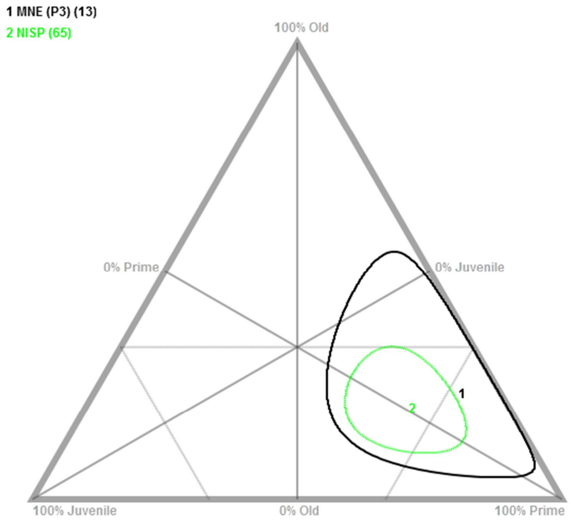

Figure 5.20 Age groups of horse from the MP

Based on a sample of teeth, the mortality pattern of the horse can be established from the MP (The sample size from the Aurignacian is too low). The age group of the horses, based on the measurement of the premolar and molar teeth, is mostly dominated by juveniles and adults in terms of NISP and adults in terms of MNE (Figure 5.20). Their abundance fits the model of living structure, which is an indication of non-random hunting that still leaves the identity of the predator open to question. Many hunted assemblages of hyenas and predators of large and middle-sized carnivores are characterized by an abundance of juveniles and older adults, which are likely to be targeted as a prey (Stiner, 1990; Stiner, 2009a). Therefore, this may reflect in part human predation on horses. However, an age profile dominated by prime-aged adults is a better signature of hominin involvement in the hunting of the animals (Stiner, 1990). Other profiles could be mimicked by other predators and could fluctuate due to seasonal variation in herd structures.

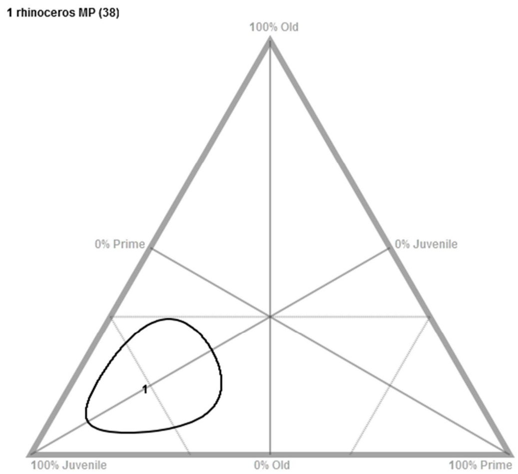

Figure 5.21 Age groups of rhinoceros from the MP

Although the sample size is relatively small, the age groups of the rhinoceros based on NISP show that juveniles are slightly better represented in the assemblage than adults and old adults (Figure 5.21). Targeting juveniles among prey animals is a common hunting strategy among predators. Therefore, the age profile supports the accumulation of kills by non-human predators. However, there are not many examples in the study of large mammal hunting such as rhinoceros by humans. Some of the archaeological assemblages show that the juveniles could be dominant in the assemblage (Scott, 1980). Based on Gamble's study (1999), it appears that there is an equal representation of juvenile, prime and old adults that may slightly have altered the pattern of age profiles.

Both taphonomic analysis and skeletal representation support the notion that carnivores had a major role in the transportation, consumption and destruction of the animal carcasses. On the other hand, the age profile does not provide a clear signature of hunting by carnivores. Therefore, it is likely that the herbivorous taxa probably derived from both human and carnivore hunting activities.

Ivory and antler

The osseous tools enter in the archaeological record towards the end of the Lower Paleolithic with the Acheulean industry in Eurasia and, for example, the bone bifaces made from elephants (Boschian and Saccà, 2010; Rabinovich et al., 2012). Bone retouchers, used to modify lithic artifacts, become one of the most common organic artifact types recovered from the Middle Paleolithic (Ahern et al., 2004; Blasco et al., 2013; Chase, 1990; Patou-Mathis, 2002; Verna and d'Errico, 2011). The use of diverse raw material for tool production is not limited to modern humans.

Nonetheless, the production of functional tools from animal remains became a prominent part of the cultural repertoire in the Upper Paleolithic (Patou-Mathis et al., 2005). Intentional modification of osseous material, similar to fashioning lithic artifacts, is a notable change in the organic tool technology, which is a contrast to expedient tools with limited modification that assist in the manufacture of lithic artifacts.

Further, the production of ivory tools is a development unique to the end of the Middle Paleolithic/early Upper Paleolithic. As noted by several studies, proboscidean use of their tusk throughout their lifetime results in polish and scratches from natural modification (Heckel and Wolf, 2014; Saccà, 2012; Wolf, 2013). Therefore, the evidence of ivory points documented at the Acheulean sites in Italy and Spain is refuted by reanalysis of these objects using criteria for distinguishing natural and anthropogenic modification (Villa and d'Errico, 2001).

Ivory is an important component of the Aurignacian culture in the Swabian Jura (Conard, 2010; Conard et al., 2006; Wolf, 2013) and in general, the use of ivory is not frequently documented prior to the early Upper Paleolithic. As such, we assume that the tusks and ivory debris will be better represented in the Aurignacian assemblage. Interestingly, ivory fragments indicate that their quantity both in terms of frequency and weight remains relatively consistent throughout the sequences (Figure 5.22). Fragments present no clear features of ivory debitage described by Heckel and Wolf (2014) such as bulbs of percussion or tongued fracture typical of organic material. None of fragments shows clear morphology that resembles segmentation, extraction and fracture (Heckel and Wolf, 2014) due to relatively frequent rounding of the ivory pieces after their burial.

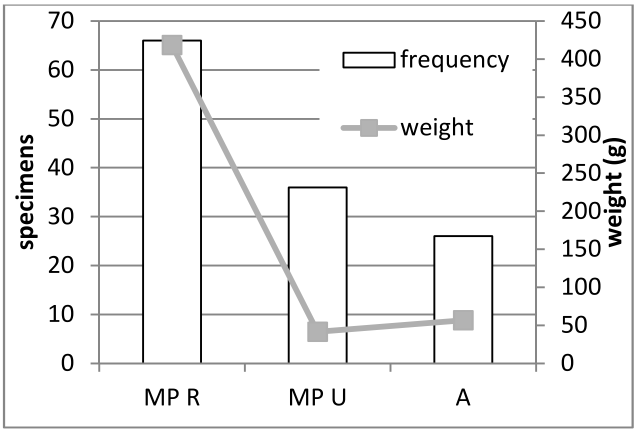

Figure 5.22 Frequency and weight of ivory fragments (excluding the tusks from the MP R which is described below and modified fragments)

However, a recent study by Wolf (2013) from the material of this site points to occurrences of ivory artifacts (aside from the Lionman and associated ornaments). Two pieces of tusks were recovered from the Middle Paleolithic during the excavation of 1939. They are relatively complete with some missing cementum from the outer surface and were segmented in equal length roughly 17 cm long. No usewear on the pieces is observed due to natural rounding and carnivore gnawing marks, obscuring the morphology of fracture (Figure 5.23) (Wolf, 2013). However, the breakage pattern of the tusk suggests that they were not naturally broken, and it is unlikely that carnivores intentionally transported segments inside the cave unlike other bone remains, which contain collagen and fat. Chisel-like forms point to the use of tusks as tools for digging. They may also have been segmented and transported by Neanderthals as blanks to work on the tusks. This, in addition to a relatively complete tusk from the lower Middle Paleolithic unit, suggests that mammoths have been possibly exploited for their ivory prior to the Aurignacian period.

Figure 5.23 Two tusk fragments from the MP, both ~17cm (Photo courtesy of Kurt Wehrberger, Ulmer Museum)

Antlers can also be included in the diversification of raw material in artifact assemblages. Split points are one of the common forms of antler artifacts, typical of the Aurignacian industries and previously not documented (Bar-Yosef, 2002; Knecht, 1993). Experimental work demonstrates that the use of the thin antlers make for easier processing and modification (Tartar and White, 2013).

At the site, many of the antlers from this assemblage are identified to reindeer, which is possible due to the small diameter of the antlers. Thus far, two antlers of red deer were identified from the lower part of the Red Middle Paleolithic, characterized by greater thickness and distinctive pedicle with rose, and the rest have been identified to reindeer. Many antlers are thin, either indicating females or juveniles. Some antler fragments can be identified to juveniles (1-2 year) based on the absence of beams close towards the pedicles (Figure 5.24). The number of reindeer antlers increases from the MP to the Aurignacian significantly (χ^2 =7.47, <.01) (Figure 5.25). The same pattern applies to antlers identified generally to cervids.

Figure 5.24 shed reindeer antler with carnivore modification from the MP

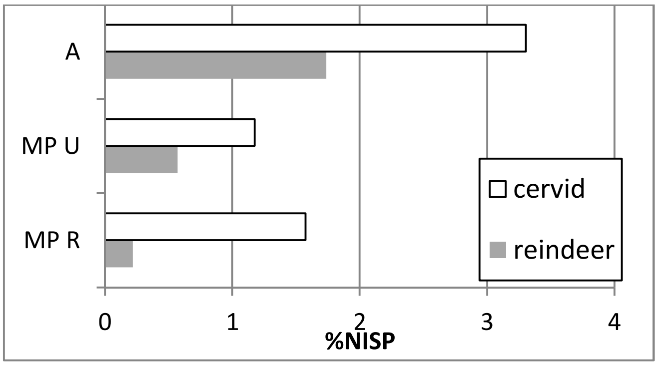

Figure 5.25 Frequency of antlers

Studies also indeed show that antlers could also be transported by other predators (Stiner, 1994). Therefore, either humans and/or carnivores favored shed antlers over antlers attached to cranium. Butt occurs infrequently compared to shed antlers, when antlers with pedicles were considered. Further, the measurement of antler diameter indicates that antler thickness formed two groups, one indicating males and the other indicating female and young individuals with indeterminate sex (Figure 5.26). During the Middle Paleolithic, the antlers of females and/or younger individuals dominate, and the adult male antlers occur infrequently. During the Aurignacian, no adult male antler is identified, and the greater bias towards smaller and thinner antlers is apparent.

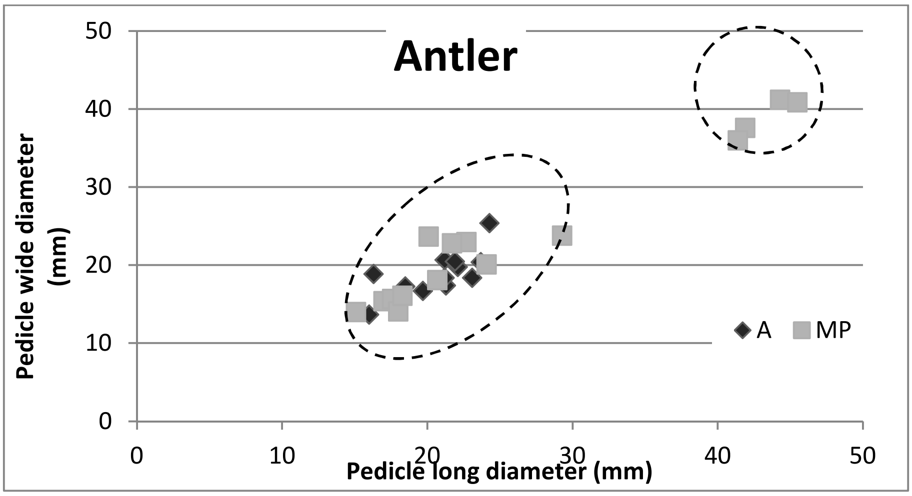

Figure 5.26 Measurement of the pedicle of reindeer antler

The collection of shed antlers most likely took place during milder seasons when snow cover was minimal. Therefore, this may be an indirect indication that humans/carnivores visited the site and deposited the antlers during spring-summer. Carnivore damage on the antlers including fragments occurs more frequently during MP R than MP U and the Aurignacian (Table 5.31). The agent responsible for the transport of antlers to the cave cannot securely be determined as Stiner (1994) demonstrates, as antlers and horns are often transported by carnivores, such as hyenas, into dens. Therefore, it is likely that antler collecting was at times practiced by non-humans as well. However, the decrease in carnivore damage on the antlers over time suggests that they were increasingly transported by humans. Therefore, humans potentially visited the site and deposited antlers with a preference for shed young and/or female antlers during the Aurignacian period.

reindeer antler MNE	MP R	MP U	A
shed	2	11	14
unshed	2	1	3
Antler specimens			
unmodified	70	95	241
carnivore modification	21	11	27
% w/ modification	23,1	10,4	10,1
total	91	106	268

Table 5.31 Frequency of shed and unshed reindeer antler and carnivore damaged antlers

Small animals

Hares were the smallest mammalian taxa that occurred consistently. There are clearly preservational biases against smaller animals, as discussed above, from chemical and mechanical weathering. However, some hare specimens exist in the MP, although they are mostly represented by dental remains. They become more common in the Aurignacian period as post-cranial elements become more common as well. Carnivore modification is not significant but exists on some specimens.

Foxes, which probably were hunted by other carnivores or which frequented the site, occur consistently through the horizons. There is no significant change in the NISP values and their presence also adds to the diversity of carnivores that occur at the site. There are no clear indications that humans actively exploited foxes in the MP.

The recovery of aquatic source at caves requires a consideration of taphonomic processes and agents responsible for its occurrence away from water sources. Although the exploitation of aquatic remains by hominins is documented in the Plio-Pleistocene period and geographically appear to be a common part of subsistence (Colonese et al., 2011; Stiner and Munro, 2002), the degree to which aquatic resources are consumed vary across geographic locations, especially of water sources that favor a diversified diet with terrestrial and aquatic animals, as opposed to inland locations or areas with relatively little access to a body of water.

Biological observations of extant brown bears and felids indicate that they are at times known to consume fish. Therefore, medium to large carnivores and bears from the past possibly also consumed aquatic resources. Recent stable isotopic analysis revealed that cave bears and cave lions that were found in a cave with anadromous salmon remains contradict this view, since they did not show an isotopic signature of fish consumption with lower ^{15}N isotopic ratio (Bocherens et al., in press). Through the process of elimination, the study concludes that Neanderthals are the likely agent that brought the fish remains for consumption to the site. However, the variability in the diet of bears and large felids remains to be evaluated and the possibility that non-human predators transported the fish as scats into the cave cannot be entirely excluded.

The dietary role of fish in the Swabian Jura is explored towards the end of the Upper Paleolithic period. The number of fish remains is relatively low during the Aurignacian period, and later sees an increase starting from the Gravettian period (Owen, 2013; Torke, 1998). At Hohlenstein-Stadel, some remains are identified to Cyprinid (carp) pharyngeal (Figure 5.27) and Salmonid vertebra from the MP R. The presence of relatively large fish remains is tentatively indicative of fish consumption by Neanderthals and modern humans in non-coastal settings, but this remains to be tested.

Figure 5.27 pharyngeal of Cyprinid from the MP R

Most of the bird remains were recovered from the excavation between 2009-2011 and studied by P. Krönneck. The abundance of bird remains is not heavily biased in one horizon but is consistent. Many derive from the layer of MP R. Besides unidentifiable bird remains, there are a few ptarmigans, geese and ducks. From the MP U, there are also a few unidentified grouse (Hazel grouse or black grouse) and duck. The bird remains from the Aurignacian include grouse and ptarmigans.

No carnivore and anthropogenic modification has been identified on the remains. While carnivores or hominins could have transported the bird remains, remains of small animals often exhibit a few evidence of butchering and due to the lack of carnivore damage. Thus, it is possible that hominins exploited the birds. The use of bird remains in the Middle Paleolithic is not common, but growing number of sites have yielded evidence of bird procurement by Neanderthals (Blasco and Peris, 2009; Conard et al., 2013; Finlayson et al., 2012; Morin and Laroulandie, 2012; Peresani et al., 2011). However, the evidence for the exploitation of small game by hominins remains equivocal based on the current assemblage.

Seasonality

Reindeer and horses were two taxa that enable us to deduce the seasons in which the prey was procured and the site was occupied. The sample size of specimens with information on seasonality is rare and the signals are mixed. Here, the length of the metapodial from a neonate horse as well as reindeer skull with attached antlers is an indicator of seasons in which the animals died and were deposited at the site. The neonate of the horse indicates that the fetus developed for around 20 weeks, broadly pointing to summer-fall as represented in the MP R. Further, the measurement of the unshed antler attached to the cranium puts the death of the individual at fall. During the MP U, one individual of reindeer with antlers is associated with spring procurement. Due to a small sample size, this is not a clear indication of seasonality in the occupation of humans or other predators.

Carnivores

Traces of carnivore activity occur in the faunal assemblages in the cave and the abundance of predators is a unique feature in the assemblage of Hohlenstein-Stadel. This calls into question how the cave was utilized by non-human predators and the role that humans had on the faunal assemblage. Stiner highlights the abundance of large predators in Paleolithic hyena and wolf dens in Italy as one of stark contrasts between dens and human accumulated assemblages (2004:773).

It appears that, based on some studies, ~>10% of carnivores indicate predator-collected assemblages (Cruz-Uribe, 1991; Stiner, 2004a). Although carnivore abundance remains relatively low in the MP, at 6.4-7.2%, it is unlikely that the carnivores were systematically targeted by hominins in the Paleolithic (but see Blasco and Rossell, 2010; Gabucio et al., in press; Kitagawa et al., in press). Therefore, this assemblage likely represents a mix of human, carnivore and cave bear occupation.

The NISP of carnivores indicates that, in the MP, hyenas were the most frequent carnivore to visit the sites, outnumbering wolves both in NISP and MNI. Therefore, it is likely that hyenas are the major agent that used the site for denning, resulting in the accumulation of fauna. Wolves become better represented in the Aurignacian, when the hyena remains become scarce, which may partially reflect a local demise of the population. The ecological niche of hyenas became occupied and replaced by wolves, which then became more frequent. The gradual disappearance of other competitors appears to have positively affected at least the use of the caves by wolves in the Aurignacian period.

The skeletal abundance for hyenas shows that there is an overabundance of tooth elements in all the horizons (Figure 5.28). Other elements are absent except in the Aurignacian period, in which more forelimbs were recovered. Nonetheless, the bias of teeth again characterizes the general skeletal representation of many taxa at the site.

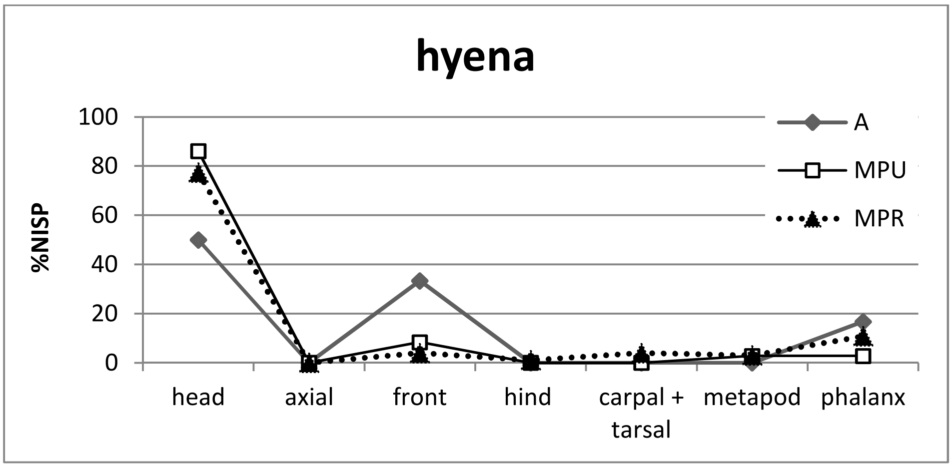

Figure 5.28 %NISP of body part for hyena

Wolves show a slightly different pattern (Figure 5.29). While the skull/mandible remains the most common element in the Middle Paleolithic, we observe a greater proportion of metapodials in the Aurignacian compared to the head. Further, across all strata, forelimbs are also present in the assemblage. There is a difference between hyena and wolf skeletal abundance. Predators especially hyenas often face intraspecific as well as interspecific confrontation with other predators, which may lead to mortality and exploited the carcasses of competitors after confrontation. Therefore, it appears that hyena remains were exposed to greater levels of carnivore destruction than wolves, reflecting the complex interaction and competition among predators.

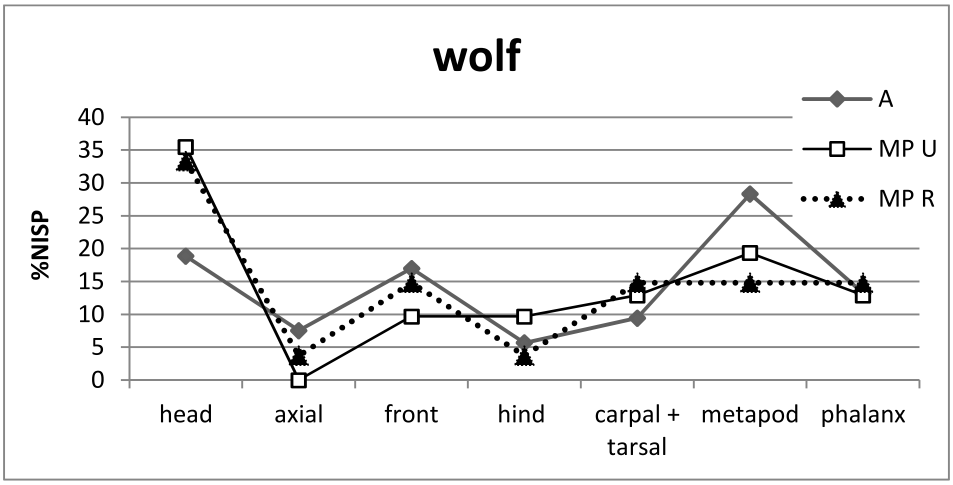

Figure 5.29 %NISP of body part for wolf

The age groups of hyena indicate that juveniles and adults are represented equally in the MP. They point to a living structure that is well represented by young followed by prime-aged individuals for NISP and young for MNE (Fig 5.30). Old adults are less represented. The cause of mortality for these predators is not as clear as other mammalian taxa in cave contexts. However, a number of juveniles hint at the use of the site as den, considering that deciduous teeth are subject to greater *in situ* attrition.

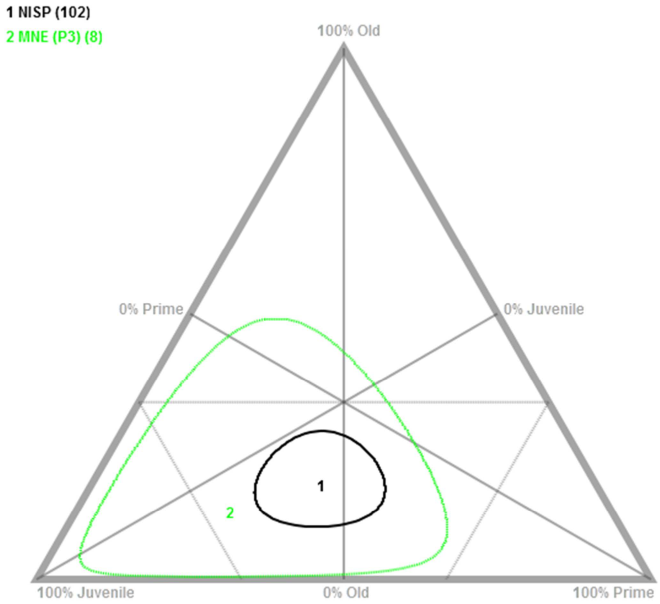

Figure 5.30 Age group of hyena from the MP

If similar reproductive behavior and ontogeny apply to cave hyenas, the paleontological record may preferably preserve their remains over other carnivores due to their prolonged use of dens and possible communal ones where more than one family may be represented. Further, competition among the young is high and may lead to mortality, possibly due to advantages of an individual for having greater access to food (Kruuk, 1972). This also leads to a greater presence of juveniles at hyena dens compared to other carnivores that make use of sheltered space.

Also, while the sample size is relatively small, the number of juveniles is relatively high in comparison to prime and old adults for the wolves in the Middle Paleolithic, a similar pattern to hyenas. Denning behavior of carnivore best explains the abundance of juvenile remains. Therefore, it is likely that the wolves, albeit at a lesser scale, also used the site as a den interchangeably with other predators.

Cave lions occur infrequently in the assemblage. Some have emphasized the importance of cave lions in the assemblage, despite its low NISP, linking the animal to the finding of the Lionman figurine. The cave lions in general are less present in cave contexts than other predators, a phenomenon directly related to their reproductive as well as foraging behavior. Many of the remains are represented by teeth, and a few juvenile remains were recovered from the site.

Coprolite

Coprolite mostly consists of bone matrix, which is chalk like and includes organic digested hair and bone chips. Coprolites from modern African fauna have been compared to the Pleistocene coprolites, which are 22-32 % bigger (Larkin et al., 2000). Coprolites are composed of hydroxyapatite and the organic component of bony remains becomes digested (Horwitz and Goldberg, 1989). The high proportion of mineral in the droppings can be distinguished from those of other carnivores, including striped hyena that has a more diverse omnivorous diet. Complete coprolites of hyenas usually have a circular form with one concave end and a more convex end, and chemical analysis shows high levels of calcium and phosphorous that can be identified in sediments (Larkin et al., 2000).

Droppings from other carnivores usually contain larger proportions of bone fragments, and the overall shape of the coprolite also differs (Brugal, 2010). Recovery of coprolites withdifferent morphology from Pleistocene deposits shows that in contrast to the rounded coprolites, feces of wolves produce rather tube-like forms (Brugal, 2010). Further, the high density of the coprolite made it less vulnerable to scattering or trampling by large animals

(Larkin et al., 2000). The diameter of the feces is an indication of the body size of carnivores (Harrison, 2011). The spotted hyena and lion are both large and produce feces larger than 35 mm in diameter (Harrison, 2011). Typically, the coprolites from larger carnivores produce scats with digested bones that are less identifiable than feces from smaller animals that produce lower levels of damage on bones (Horwitz and Goldberg, 1989; Matthews, 2002)

Twenty-four pieces of coprolites were recovered from the MP, 17 pieces from the MP R and 7 from the MP U. It appears to be like compact bones, with granular structure and pits (Figure 5.31). The color is similar to other skeletal remains that are orange/yellow color with manganese stains. None of the coprolites is complete in form, making it difficult to determine the species of carnivore from the gross morphology of the coprolites alone. Among animals that produce scats, which include hyena, wolf and cave lions, hyena is the most abundant carnivore in the assemblage, a possible indication that the coprolites belong to the hyenas. It appears that hyena coprolite also contain more corroded unidentifiable bones in contrast to other scat-producing animals, which are likely to preserve bone remains through the digestive tract, bone remains that are well preserved with fragments that remain sharp on the edges (Larkin et al., 2000).

Figure 5.31 Coprolite fragments from the MP

In the Ach Valley, S. Münzel identified few pieces from Hohle Fels and Geißenklösterle. The evidence of coprolites is also observed microscopically at other sites. Miller (2009) documented a high degree of phosphate in the micromorphological samples from Geißenklösterle and Hohle Fels in the Middle Paleolithic. Micromorphologial analysis from Hohlenstein-Stadel will clarify whether this pattern is consistent at Hohlenstein-Stadel.

Summary

Several lines of evidence suggest that the cave served as a shelter for a number of predators, including human and other carnivores, as well as cave bears. First, the abundance of cave bears in all layers shows that this site was often available for use during winter and that hominins did not occupy the site intensively to the degree that would deter animals from visiting the site. There are also certain indicators that the cave served as a den for hyenas and to a lesser extent for wolves. The mortality profile of the carnivores appears to be dominated by juveniles. Further, extensive carnivore modification observed on the bone assemblages from several levels attest to their frequent presence in the cave. Therefore, it appears that the herbivore taxa resulted from both human and carnivore predation of the animals. The degree of the contribution by humans and non-predators cannot be assessed quantitatively, but this faunal assemblage clearly shows greater carnivore signatures than many Paleolithic assemblages. The abundances and diversity of carnivores in the assemblage is uncommon in most archaeological contexts. For this reason, the site differs from other caves in the Swabian Jura and probably points to the site’s unique function as an area occupied, inhabited and frequented by different animals for various purposes.

6 Regional perspectives in the Swabian Jura

This chapter presents a comparison of the faunal data from Hohlenstein-Stadel with sites in the Swabian Jura in order to assess similarities and differences, which in turn enable us to understand the role of Hohlenstein-Stadel on the landscape of Swabian Jura for hominin settlement. Further, the regional pattern of the Swabian Jura also serves as a study case in the transition from the Middle Paleolithic (MP) to the Aurignacian. The subsistence behavior of hominins and the use of caves are the two main foci of this chapter. We begin with a summary of the faunal work on each site.

The Lone Valley: Bockstein and Vogelherd

The MP fauna of Vogelherd (VH) is characterized by a relatively limited assemblage size from four cultural layers. The most common taxon is horse, followed by woolly rhinoceros and large bovids. While adult horses probably indicated Neanderthal hunting episodes, the faunal assemblage is a combination of carnivore and human accumulations (Müller-Beck, 1988; Niven, 2006). Carnivores are not so common, but there is a high degree of carnivore damage on the MP assemblage.

The Vogelherd fauna from the Aurignacian deposit are dominated by reindeer followed by horse, pointing to hunting between late summer and late fall (Niven, 2006). This season corresponds with the migration of reindeer. Butchering and breakage patterns show intensive processing of appendicular elements, especially those of lower hind limbs from reindeer. The two taxa were exploited for meat in addition to marrow, a subsistence strategy which remained consistent throughout the Aurignacian period. This is evidenced by selective processing of body portions, such as horse crania. They are well represented in the assemblage, which probably reflects the nutritional value of the skull for fat. The economic decision of ungulate hunting and the exploitation strategies are well documented at this site.

VH is also the only site with enough post-cranial remains from mammoths to assess their economic utility as food resources (Niven, 2006).

The largest MP faunal assemblage at Bockstein (BS) derives from Bocksteinschmiede III, a cultural layer with relatively high density of lithic artifacts and fauna. Equid is the dominant species, followed by reindeer. (While Krönneck differentiated *E. hydruntinus* from *E. ferus*, not many *E. hydruntinus* were identified and the equids were all grouped together.) According to Krönneck and colleagues, “anthropogenic involvement with the Bocksteinschmiede III fauna is evident in burnt bone, cut or impact marks, and several worked bone specimens” (2004: 218). There is a relatively low frequency of carnivore damage on the faunal material. The Aurignacian is represented by Bocksteintörle VII. The assemblage size is limited, but horse is the most common taxon followed by reindeer. Despite the small sample size, there is a higher frequency of anthropogenically modified fauna.

The Ach Valley: Hohle Fels, Geißenklösterle and Kogelstein

Hohle Fels (HF) and Geißenklösterle (GK) have produced comparable faunal assemblages that are dominated by cave bears as well as ungulates that were most likely transported by hominins. At Hohle Fels during the MP, non-ursid remains are scarce with little input of exogenous animals. The cave was mostly occupied by cave bears during winter and shows little evidence of activity by other animals. Future study will confirm whether the current sample is representative of the species composition at the site, but the general predominance of cave bears will likely not alter (Münzel, in preparation).

During the Aurignacian, there is also a similar pattern in the greater dominance of herbivores, namely reindeer followed by horses. While cave bear still persists, there is a more clear presence of humans in the archaeological record. Ivory fragments increase considerably, also attributed to their importance as raw material, so the utility of mammoth in terms of subsistence still remains an open question (Münzel, 2001; Münzel, in press). There is also an abundance of anthropogenic modification on carnivores and cave bears (Kitagawa et al., 2012), a trend that continues into the Gravettian.

At Geißenklösterle, the MP assemblage is characterized by a high frequency of cave bears, followed by small ruminants such as ibex, and middle and large-sized carnivores such as wolf, lion and hyena (Münzel, in press; Münzel and Conard, 2004b). Further, shed reindeer antlers remain a common finding at the site. Münzel (in press) interprets the relative scarcity of typical prey animals such as horse, mammoth and reindeer as the tendency to process animal carcasses at the kill site and the lack of interest by Neanderthals in the exploitation of animals for tool production.

During the Aurignacian, there is an increase in the input of prey game at both sites. At Geißenklösterle, horses are the most common taxon besides cave bear. There is also a significant amount of ivory fragments and a greater importance of mammoth. According to Münzel, long bones of equids and rib fragments of mammoths served as raw material and may have been intentionally selected (Münzel, in press). Seasonal data suggest that horses were targeted between late fall and spring while the mammoths were probably hunted in spring due to the abundance of juvenile mammoths (Münzel, in press).

The zooarchaeological interpretation of the site reveals a different history of the use of Kogelstein (KG). It is characterized by the dominance of small animals including fox, hare and marmots, the latter being extremely rare at other sites. The most abundant middle to large-sized animal in terms of MNI is the hyena. Only a few post-cranial elements were recovered and more than half of the teeth were deciduous (40 deciduous and34 permanent teeth) (Ziegler in Böttcher et al., 2000). Considering the taphonomic biases against juvenile remains, the abundance of milk teeth suggests that juveniles account for the majority of hyenas found at the site. Further, 50 specimens show gnawing marks, with hyenas, wolves and foxes being the probable agents. Other remains show extensive polishing that indicates digestion or extensive gnawing by hyenas. Fish remains including graylings and burbots were likely consumed by Neanderthals, although carnivorous birds, such as eagle owls, may also have contributed to the accumulation of fish remains. Faunal remains in Kogelstein with anthropogenic modification are seldom (Böttcher et al., 2000; Münzel and Conard, 2004b). The faunal remains clearly indicate the use of caves predominantly by hyenas as a denning site (Ziegler in Böttcher et al., 2000).

Comparison: stratigraphy and sampling

Table 6.1 lists the cultural layers from which the assemblages were recovered and utilized in this study. There are some discrepancies in the number of strata representing the MP and the Aurignacian layers. In VH, four MP sequences exist while the two Aurignacian layers were identified. At Bockstein three MP layers from two deposits (Bocksteinschmiede and Törle) exist. The MP and Aurignacian are represented by three discrete layers at HF. At GK, five MP layers and two Aurignacian layers exist. Lastly, KG, represented by the MP, consists of three distinct layers. The fauna have been studied by P. Krönneck, L. Niven and S. Münzel. All of the material was studied in VH and BS. The material from GK consists of recovered finds that are larger than 3 cm long. The sorted material in the screenwashed sediment has not been systematically studied. Approximately half of the material from each cultural layer at Hohle Fels has been analyzed by S. Münzel, who provides us with a representative sample from the Aurignacian and MP layers.

Site	Valley	Middle Paleolithic	Aurignacian	Source
Hohlenstein-Stadel	Lone	1939: VI-XI, 2009-2011: 3-8	1939: IV-Va , 2009-2011: 1o-1u	current study
Vogelherd	Lone	VI-IX	IV-V	Niven 2006
Bockstein	Lone	Törle X, Schmiede III-IV	Törle VII	Krönneck 2012
Hohle Fels	Ach	VI-VIII	III-V	Conard et al. 2013, Münzel unpub
Geißenklösterle	Ach	IV-VIII	II-III	Münzel in press
Kogelstein	Ach	Io, Iu, II	n/a	Böttcher et al. 2000

Table 6.1 Name of the site and geological layers that were compared in this study

The sample size is not equal among the assemblages. Overall, the size of the VH and HF assemblage is small in the MP. Continuing excavation and analysis at HF may provide us with an adequate sample size in the future. The BS assemblage is rather limited in the Aurignacian. Further, I do not attempt to correlate each layer of the different deposits, as there has been previous work on the correlation of HF and GK strata (Miller, 2009). The assemblages are compared on a coarse scale, bearing in mind that there are differences in the sample size.

Species abundance

The dominant animal varied among the cave sites both during the MP and the Aurignacian. In the MP of the Lone Valley, at Vogelherd and BS, the NISP of herbivores is well represented, comprising 90% and 86% of the assemblages, respectively. The relative proportion of cave bears at VH and BS is comparable, with 5% at VH and 3.8% and BS. Carnivores consist of 3.7% of the assemblage at VH, which is low compared to BS, where there is a greater proportion of middle and large carnivores (7.8%) and small carnivores (2.2%). Lagomorphs and rodents are scarce, but likely reflect a different recovery method.

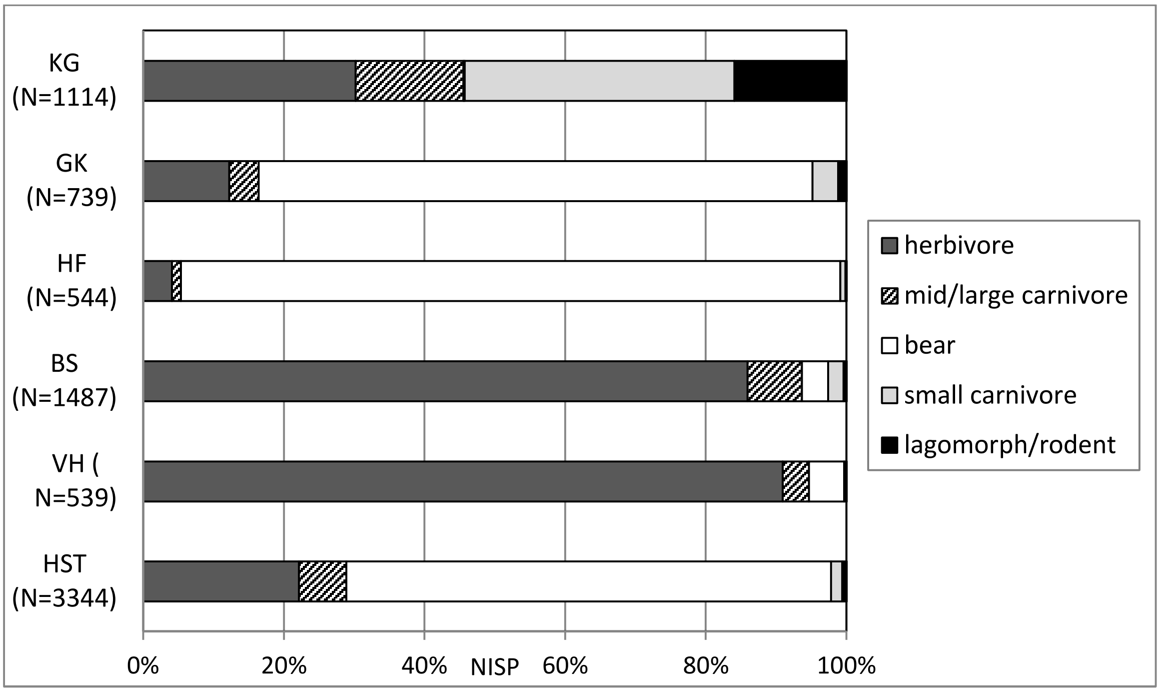

Figure 6.1 Identified faunal remains grouped by animal group (herbivore, middle/large carnivore, bear, small carnivore, lagomorph/rodent) for MP

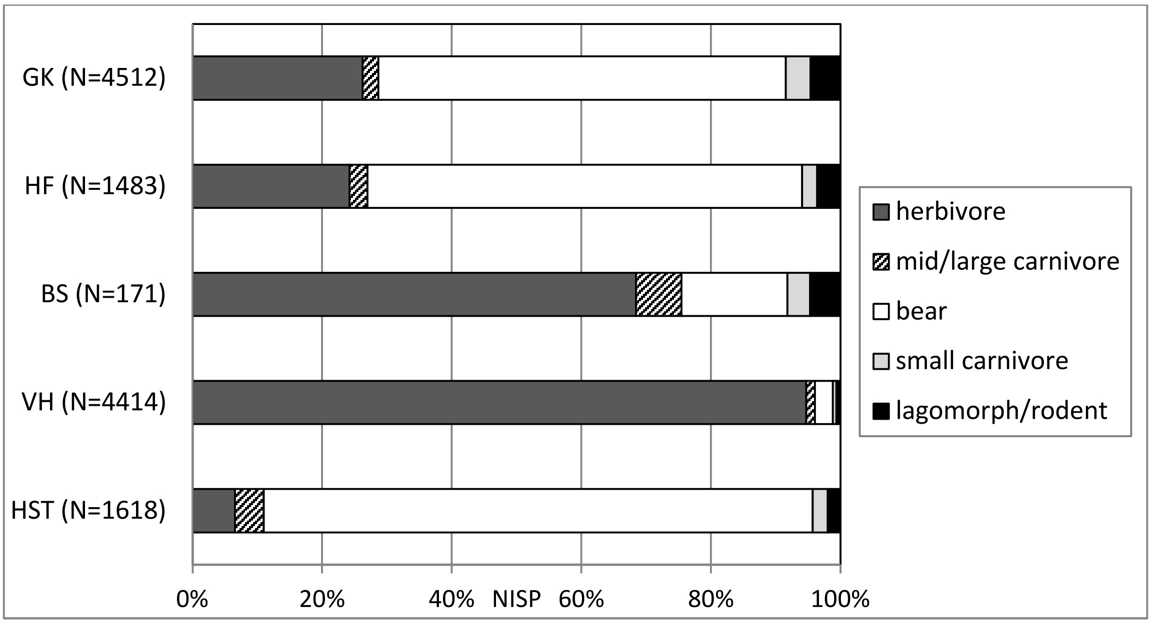

Figure 6.2 Identified faunal remains grouped by mammalian group (herbivore, middle/large carnivore, bear, small carnivore, lagomorph/rodent) for Aurignacian

In the Ach Valley, the MP at GK and HF shows relative similarities in the composition of taxonomic groups. Cave bears dominate both assemblages, but herbivores and carnivores are more frequent in GK than HF. The NISP proportion of cave bear is the highest in HF, making up 94% of the sampled fauna. At KG, small carnivores are most frequent. KG is the site with the greatest proportion of middle to large-sized carnivores compared to the rest of the sites. This variability in cave bear frequency indicates the preference of cave bears for certain sheltered sites.

During the Aurignacian, the broad pattern of species abundance remains consistent with that of the MP. Bears dominate at HS, HF and GK while herbivores dominate the fauna in VH and BS. Among all sites, VH is the site with the most frequent herbivore remains (95%). The abundance of bear is highest at HS, comprising 85% of the assemblage. However, the relative proportion changes. At the site of VH, GK and GK, the input of herbivores increases while bears proportionally increase at HS and BS. The %NISP of middle and large carnivores is the highest at BS and HS, and the %NISP of small carnivores is highest at GK.

The abundance of animal species measured in weight mirrors the same patterns as the NISP. The proportion slightly changes, with increased representation of herbivores. As expected, small-sized animals such as lagomorphs and small carnivores decrease significantly. The proportion of cave bears is smaller in weight in contrast to NISP. The NISP and weight of middle and large-sized carnivores are comparable except for VH, where carnivores are better represented in NISP than weight.

Squared Euclidean distance values have been calculated based on proportion of NISP among mammalian groups: herbivore, middle and large-sized carnivore, bear, small carnivore, lagomorph/rodent (Table 6.2). Based on proportions, the distance values reveal that the MP assemblage of HS is least dissimilar to GK, followed by HF. This is mostly driven by the large proportion of cave bear as well as middle and large-sized carnivores that closely mirror one another. Hohle Fels is slightly dissimilar to GK due to the low proportion of carnivores. Despite the close vicinity, Bockstein and Vogelherd differ significantly from HS. The number of cave bear is low at these sites and is characterized by a high frequency of herbivores. The KG assemblage differs compared to HS, due to the abundance of small carnivores.

MP sites	HS	VH	BS	HF	GK	KG
HS	-	-	-	-	-	-
VH	0,88		-	-	-	-
BS	0,83	**0,00**	-	-	-	-
HF	**0,10**	1,54	1,48	-	-	-
GK	**0,02**	1,17	1,11	**0,03**	-	-
KG	0,65	0,56	0,47	1,13	0,80	-

Table 6.2 Squared Euclidean Distance values based on mammalian group of the MP

A sites	HS	VH	BS	HF	GK
HS	-	-	-	-	-
VH	1,45	-	-	-	-
BS	0,85	**0,09**	-	-	-
HF	**0,06**	0,91	0,45	-	-
GK	**0,09**	0,83	0,40	**0,00**	-

Table 6.3 Squared Euclidean Distance values based on mammalian group of the Aurignacian

Among all the sites, BS and VH display the least difference in proportion of mammalian groups. Both assemblages are heavily herbivore dominated with a low frequency of bear, carnivore and small mammals. Further, GK and HF show small SED values due to the high frequency of cave bears. We observe the greatest divergence with a high SED value between HF-VH and HF-BS. The faunal composition of KG is distinct from other assemblages, showing the least dissimilarity to BS and the greatest discrepancy to HF. The high abundance of small game including carnivores, lagomorphs, and rodents is in part an artifact of recovery technique, but the scarcity of bears and high abundance of middle/large carnivores make KG a distinct assemblage.

In the Aurignacian, the degree of similarity with HS and other sites remains relatively consistent (Table 6.3). SED values between HS-HF and HS-GK are high. Cave bears dominate all these assemblages, followed by herbivore taxa. The SED value between HS and BS remains similar to the MP, while the distance between VH and HS becomes more pronounced in the Aurignacian, which is driven by low frequency of bear and high frequency of herbivores. The SED values of HF and GK share the least discrepancy among all Aurignacian assemblages. The SED value of BS-VH also remains high.

Individual species

The NISP and weight of individual taxa is provided (Table 6.4-6.7). In the MP based on NISP, cave bears are underrepresented in VH and BS compared to HS, while herbivores including horse, woolly rhinoceros, red deer, and aurochs/bison are better represented in the two sites compared to HS. The exception is mammoth, which is better represented in HS than in VH. In addition, reindeer and wolf are also better represented in BS than HS. Relatively speaking, GK and HF are characterized by fewer hyenas, mammoth and horse. In comparison to HS, woolly rhinoceros is underrepresented at HF. Foxes are better represented in GK than HS. KG shows faunal abundance distinct from HS. KG is represented by greater abundance of small mammals (rabbit and fox), carnivores (hyena and wolf) as well as ungulates including horse, red deer, reindeer and aurochs/bison. Compared to KG, the proportion of mammoth and cave bears is high at HS.

Great abundance of horse by NISP and weight is unique to BS and VH in the MP. This is a reflection of the availability of prey in the Lone Valley that was dominated by horses. Woolly rhinoceros and reindeer are the second most abundant species in VH and BS, respectively, followed by aurochs/bison. Mammoths are also relatively low in abundance compared to other herbivorous taxa. Cave bears comprise merely 5% of the assemblage, and hyena and wolf are better represented in BS than in VH.

MP/Taxon	HS (N=3345)	VH (N=539)	BS (N=1487)	HF (N=544)	GK (N=739)	KG (N=1114)
Lepus sp.	22	2	6	1	8	65
Marmota marmota			1		1	113
Canis lupus	60	8	47	5	19	44
Vulpes/Alopex	50	0	25	4	26	418
Ursus spelaeus / Ursus sp.	2303	25	55	507	581	2
Ursus arctos	3	2	1	3	1	
Panthera leo spelaea	13	2	9	1	3	
Lynx lynx	2	0	1		1	
Felis silvestris						
Mustela sp.	1					8
Martes sp.	1				1	
Gulo gulo			1			
Meles meles			6			1
Crocuta crocuta spelaea	150	10	58	1	8	127
Elephas antiquus		1				
Mammuthus primigenius	211	15	65		3	5
ivory	102	1	0?		17	
Equus sp.	355	342	842	10	21	143
Coelodonta antiquitatis	98	57	93	2	8	12
Sus scrofa			4			
Megaloceros giganteus	0	7	0		7	1
Cervus elaphus	2	11	15	1	2	34
Capreolus capreolus			1		2	
Rangifer tarandus	59	8	141	5	22	37
antler	45	4	7	2	31	
Alces alces			2			
Bos/Bison	14	49	103			53
Ovibos moschatus			2			
Capra ibex	0	0	2	4	20	5
Rupicapra rupicapra	0	0	7		5	46

Table 6.4 NISP value of individual taxa for MP

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A	HS (N=1618)	VH (N=4414)	BS (N=171)	HF (N=1483)	GK (N=4512)
Lepus sp.	31	27	8	53	209
Marmota marmota	0	0	0	0	0
Canis lupus	54	38	5	26	94
Vulpes/Alopex	36	20	6	34	167
Ursus spelaeus / Ursus sp.	1369	120	28	992	2837
Ursus arctos	2	2	0	3	1
Panthera leo spelaea	12	4	0	9	1
Lynx lynx	0	0	1	1	2
Felis silvestris		3			
Mustela sp.	0				2
Martes sp.	1				2
Gulo gulo		1			
Meles meles				1	
Crocuta crocuta spelaea	6	17	6	5	13
Elephas antiquus					
Mammuthus primigenius	8	1127	6	21	220
ivory	21	2413	0	12+	4726
Equus sp.	45	1423	72	121	481
Coelodonta antiquitatis	12	124	0	4	58
Sus scrofa		8			
Megaloceros giganteus		0	0		1
Cervus elaphus		19	1	9	10
Capreolus capreolus					3
Rangifer tarandus	40	1418	30	176	272
antler	44	215	2	47	206
Alces alces					
Bos/Bison	1	61	8		1
Ovibos moschatus		0			
Capra ibex		0	0	27	103
Rupicapra rupicapra		2	0	1	35

Table 6.5 NISP value of individual taxa for Aurignacian

MP	HS	VH	BS	HF	GK
Lepus sp.	19,3	6	5,4	0,2	8,8
Marmota marmota			1,1		0,1
Canis lupus	546,9	58	318,4	25,7	103,6
Vulpes/Alopex	54,1		32,6	6,9	34,5
Ursus spelaeus / Ursus sp.	19146,6	573	603,7	4797,6	2928,31
Ursus arctos	14,1	336	2,6	6,7	17,3
Panthera leo spelaea	364,8	23	92,5	46,1	13,1
Lynx lynx	11,2		2,7		1
Felis silvestris					
Mustela sp.	0,4				
Martes sp.	1,2	1			0,2
Gulo gulo			5,1		
Meles meles			13,5		
Crocuta crocuta spelaea	1434,9	54	594	0,2	28,8
Elephas antiquus		275			
Mammuthus primigenius	6039,8	2017	7844,5		25,2
ivory					
Equus sp.	7761,7	19293	25116,9	263,7	316,6
Coelodonta antiquitatis	3758,9	5809	2575,6	11	129,2
Sus scrofa			21,5		
Megaloceros giganteus	30,9	94			68,9
Cervus elaphus		112	164,5	18,8	250,1
Capreolus capreolus			1,8		5,9
Rangifer tarandus	564,2	298	1285,9	50,1	1106,8
antler					
Alces alces			267		
Bos/Bison	966,4	4441	3818,5		
Ovibos moschatus			392		
Capra ibex			18,6	28,4	268,1
Rupicapra rupicapra			55,7		30,5

Table 6.6 Weight value of individual taxa for MP * no weight provided for KG

A	HS	VH	BS	HF	GK
Lepus sp.	30,2	78	2,6	41,6	222,1
Marmota marmota					
Canis lupus	647	105	28,6	291,5	417,4
Vulpes/Alopex	53,2	102	9,1	55,24	118,91
Ursus spelaeus / Ursus sp.	23666,36	2719	141,5	10597,4	12729,6
Ursus arctos	13,8	49		31,5	8,2
Panthera leo spelaea	499,7	15	139,1	221,7	4,1
Lynx lynx	0		1,3	2,2	1,7
Felis silvestris		12			
Mustela sp.	0				0,4
Martes sp.	0,8				0,7
Gulo gulo		14			
Meles meles				0,6	
Crocuta crocuta spelaea	62,9	184		22,5	21,8
Elephas antiquus					
Mammuthus primigenius	477,3	290360	11,3	1456,9	7638,79
ivory					
Equus sp.	1386,9	41833	1098,4	1919,6	6593,2
Coelodonta antiquitatis	3028,7	7596		70,8	868,8
Sus scrofa		139			
Megaloceros giganteus	0				51,8
Cervus elaphus		1614	380	70,2	143,3
Capreolus capreolus					18,5
Rangifer tarandus	591,2	21020	407,7	2041,39	2929,5
antler					
Alces alces					
Bos/Bison	44,2	2681	164,8		12,5
Ovibos moschatus					
Capra ibex				395,1	524,3
Rupicapra rupicapra		8		0,2	115,8

Table 6.7 Weight value of individual taxa for Aurignacian

HF and GK are relatively similar although, after cave bears, horses at HF and foxes at GK are the second most common fauna. Other taxa in HF are scarce, while horse, reindeer, ibex and wolf each make up roughly 3% of the assemblage. The most abundant taxon in KG is fox, comprising 44% of the assemblage. The second common taxon is horse. Hyenas are the third abundant taxon, and both hyena and wolves show the highest %NISP and weight across all sites. Hares are also common, followed by aurochs/bison, and an equal proportion of red deer and reindeer.

During the Aurignacian, HS is dominated by cave bear and relatively low frequency of other taxa including horse, reindeer and wolf. The assemblage of VH is dominated by the prey animals including horse and reindeer, both equally representing the majority of the assemblage. Mammoth is the third common taxon, and other animals are less represented. At BS, horse is the most abundant taxon followed by reindeer. Cave bear increases in proportion, making up 16% of the assemblage, and other animals are found in lower frequency including aurochs/bison and hare. At HF, the cave bear still comprises more than half of the assemblage, but ungulates such as reindeer and horse are also abundant. Small animal such as hare and fox become more abundant. The majority of the assemblage in GK is also cave bear, followed by horse. Reindeer is the third common taxon, and mammoths and hare also are abundant.

The χ^2 analysis and adjusted residual values of species abundances based on raw NISP values enable us to evaluate the abundance of individual taxa. We observe significant differences from the Middle Paleolithic to the Aurignacian. At all sites, χ^2 values indicate differences at a significant level (<0.001). Therefore, the species composition of the Middle Paleolithic and Aurignacian indicates some change in the species abundance.

MP/A	HST	VG	BS	HF	GK
Hare	**4,04**	0,67	**5,75**	**4,20**	**4,44**
Wolf	**3,40**	-1,46	-0,19	1,35	-0,91
Fox	1,85	1,55	1,64	2,29	0,18
Bears	**11,87**	-2,57	**7,13**	**-12,09**	**-8,97**
Cave lion	1,65	-1,79	-1,03	1,20	**-3,53**
Hyena	**-7,79**	**-4,43**	-0,28	0,56	**-3,21**
Mammoth	**-9,35**	**11,74**	-0,56	2,79	**5,54**
Horse	**-9,51**	**-14,64**	**-3,80**	**5,12**	**6,62**
Woolly Rhinoceros	**-4,75**	**-9,19**	**-3,39**	-0,36	0,42
Red deer	-0,98	**-4,60**	-0,55	1,20	-0,28
Reindeer	1,67	**14,72**	**3,22**	**7,65**	**3,27**
Aurochs/ Bison	-2,15	**-11,58**	-1,15		0,40
Ibex			-0,48	1,76	-0,77
χ^2	325,65	**665,00**	**113,36**	**153,62**	**149,98**
p value	0,00	0,00	0,00	0,00	0,00

Table 6.8 χ^2 Value and adjusted residual values between MP/Aurignacian for each site

At HS, the combined MP assemblage is compared with the Aurignacian, showing differences in abundance among many taxa. There is a significant increase in bears, hares and wolves, while many of the herbivorous taxa such as mammoth, horse and woolly rhinoceros, in addition to hyena, decrease. At Vogelherd, the number of hyena, horse, woolly rhinoceros, red deer and aurochs/bison sees a decline, while the number of mammoth and reindeer increases significantly relative to the assemblage size. Other animals included in the adjusted residual analysis, including hare, wolf, fox, bear and cave lion, remain consistent in terms of abundance. At Bockstein, a different pattern is observed. Similar to Vogelherd, the Aurignacian assemblage is characterized by abundances of reindeer. In addition, the decline of horses and woolly rhinoceros is also a pattern observed both in Vogelherd and Bockstein. Hares and cave bears appear more frequently in the Aurignacian. Other animals show a slight decrease, which may be due to the relatively small sample size of the Aurignacian relative to the MP.

MP	HST	VH	BS	HF	GK	KG
HST	-	-	-	-	-	-
VH	0,71	-	-	-	-	-
BS	0,66	0,02	-	-	-	-
HF	**0,08**	1,20	1,14	-	-	-
GK	**0,03**	0,97	0,90	0,02	-	-
KG	0,65	0,46	0,37	1,07	0,81	-

Table 6.9 Squared Euclidean Distance values based on individual taxa of the MP

A	HST	VH	BS	HF	GK
HST	-	-	-	-	-
VH	0,91	-	-	-	-
BS	0,65	0,10	-	-	-
HF	**0,04**	0,58	0,38	-	-
GK	**0,06**	0,53	0,34	**0,01**	-

Table 6.10 Squared Euclidean Distance values based on individual taxa of the Aurignacian

SED values based on individual species with sample size on average (5<) were recalculated to compare differences between sites in the Swabian Jura for the MP and the

Aurignacian separately (Table 6.9+6.10). SED values of the taxa based on the relative proportion again mirror the general similarity and differences described above. In MP, HS resembles GK, showing low SED values followed by Hohle Fels. HS-VH resulted in the highest SED value, reflecting greater dissimilarity, followed by KG and BS. VH is most similar to BS, while HF exhibits greater dissimilarity to VH, indicated by the highest SED values among all MP assemblages. GK also exhibits a relatively stark contrast, and SED values of VH-HS are greater than VH-KG. BS compared with HF, GK, HS and KG resulted in high SED values. The SED value is the lowest between HF and GK as well as between VH and BS. KG, a known carnivore den, remains unique in its faunal composition, with high SED values.

In the Aurignacian, HS-HF becomes least dissimilar, and GK shows greater difference. The degree of dissimilarity between HS and BS remains consistent while the VH assemblage reveals greater discrepancy to HS. The SED value is the lowest between HF-GK among all the Aurignacian assemblages. VH-BS shows greater dissimilarity compared to the MP. In contrast, comparison between BS-GK, VH-GK, VH-HF and BS-HF of the Aurignacian reveals lesser dissimilarity than in the MP.

SED values are recalculated after removing the cave bear to consider variability in faunal composition, since the depositional history of cave bears differs from other fauna. Overall SED values decrease, exhibiting lesser dissimilarity among sites. This is a clear indication that cave bears drive patterns of species abundance. HS shows the least dissimilarity with HF, but the SED values are lower for HS-BS and HS-GK. VH and KG still present greatest dissimilarity in relation to HS. The degree of difference for VH and BS remains the same, since cave bears were infrequent, and VH remains dissimilar to HS, HF, GK and KG. With the exception of VH, BS has relatively lower SED values for HS, GK and KG. HF is still similar to GK, and the difference with other sites becomes relatively insignificant. SED between GK and HF is small, followed by KG, HS, BS and VH. KG again is different from other assemblages, but closest to GK without bears.

MP	HST	VH	BS	HF	GK	KG
HST	-	-	-	-	-	-
VH	0,17	-	-	-	-	-
BS	0,11	0,02	-	-	-	-
HF	0,08	0,22	0,14	-	-	-
GK	0,12	0,39	0,27	0,03	-	-
KG	0,24	0,51	0,40	0,18	0,12	-

Table 6.11 Squared Euclidean Distance values based on individual taxa of the MP, excluding cave bear

A	HST	VH	BS	HF	GK
HST	-	-	-	-	-
VH	0,19	-	-	-	-
BS	0,17	0,10	-	-	-
HF	0,08	0,07	0,10	-	-
GK	0,05	**0,07**	**0,07**	**0,05**	-

Table 6.12 Squared Euclidean Distance values based on individual taxa of the Aurignacian, excluding cave bear

During the Aurignacian, SED values indicate that HS maintains the same degree of dissimilarity with other sites. However, VH shows lesser dissimilarity with GK and HF than BS, one clear contrast with the SED values including bear. The SED values for all sites compared with GK are lower than in the MP. The similarity increases in the Aurignacian when cave bears are excluded among VH, HF and GK, while HS and BS maintain greater degrees of discrepancy. In all, the calculation of SED without bears still attests to general similarity in the MP, but a slight difference in the degree of closeness in the Aurignacian.

SED values show that when the MP and Aurignacian assemblages of each site were compared, HS, BS and GK exhibit relatively small dissimilarity. Therefore, in terms of proportion, the differences are relatively small. In contrast, VH shows a greater discrepancy between the MP and Aurignacian, a telling sign that the change in the abundance is marked in VH and to a lesser degree in other deposits. SED values excluding cave bears reveal that there are greater differences between MP and Aurignacian assemblages in VH and HS than among other sites, such as BS, GK and HF.

The NISP of herbivores and carnivores for each site is plotted to test whether there is a positive correlation. Among the MP assemblages, there is a positive correlation between middle/large carnivore and herbivore abundance at $p<0.07$, while the Aurignacian assemblages show no significant correlation. While correlation does not signify causation, the positive correlation indirectly suggests that the herbivore abundance in part reflects activity of carnivores at the site.

There is a clear increase in some of the important prey game in the Aurignacian at Hohle Fels, marked by a clear increase of horses and reindeer, the two prominent taxa targeted by hunters. Conversely, the abundance of bears declines. Although not significant (at 0.05 level), mammoths become more dominant, but not to the degree to which ivory fragments increase. Hares also increase in abundance. The pattern of species abundance at Hohle Fels is similar to that of GK with additional changes. Horses, reindeer and hare increase significantly in the Aurignacian. Mammoths also show a significant increase. In addition to the decline of bears, carnivores such as cave lions and hyenas decrease relative to the MP.

In summary, herbivore abundances reveal certain temporal trends, some of which are particular to the Lone Valley and others that are across all sites. Based on adjusted residuals, there is a decrease in the relative proportion of horses in the Lone Valley, a pattern that is reversed in the Ach Valley, representing a significant increase from the MP to the Aurignacian. In the Lone Valley, woolly rhinoceros was consistently more abundant in the MP than the Aurignacian period, while there is no change in HF and GK. Another megafauna, mammoth, increases at VH and GK, mirroring the significant input of ivory during the

Aurignacian, but declines significant at HS, also mirroring the amount of ivory fragments, and shows no difference at Bockstein and HF. Further, reindeer become more abundant in the Aurignacian period in the Swabian Jura sites, except for HS.

In contrast to reindeer, red deer appear to occur without any significant changes with the exception of VH which shows a clear decrease. With the growing presence of reindeer, it is possible to deduce that reindeer, which favor tundra and steppe environments, became more abundant in the Aurignacian period, either a reflection of a changing floral community over time or behaviors of deer such as migration routes that led to an overall increase of reindeer on the landscape that were targeted for prey. At Vogelherd, the aurochs/bison also decrease in number. Ibexes, recovered from BS, HF and GK, show no significant changes over time.

Hunting of reindeer appears to be a regional trend among hunter-gatherers that emerged in the Aurignacian period. On the other hand, it appears that horses were regularly hunted throughout the period of the Middle Paleolithic and onto the Aurignacian period with varying degrees of preference, changing the patterns of prey game abundance at sites.

When compared across sites, hares show a consistent increase except for Vogelherd. It is known that many smaller specimens were excluded from the analysis and thus likely creating a particular strong bias against small animals. Therefore, the increase of hare appears to be a regional signal in both valleys or is due to the differential preservation of smaller animals. However, this increase is not observed in foxes and thus partially appears to reflect actual increases in the input of hares in the assemblages. Besides the hares, there is variability in patterns of species abundance between the Middle Paleolithic and the Aurignacian.

For bears, we observe a decrease in HF, GK and VH, while the decline is not significant at VH. In contrast, bears increase in proportion at HS and BS. There is an intersite variability of cave bear abundances in the two valleys. Hyenas decline in proportion at HS, VH and GK, but do not change in frequency at BS and HF. At Hohle Fels, hyenas are not an abundant taxon in both periods, so it appears that the diminishing presence of hyenas in the Swabian Jura is, perhaps, a regional signal. Wolf shows a significant increase at HS only and continues to be present in deposits without changing frequency. Cave lions and foxes, two other common carnivores at these deposits, do not reflect any temporal trends.

Diversity

Several measures of diversity provide a basis of comparison for the evenness in the faunal composition (Table 6.13). For all these values, there is little correlation between the sample size and the evenness measure. When all faunal species are compared, the KG assemblage is the most diverse MP assemblage expressed both in terms of the Shannon and Simpson's indices. After KG, BS and VH have a relatively high degree of evenness according to the Shannon index, while HS has a greater evenness based on the Simpson's index. HF and GK assemblages show the lowest evenness value in the Shannon and the Simpson's index of evenness, respectively. Cave bear accounts for the low diversity in GK and HF. During the Aurignacian, the diversity is highest in BS. However, BS differs from others due to a small assemblage size. After BS, VH exhibits the highest diversity. HS has the lowest evenness, although the evenness values based on Simpson's index are comparable among HS, GK and HF. The diversity of KG is partially due to the recovery method but also is accounted for by the fact that the assemblage is large as a result of the use of the cave by hyenas as a den.

From the MP to the Aurignacian, the diversity measure for Shannon's index of evenness increases for BS, GK and HF, but remains consistent at VH and decreases at HS. Based on Simpson's index, diversity increases for BS and GK, and remains consistent for VH and HF, but decreases for the HS assemblage. Diversity measures do not indicate significant correlation with the abundance of bears or carnivores. The only correlation of significance is a positive relationship between herbivores and the diversity measures in the MP. Therefore, the higher abundance of herbivores equates to greater diversity. However, this is not reflected in the Aurignacian.

	MP						A				
	HS	VH	BS	HF	GK	KG	HS	VH	BS	HF	GK
NTAXA	17	14	22	12	19	17	14	17	11	16	20
Shannon index of evenness	0,43	0,53	0,54	0,16	0,35	0,73	0,28	0,53	0,74	0,45	0,48
Simpsons index	0,49	0,43	0,34	0,87	0,62	0,08	0,72	0,27	0,24	0,47	0,42
1/D	2,03	2,35	2,91	1,15	1,61	12,28	1,39	3,65	4,18	2,13	2,40

6.13 Measure of diversity for MP and Aurignacian

Prey Animals

Horse was the most abundant prey animals in the Lone Valley and the Ach Valley. This is mostly true for the MP and the Aurignacian. In the MP, there is also a variation in the abundance of other prey animals. At VH, woolly rhinoceros is the second most abundant prey animal while mammoth is more common in HS, and reindeer is the second most important prey animal at BS. KG also affirms the importance of horse as well as hare and aurochs/bison during the MP, as prey for hyenas. Other prey represented across sites in small quantities includes red deer, ibex, muskox, elk, chamois, wild pig, roe deer, Giant elk and straight-tusked elephant.

In the Aurignacian, horse remains a common prey but reindeer increases across the sites. Aside from these two taxa, mammoth gains greater importance at some sites: VH and GK. There are prey animals that are less common in the Aurignacian, such as red deer, aurochs/bison and woolly rhinoceros. Ibex is present in relatively high quantities but only in - the Ach Valley. Other prey animals include wild pig, giant elk, red deer, roe deer, elk and chamois.

	MP						A				
	HS	VH	BS	HF	GK	KG	HS	VH	BS	HF	GK
NTAXA	5	5	6	4	5	5	5	5	4	5	6
Shannon index of evenness	0,27	0,19	0,18	0,34	0,32	0,24	0,30	0,26	0,29	0,27	0,27
Simpsons index	0,32	0,55	0,48	0,26	0,21	0,28	0,25	0,30	0,40	0,30	0,23
1/D	3,14	1,83	2,09	3,90	4,87	3,56	4,03	3,28	2,51	3,31	4,41

6.14 Measure of herbivore diversity for MP and Aurignacian

The measure of diversity based solely on an array of potential prey, which includes ungulates and proboscideans, does not allow for a simple interpretation. Both the Shannon index of evenness and Simpson’s measure of evenness indicate that the fauna are more evenly represented in the Lone Valley in the Aurignacian when compared to the Middle Paleolithic. This is in contrast to the Ach Valley where both GK and HF reveal lower values in the Aurignacian. Across all sites, the diversity of the HF assemblage is high in the MP though the sample size is relatively small. BS has the lowest prey diversity, followed by VH. This is likely due to the heavy dominance of horses. During the Aurignacian HS, BS and HF have a higher Shannon index for evenness and HS has the higher Simpson’s index.

The sample size of each assemblage indicates no significant relationship. Such observations reveal that the diversity values are not an artifact of sample size. Further, the evenness indices do not correlate with the abundance of middle and large carnivores, and no clear patterns in diversity are apparent. That being said, it appears that the diversity is higher in assemblages with smaller sample size. When the assemblage is larger, it appears that one or two prey animals usually dominate.

However, the diversity measures vary both geographically and temporally. This variability cannot be accounted for either by increased presence of modern humans at the sites and greater contribution to the accumulation of animal carcasses or through environmental shifts, as both valleys, being in the vicinity of one another, would have experienced similar climatic fluctuations. In all, the diversity measures of herbivores do not appear to provide a clear regional signal of hominin prey choices or subsistence strategies. Local factors override general patterns of species abundance in the faunal assemblages of the sites in the Swabian Jura.

Horse: Skeletal representation and Age

The skeletal representation of common prey differs for horse and reindeer. The skeletal representation of GK, BS, VH and HS are compared. During the MP, the head is overrepresented in the assemblages, making up 65-89% (Table 6.3). The exception is HF, but the NISP of horse is small compared to other sites. Therefore, bias towards teeth elements of horse exists across most deposits in the Swabian Jura. Most likely there are several factors that lead to this regional pattern. The skeletal representation of HS mirrors that of VH, which has been interpreted by Niven (2006) as resulting from carnivore ravaging. Due to heavy carnivore damage, it appears that the skeletal material was significantly altered to the degree that only the most durable part of the carcasses remained for analysis

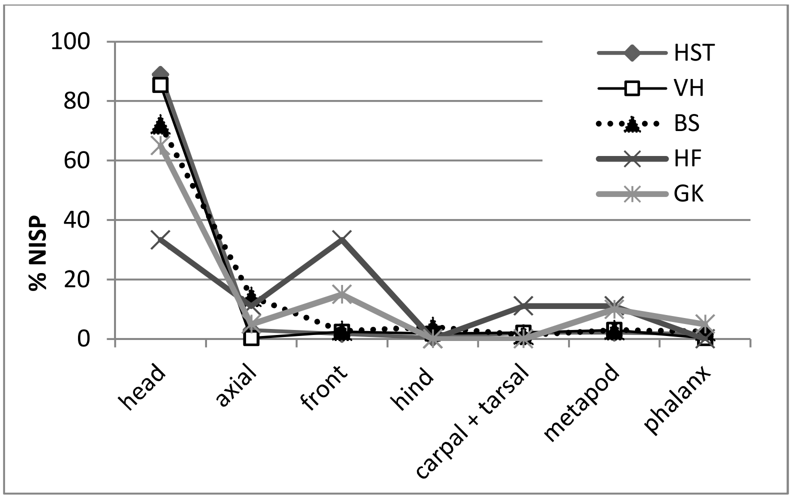


Table 6.3 %NISP of body parts of horse, MP

As Niven (2006) discusses the economic utility of crania of horses, there are relatively high abundances of meat and other tissues such as brain with nutritional values (Lupo, 1998) despite the fact that the general utility index is low for skulls (Outram and Rowley-Conwy, 1998). Ethnological observations on Hadza hunters reveal that meat is removed and other tissues of crania are consumed at the kill or butchery site and, half of the time, are not transported back to the habitation site (O'Connell et al., 1988). However, the energetic return of the skull was probably high if the hunt took place in the vicinity of the valley. Therefore, it is likely that the skull is abundant due to its dietary value and the likelihood that the hunt took place within the proximity to the cave.

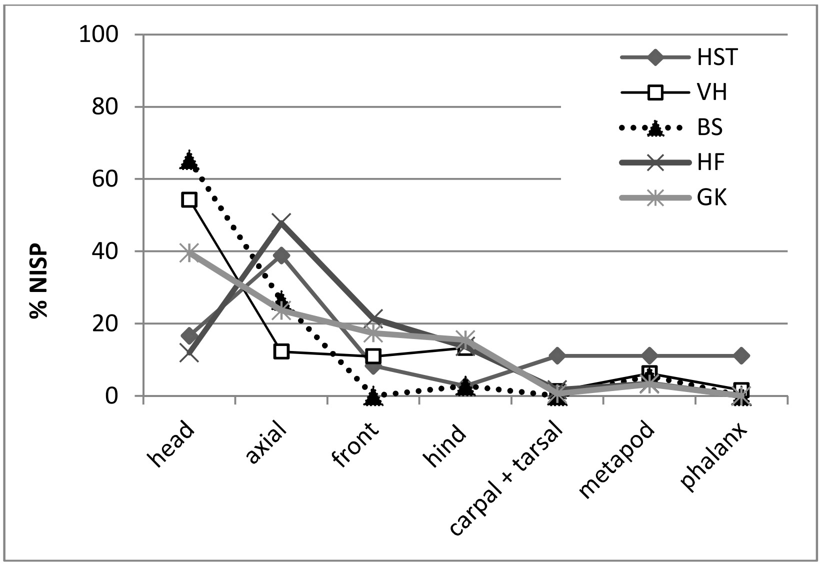


Table 6.4 %NISP of body parts of horse, Aurignacian

During the Aurignacian, the patterns change slightly (Table 6.4). The BS, GK and VH remain dominated by cranial elements, but the overall representation becomes more equal, with increasing abundance of axial elements at BS and fore and hindlimbs at VH. GK is represented by cranial elements, followed by axial and limb proportion. At HS and HF, the assemblages show axial elements to be well represented. This is due to the abundance of ribs; besides the axial element, the frontal limb is also frequent at HF.

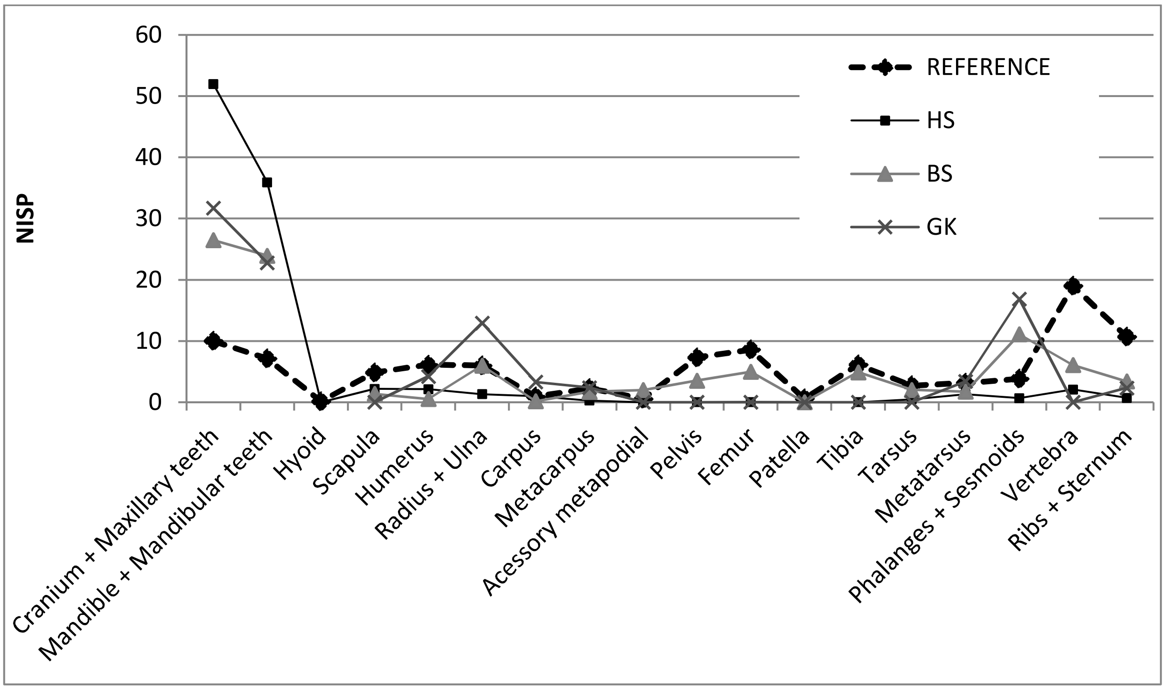


Figure 6.5 %Weight of skeletal element for horse from reference skeleton (EQ42) and assemblage from MP

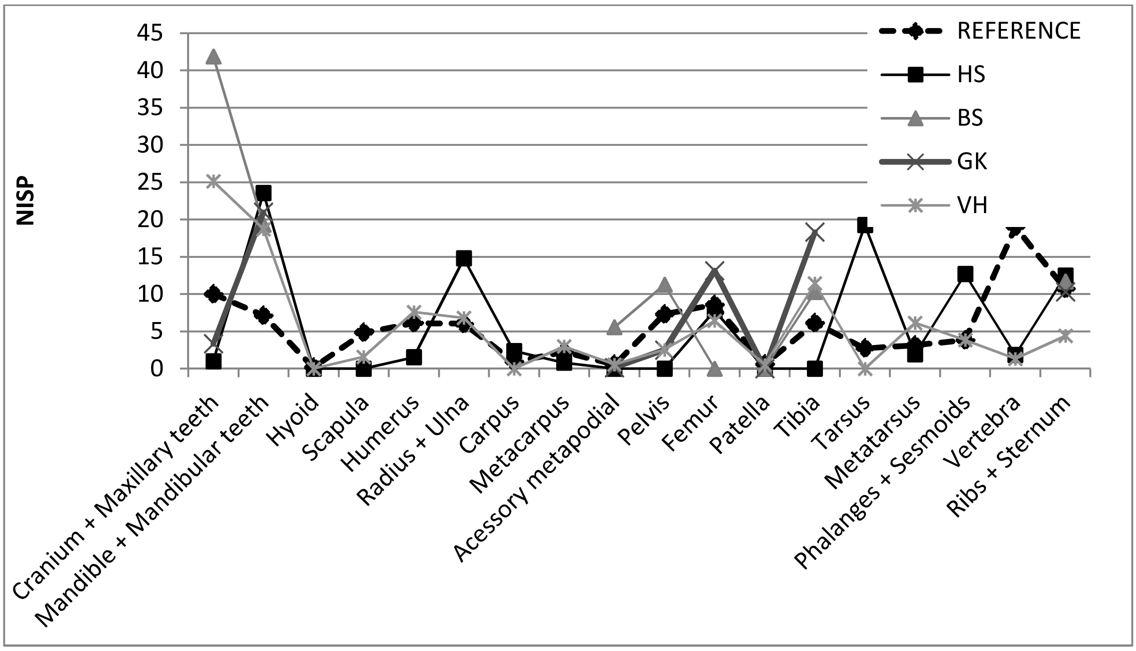


Figure 6.6 %Weight of skeletal element for horse from reference skeleton (EQ42) and assemblage from Aurignacian

Further, the comparison of weight with the comparative skeleton is similar to the skeletal abundance based on NISP. The cranial element is overrepresented at all sites. At HS, this pattern is extreme, and most of the skeletons are dominated by skulls and mandibles. In all assemblages, the axial element is underrepresented. Comparative skeleton and MP assemblages exhibit relatively low correlation. This pattern becomes diverse in the Aurignacian. The weight of the cranial elements decreases at most sites with the exception of BS. Low survival elements, including vertebra and pelvis, remain underrepresented at all sites. There is an overrepresentation of mandible, radioulna and tarsal remains at HS, while VH exhibits overrepresentation of some limb elements such as the tibia. Further, the GK assemblage is also characterized by the overrepresentation of crania and hindlimbs, or the femur and tibia. The correlation between the weight of comparative skeletons and the assemblages continues to be low. Therefore, in the MP, there is a clear sign of *in situ* attrition, but the Aurignacian assemblage indicates variation in the skeletal abundance not attributed to a single cause. This is also noted by Niven's analysis (2006) of density-mediated attrition. She notes that a degree of *in situ* attrition alone does not account for the skeletal pattern. Horse remains from GK and VH are well represented by limb proportions with a greater utility index.

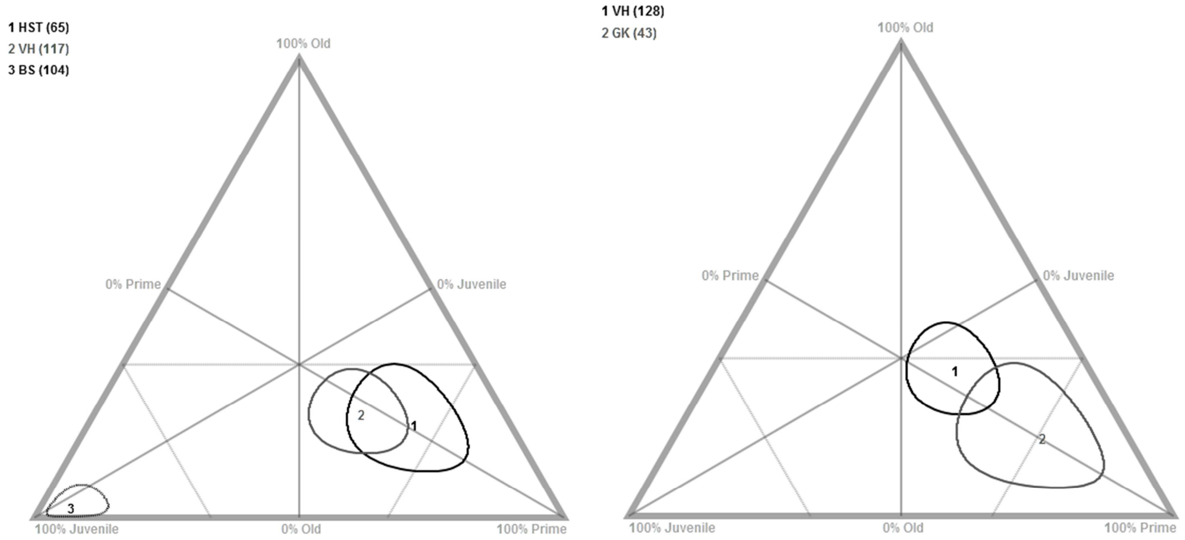


Table 6.7 Age group of horses for MP assemblage on the left and Aurignacian assemblage on the right

The abundance of horse remains in some deposits allows for a reconstruction of the mortality profile, which provides clues to hunting strategies and predators. The mortality profile is determined by the identification of deciduous teeth and measurement of permanent premolar/molar teeth. During the MP, the age profiles are provided for the sites of the Lone Valley. VH and HS assemblages consist of a large proportion of prime adults followed by an equal proportion of old adults and juveniles. This reflects a catastrophic mortality, an expected pattern among living animal populations. Juveniles are not as well represented in archaeological cases due to the attritional bias against deciduous or unmineralized permanent teeth. The pattern reflects non-selective predation that results from stalking or traps as a hunting strategy or focus on solitary individuals instead of herds (Steele, 2005; Stiner 1990, 1994).

BS is an outlier within the Lone Valley. There are 10 adult individuals based on teeth MNE count (Krönneck, 2012). Most of the teeth derive from juveniles. The high frequency of juveniles and old aged individuals characterize a typical attritional mortality with an overrepresentation of vulnerable individuals. However, the extreme underrepresentation of old adults is striking at BS. It appears that juveniles were preferentially targeted for predation, suggesting that the hunters focused on family herds. The low abundance of prime adults will nonetheless lead us to conclude that this demographic pattern is a variation of an attritional mortality marked by the rarity of old adults.

During the Aurignacian, there is a large enough sample in VH and GK. At VH, the prime adults are slightly dominant and juveniles are underrepresented compared to the other age groups (Niven, 2006). The aged MNI also show that prime adults dominate the assemblage (Niven, 2006). There is continuity in the demographic pattern compared to the MP, which represents a living structure and points to a non-selective predation by humans. Further, based on the lack of canines, Niven (2006) concludes that hunters focused on family herds, which would have very low numbers of males (one or two males per herd). The GK assemblage is also comparable. While the sample size is small, it is clearly pointing towards a living structure with a dominance of prime adults and an equal proportion of old adults and juveniles.

In all, the age groups of horses mostly show that predators systematically targeted prime adults. BS remains the only exception to this pattern, which can be interpreted as a form of attritional mortality with a skewed focus on juveniles. Based on the literature, this pattern occurs often in kills of non-human predators such as wolves, coyotes and hyenas that chase prey over distances or through scavenging (Steele, 2005; Stiner, 1990, 2009). In contrast, stalking and ambush as a hunting strategy result in a random selection of individuals regardless of their age and fitness. This form of hunting is practiced by felids, but humans also produce animal accumulation without particular preference of age that would result in living structures of the prey population (Stiner, 1990).

Reindeer

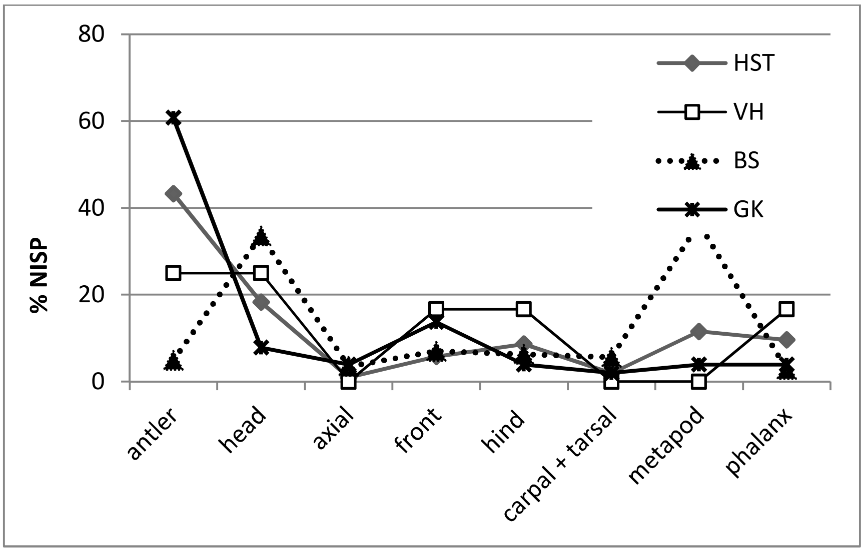


Figure 6.8 %NISP of body parts of reindeer, MP

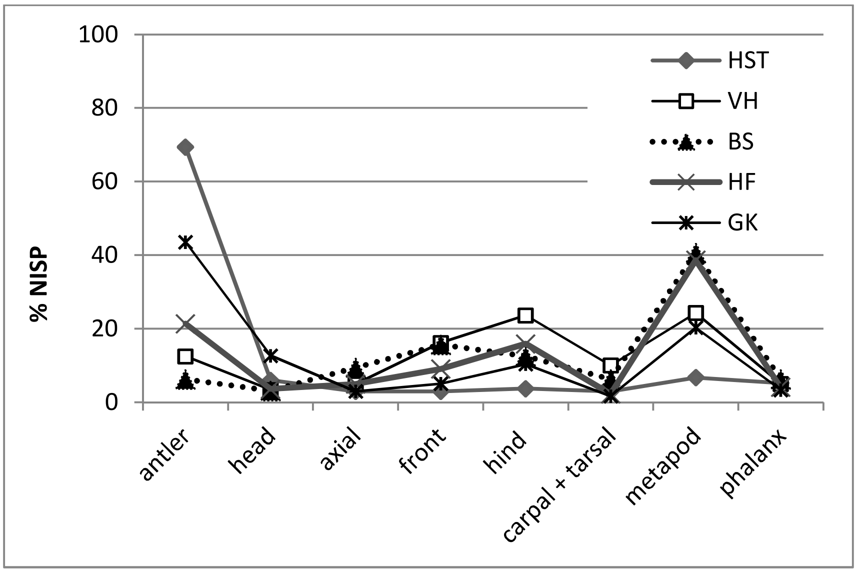


Figure 6.9 %NISP of body parts of reindeer, Aurignacian

The skeletal representation of the reindeer varies across sites. At HS, the MP assemblage is largely head dominated with a high frequency of antlers and cranial parts. Besides the heads, metapodials are more common. At VH, the axial elements and the extremities are underrepresented, although the small sample size makes this assemblage rather limited in deducing patterns. Similar to HS, reindeer remains of BS are dominated by cranial elements and metapodials although antlers are infrequent. The number of reindeer remains in HF is low and not considered here. GK is characterized by an abundance of antlers followed by forelimbs. The skeletal representation shows no consistent pattern.

During the Aurignacian, HS is characterized by an abundance of antlers, while the other body part frequency is proportional. At VH with the largest assemblage size, antlers are not so common, but the majority of the remains are represented by hindlimbs and metapodials. At BS, the assemblage is small but limbs are well represented. The reindeer remains at HF are characterized by a high proportion of metapodials, followed by antlers and hindlimbs. After antlers, metapodials, crania and hindlimbs occur frequently at GK.

The frequency of antler does not show a temporal trend, but a spatial variation. Antlers remain comparatively frequent in HS and GK during the MP and Aurignacian. Antlers from the Aurignacian strata in GK exhibit anthropogenic modification with traces of polishing and breakage (Münzel, in press). Therefore, collection of antlers is attributed to humans during the Aurignacian while carnivores may have contributed to the assemblage in the MP. Carnivore modification is insignificant at GK in both strata, but occurs at a higher frequency at HS. As noted in the previous chapter, the frequency of carnivore damage on antlers at HS decreases from the MP (16%) to the Aurignacian (10%). Relative frequency of antlers has been documented at carnivore dens or caves with mixed assemblages (Stiner, 1994) but anthropogenic modification at GK demonstrates the use of antlers for tool production in the Aurignacian. Antler distribution at GK and HS cannot be easily explained, but reflects both carnivore behavior in the MP and hominin activity in the Aurignacian.

Cranial elements are better represented in the MP than in the Aurignacian. There is a clear overrepresentation of metapodials at all sites in the Aurignacian as well as in the BS assemblage during the MP. Hindlimbs are also well represented while cranial elements are underrepresented in the Aurignacian compared to the MP. There is a greater representation of limb portions, which correlate with the meat index as well as marrow index. Further, Münzel notes that the metatarsals of reindeer also served as raw material for tool production (in press).

There are not enough reindeer remains in most sites to reconstruct the mortality profile, with the exception of VH. There is a clear dominance of prime adults and relatively scarce juveniles and old individuals. This is a signature of human predation, focusing on prime adults (Stiner, 1994). GK is represented by equal representation of the population (Münzel, in press).

Mammoth

Mammoth also gains considerable significance in the Aurignacian that is heavily represented at VH. At other sites, mammoth is heavily biased towards teeth and the exploitation pattern of mammoths by modern humans is not evident. At VH, Niven (2006) concludes that the selection and transportation of body parts were not based on meat utility but non-nutritional importance, such as the use of fauna for architectural purposes, tool production and fuel for fire. Ivory becomes a prominent component of the Aurignacian assemblages, which is found in the form of artifacts and debitage (Münzel, in press; Wolf, 2013). Increased mammoth exploitation is better documented through the exploitation of non-nutritional elements than of elements with high caloric return for food.

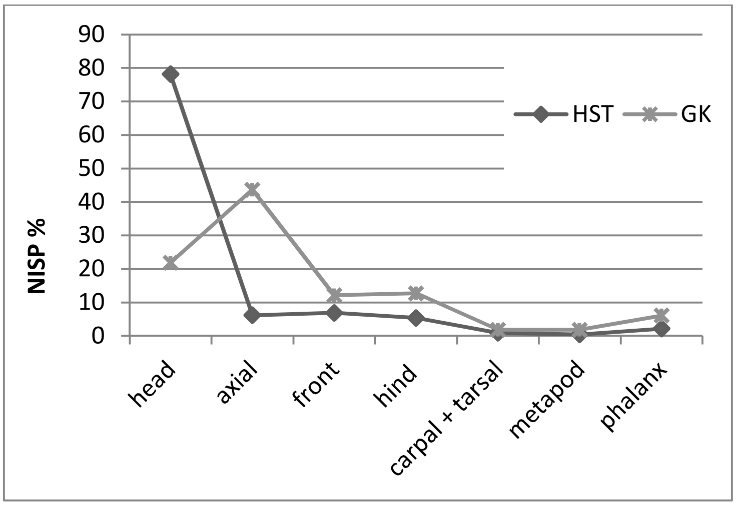
Seasonality

There are relatively few signatures of seasons that Neanderthals and modern humans occupied the Swabian Jura. The seasonality of the MP of Bockstein (in Bocksteinschmiede III) shows that hunting horses took place during spring, documented by juvenile equid teeth (Krönneck, 2012). During the Aurignacian, remains from GK indicate occupation in winter, documented by the presence of foals, and spring to early summer evidenced by the presence of young mammoth remains (Münzel, in press). At Vogelherd, the hunting of reindeer and horse likely points to the occupation of the site between late summer and fall (Niven, 2006).

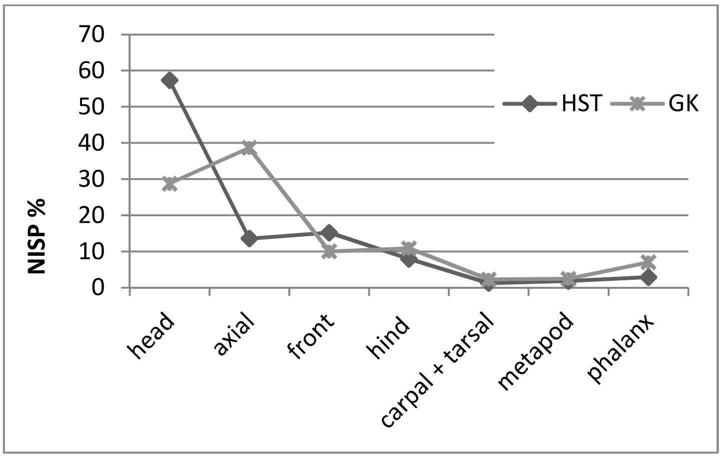
Cave Bear

Skeletal representation of bears is expressed in terms of NISP and weight. For NISP all the sites were taken into account while the weight for GK and HS were considered.
The %NISP (Figure 6.10+6.11) consistently shows the clear dominance of skull and mandible across sites with the exception of GK, which is represented by the overrepresentation of axial elements, especially of ribs. Besides GK, there is no intersite variation that appears significant. Such a pattern reinforces the notion that the process of natural attrition was consistent among

all sites. Therefore, the skeletal abundance of cave bears, much like horse, appears to be a product of *in situ* attrition.



6.10 %NISP of body parts for cave bear, MP



6.11 %NISP of body parts for cave bear, Aurignacian

During the Aurignacian, the general pattern remains similar: the cranial elements are dominant, but their proportion increases and other elements including axial proportions become more abundant. GK is the exception to this pattern and the assemblage size of BS is small. Overall, the axial elements are better represented in the Aurignacian. The proportion of extremities indicates that these elements are subject to attritional processes and remain consistent in cave bear assemblages.

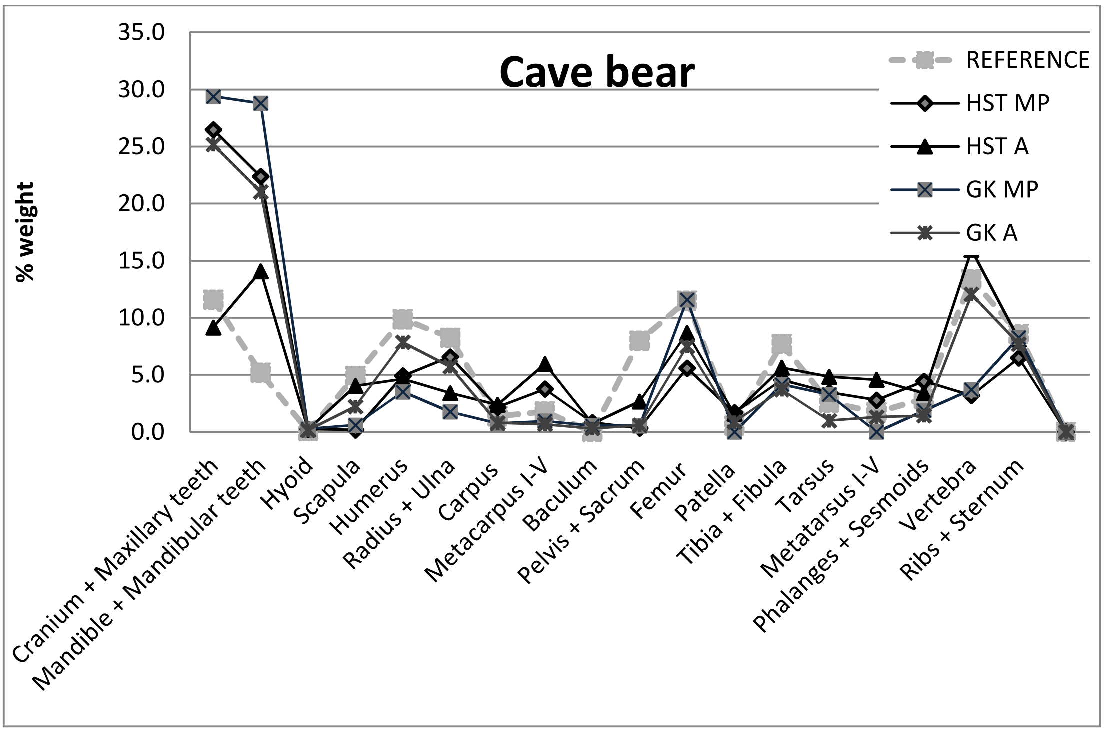


Figure 6.12 % Weight of skeletal element for cave bear from reference skeleton (UR 7) and assemblage from Aurignacian

The weight shows that despite differences at GK and HS, the overall pattern is similar (Figure 6.12). *In situ* attrition affected the survivorship of the skeletal elements in the MP. There is a clear bias towards the cranium and mandible, including teeth, and a bias against the pelvis and vertebrae. There is a slight variation in the abundance of certain elements, but the underrepresentation of axial elements with greater fragility and the overrepresentation of teeth are consistent among both sites. The Pearson correlation shows that there is no significant fit between the comparative material with the cave bear remains of HS and GK.

In the Aurignacian, GK indicates a similar pattern whereby the cranial elements are overrepresented; but other elements, with the exception of the pelvis, remain proportional to that of the comparative skeleton. HS also shows a relatively similar pattern but the crania are underrepresented. The correlation between the weight of the comparative skeleton and the archaeological assemblages also becomes significant.

Münzel			Stiner		
HS	MP	A	HS	MP	A
juvenile	171	56	juvenile	186	62
prime adult	61	18	prime adult	41	10
old adult	38	8	old adult	23	6
BS	MP	A	VH	MP	A
juvenile	15	7	juvenile	2	2
prime adult	22	6	prime adult	1	9
old adult	0	0	old adult	0	5
GK	MP	A			
juvenile	221	1321			
prime adult	54	179			
old adult	10	60			

Table 6.15 NISP of cave bear based on teeth for each age group category

The age of cave bears represented at the sites shows that there are relatively consistent patterns among sites with large cave bear remains (Table 6.15). This mortality profile supports the notion that certain caves served as a den. Despite the decrease of cave bears in the Aurignacian, the age mortality pattern does not alter. The method of age determination differs among sites. BS and GK are based on Münzel’s scheme while VH is based on Stiner’s scheme. HS was assessed on both and shows that there is little discrepancy between these two methods, which are therefore comparable. HS and GK represent a clear juvenile-dominated pattern with a temporal continuity from the MP and the Aurignacian. Despite the lower survivorship of juvenile remains, there is a clear dominance of juveniles in these cave deposits. The cave bear teeth are not so abundant in the BS and VH, but prime adults are slightly better represented. The age profile possibly indicates that these caves were not used as the hibernation as well as denning site for female cave bears.

Cave bear preference for a denning site is not easily explained. They prefer a protected, sheltered area with little disturbance. Therefore frequent visits of caves by other animals, such as hominins or carnivores, may have led cave bears to avoid certain caves. Cave bears possibly avoided VH due to the relative altitude and visibility of the cave from the valley. Multiple entrances and a non-enclosed setting did not provide protection from potential predators, which discouraged cave bears from the use of the site for hibernation. At Bockstein, cave bear remains are low compared to HS, GK and HF. In other deposits and cultural layers not considered in this study, there is a greater abundance of cave bears during the Gravettian period (Krönneck, 2012), though they are scarce in the MP and the Aurignacian. The location of the site complex and the abundance of niches at Bockstein would make it an ideal denning site. The relative altitude above the valley did not deter GK from cave bears and does not seem to be an adequate explanation for the scarcity of cave bears at BS. Based on abundant lithic material from the MP, it is possible that the caves at Bockstein were occupied by Neanderthals, whose presence discouraged cave bears from using the sites.

Carnivores

The carnivore guild is well represented in the cave deposits of the Swabian Jura. Middle and large-sized carnivores that occur in the Swabia Jura include wolves, hyenas, cave lions, brown bears and lynx. The most abundant small carnivore is fox, but there are occasional finds of wild cat, mustelids, including weasel/ermine, marten, wolverine and badger.

The most common middle/large carnivores are hyenas, followed by wolves. The carnivore remains are relatively few at HF and VH, but hyena shows a stronger presence at the sites in the MP with the exception of GK, where wolves are the second common taxon at other sites. Cave lion is a rare occurrence and smaller felids are also scarce in the cave deposits. It appears that canids and hyenids are the most common carnivores that exploited the caves.

Further, there are relatively few signs of brown bears in Paleolithic deposits. As described above, cave bear and brown bear overlap in the distribution during the Pleistocene, but it appears that brown bears did not visit sheltered areas for denning or hibernation. This suggests another niche separation between cave bears and brown bears. The rarity of brown bears in cave contexts suggests that the duration, scheduling, preferred location and other variables related to hibernation differed from that of cave bear. This relates to the dietary difference between cave bears and brown bears. The latter primarily exploited meat, and the availability of food sources for brown bear during winter was not limited as for cave bears (Münzel et al., 2011).

Among small carnivores, foxes occur most frequently in KG and GK. Especially the abundance of fox at KG is directly linked to the use of the cave as a hyena den. The cause of the high concentration is not explained, but dens of hyenas often result in an accumulation of preyed ungulates, but also of carnivores, and this may be possible evidence for the predation of foxes. Alternatively, foxes also may have utilized the site as dens.

During the Aurignacian, hyenas decreased significantly in the Swabian Jura. This is a clear regional signal that could be observed across all the sites. Wolves assume importance and replace hyenas as the common predators in the carnivore guild of the Swabian Jura. Foxes are still the most abundant small carnivore and increase in proportion from the MP. Other carnivores including brown bears, felids and other smaller carnivores also continue to be rare.

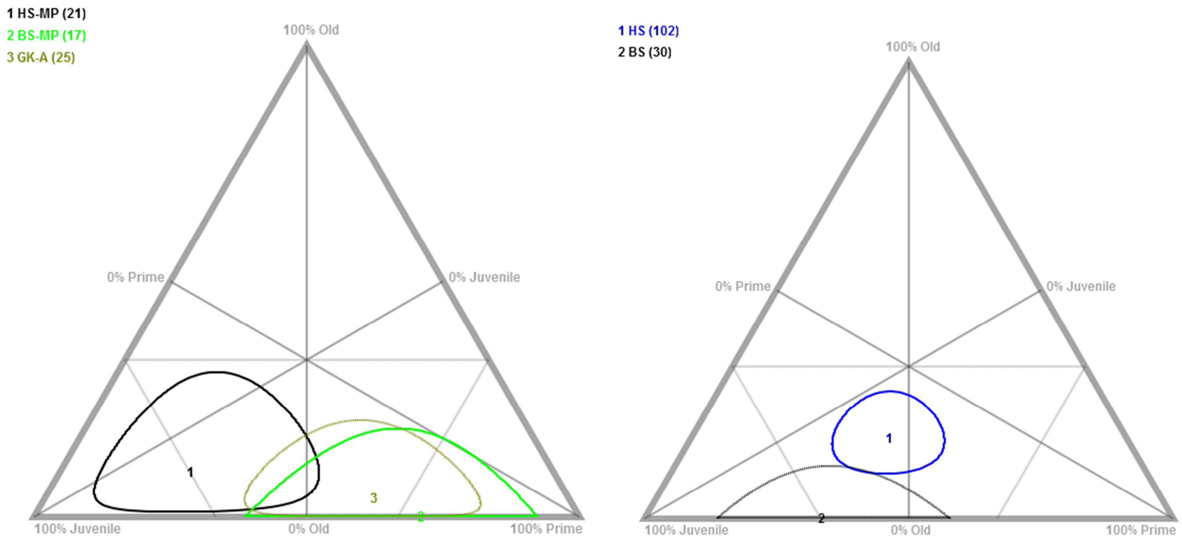


Figure 6.13 Age groups of wolf on the left and hyena on the right

The mortality profile of the wolves is relatively limited in terms of sample size, but it does show that there is a slight bias toward juveniles at HS and adults at BS during the MP (Figure 6.13). In the Aurignacian, there is a slight bias towards adults at GK, not unlike the pattern at BS. Therefore, the patterns generally point to living structures with a slight predominance of adults. The demographic pattern of hyenas differs, with a clear predominance of juveniles at HS and BS. The sample of complete permanent teeth is small and did not allow strict adaptation of Stiner's scheme (1994). However, the abundance of deciduous teeth and the wear of the permanent teeth combined demonstrate a bias towards juveniles/young adults. While the hyena assemblage in KG is not evaluated, both deciduous and permanent teeth are equal. The abundance of deciduous teeth is direct evidence of a hyena den (Cruz-Uribe, 1991). Therefore, it is possible that HS and BS were at times used as a den site similar to KG.

Taphonomy

Taphonomic processes vary greatly among cave deposits, and the sites of the Swabian Jura are no exception (Miller, 2009). Simply put, each cave has a complex history of geological and biological processes as well as anthropogenic signatures, which make a comparison of taphonomic processes a difficult challenge. However, attempts are made to understand signatures of hominin and carnivore activities on the faunal assemblages.

Carnivore modification and anthropogenic modification at the sites, with the exception of Kogelstein, are discussed. There are some differences in the identification and documentation of modification among researchers. For carnivore modification, specimens with documented gnawing, puncturing, scoring and digestive corrosion are tallied. Specimens with chemical etching, which occurs naturally through chemical alteration and through gnawing of carnivores, were grouped together in the Bockstein material. Krönneck (2012) notes that limestone shows similar etched modification at several site deposits within the technocomplex and interprets that similar processes affected faunal remains as well. Thus, the degree of carnivore modification may be underrepresented at Bockstein relative to other sites.

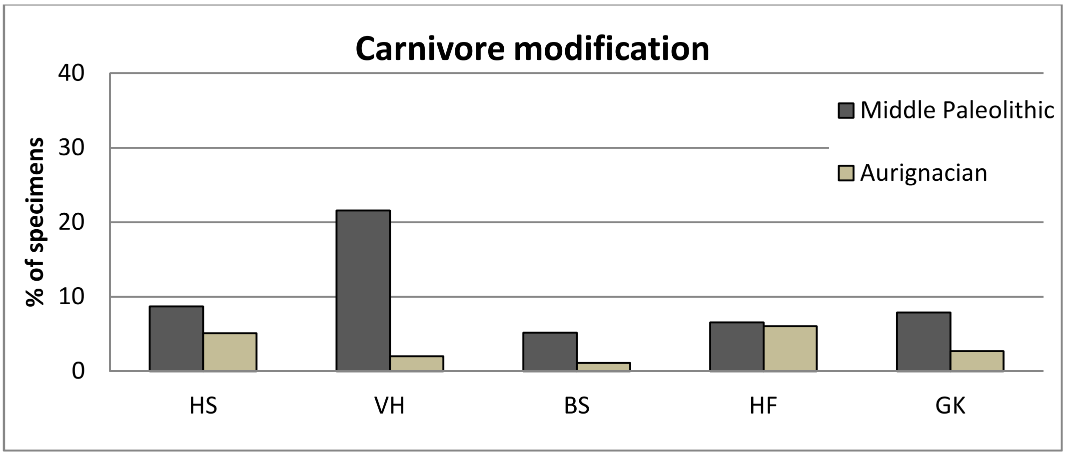


Figure 6.14 Number of specimens with carnivore modification

During the MP, carnivore modification is most frequently encountered at VH (Figure 6.14). Over 20% of specimens show carnivore damage, a relatively high proportion in an assemblage. In one MP layer, over 79% of remains show carnivore modification (Niven, 2006). The low encounter rate of carnivore modification at the site of Bockstein (5.2%) is due to the exclusion of the corroded material, which resulted from carnivore digestion. When these specimens are included in the analysis, the proportion rises to 16.4%. VH represents the largest proportion of specimens with carnivore modification (21.57%). Carnivore modification ranges between 6.5-8.7%. There is no significant correlation between the proportion of specimens with carnivore damage and the abundance of middle and large-sized carnivores, but the number of specimens with carnivore damage and the NISP of carnivore are significant during the MP ($R_s = 0.86$, $p < 0.05$).

In the Aurignacian period, carnivore modification decreases significantly ($p < .0001$) at all sites except for the assemblage of Hohle Fels, which shows a slight decline. The Vogelherd assemblage reveals the greatest change in the proportion of specimens with carnivore damage from 22% to 2% in the Aurignacian. Across all sites, there is decreasing evidence of predators modifying animal carcasses from the MP to the Aurignacian in the Swabian Jura.

One caveat in studying the temporal trend of the frequency of modification lies in the comparability of the temporal span for strata. It may not be adequate to compare cultural layers that span more than ~10,000 years to that of the Aurignacian, which roughly lasts 10,000 years in the Swabian Jura (Conard and Bolus, 2003, 2008). Nonetheless, the proportional differences on an ordinal scale should still be a rough indicator of intensified/dampened carnivore activity represented at the site. This will be especially applicable here, as there is no clear evidence of scavenging of animal carcasses from hominin hunting by carnivores. At these caves, it appears that carnivores themselves contributed to the faunal accumulation in the cave, and thus carnivore damage directly relates to the average intensity of cave use practiced by non-human predators. However, the input of fauna in relation to sedimentation rate should be verified when better chronological data are available for the MP layers.

%	HS		VH		BS		HF		GK	
	MP	A	MP	A	MP	A	MP	A	MP	A
bear	3,8	6,5	14,8	10,7	0,0	0,0	7,5	13,6	7,9	2,3
carnivore	16,8	12,0	10,0	15,3	3,5	0,0	28,6	19,5	12,9	21,8
herbivore	11,4	29,0	14,5	3,3	3,4	4,3	40,9	20,3	42,2	13,0

Table 6.16 % of carnivore modification for mammalian groups

Comparison of gnawing frequencies on identified specimens, grouped under bears, carnivores and herbivores indicates that herbivores are subjected to greater carnivore damage than bears or other carnivores (Table 6.16). The data are available for HS, HF, GK and VH. Herbivore remains with carnivore modification at all sites are more common than carnivores and ursids. After herbivores, carnivores reveal more damages from other predators. This reflects the competition which occurred within the predator guild. Bears, relative to their abundance, are not affected by carnivores during the MP, with the exception of VH, whose the bear sample is relatively small.

With the exception of HS, all the Aurignacian assemblages see a decline in carnivore modification on herbivores from the MP. HS contradicts this pattern, with an increase of carnivore-damaged ungulate and proboscidean remains. Despite the decrease, carnivore-damaged herbivore remains are relatively more common than other animal groups. VH is the outlier with low frequency of predator damage on prey animals. Carnivore damage on cave bears increases at HS and HF and decreases at GK. Further, there is an increase in carnivores with predator modification at GK and VH in contrast to a decrease at HS and HF. Some researchers argue that carnivores exploited cave bears regularly and that cave bears served as an ideal prey during winter (Diedrich, 2012). However, there is a clear tendency for carnivores to hunt herbivores, and the active exploitation of cave bears during hibernation occurred seldom in the Swabian Jura.

The comparison is solely based on animals identified to a genus level and does not include material identified to the taxonomic level of order. Nonetheless, it indicates that herbivores were modified by non-human predators more commonly than other animals that either met natural death or were killed through competition. There is a decrease in carnivore-damaged herbivore remains in the Aurignacian both in the Ach and Lone Valley, thus pointing to the greater role humans played as a predator and agent responsible for the accumulation of faunal assemblages in the caves. HS is the exception to this trend, and the contribution of herbivores to the site by carnivores proportionally increased from the MP to the Aurignacian despite an overall decrease of the carnivore presence in the cave.

Modification of faunal assemblages shows that the overlap of carnivores and Neanderthals occurred relatively frequently in the Swabian Jura in the MP, with no clear evidence of faunal signatures that exclusively derive from Neanderthal subsistence activities. Relative abundance of large and middle-sized carnivores is a direct evidence for predators occupying caves for denning and protection against other competitors, and the age profile of hyenas implies long-term use of sites for denning, which is also supported by the presence of coprolites. The frequency of carnivore modification is another indicator with which we can conclude that cave bear, carnivore and hominin are all agents in the deposits that are responsible for the presence as well as nature of the assemblages. Carnivore and hominin contribution to the fauna is intricate and does not allow for easy distinction. However, the decrease of carnivore abundance and damage on faunal remains is a phenomenon that occurs on a regional level, mirrored in part at HS.

Anthropogenic modification includes burning, cutmarks and other forms of butchering activity. Recovery bias against non-diagnostic specimens at Vogelherd has led to the exclusion of burnt material in the analysis. Organic artifacts and debitage are not considered in this study. Quantification of anthropogenic modification is not a simple task, since most burnt faunal remains are more prone to fragmentation, and anthropogenic modification on highly fragmented material is difficult. Here, the number of specimens is used.

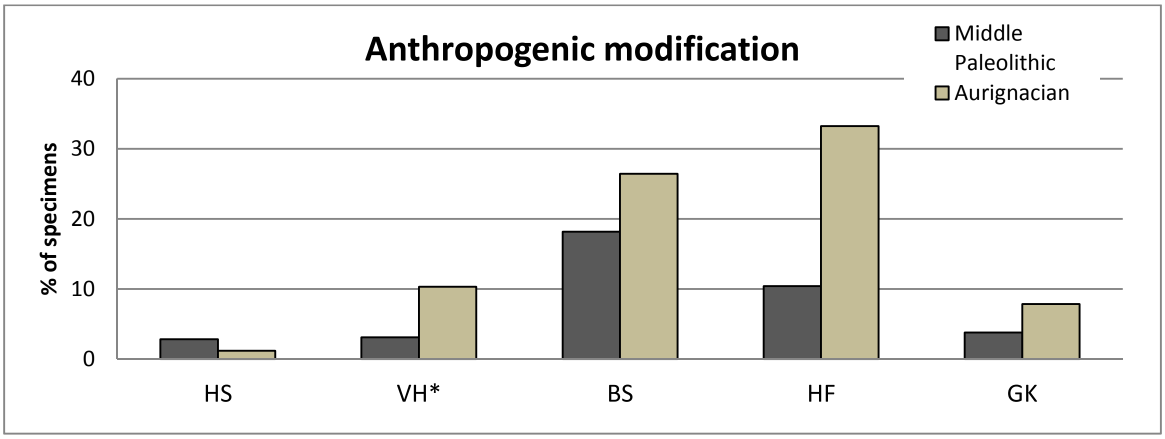


Figure 6.15 Number of specimens with anthropogenic modification. *VH burning specimen not collected

During the MP, there is a large variation in the frequency of anthropogenic modification (Figure 6.15). Altogether, 18.2 % of all specimens at BS show processing and burning traces. Relatively high proportions of anthropogenic modification attest to the major human contribution to faunal remains. Despite the fact that HF is the assemblage with few herbivores, the high frequency of anthropogenic modification after BS is significant. In contrast, GK, VH and HS have a low frequency of intentionally modified bones, with HS representing the lowest frequency of anthropogenic modification (2.9%).

In the Aurignacian, the rate of anthropogenic modification is high at HF and BS, with 33.2% and 26.4%, respectively. VH is also significant at 10.3%. It is somewhat lower at GK and the lowest at HS. This excludes ivory fragments resulting from artifact manufacturing, which would increase the input of organic material modified by hominins especially at HF, GK and VH, all of which are known for clear evidence in systematic production of ivory tools and artifacts (Wolf, 2013). With one exception, the anthropogenic modification raises in proportion from the MP to the Aurignacian. HF, GK and VH show a two to three fold increase in the proportion of animal remains with anthropogenic modification. The exception to this trend is Hohlenstein-Stadel. Traces of human activity on fauna are relatively infrequent in the MP and Aurignacian compared to other sites, and there is a decrease from 2.8 to 1.2% in frequency. This decrease is relatively small, but still significant (p<.0001).

	MP		A	
burning	Frequency	%	Frequency	%
HS	303	2,76	48	0,91
VH*	0	0,00	14	0,11
BS	407	11,94	230	25,53
HF	64	8,57	726	25,50
GK	10	0,80	335	3,61

Table 6.17 Frequency and % of specimens with burning. *VH burning specimen not collected

The use of bone as fuel is the most frequent form of anthropogenic modification with the exception of GK in the MP (Table 6.17). Burning occurs most frequently at Bockstein (11.9%) and Hohle Fels (8.6%) while it is least encountered in the GK (0.8%) and HS assemblage (2.7%). We observe a clear increase of burnt animal remains at BS and HF (26%) and relatively low occurrence of burning at GK but a significant increase from the MP. This pattern speaks to an intensified use of combustion features associated with modern humans. The use of bone as fuel is underestimated at VH due to a bias against unidentifiable faunal material, but there is clear documentation of combustion features with a concentration of burnt material in the Aurignacian layer uncovered during excavation (Niven, 2006; Riek, 1934), and it is likely that burnt faunal remains also increased over time. It is only at HS where there is a reduced amount of burnt material in the Aurignacian.

	MP		A	
butchering	Frequency	%	Frequency	%
HS	11	0,10	16	0,30
VH	21	3,10	1357	10,21
BS	212	6,22	8	0,89
HF	14	1,87	220	7,73
GK	38	3,03	395	4,26

Table 6.18 Frequency and % of specimens with butchering marks.

Some anthropogenic modifications are more susceptible to other post-depositional processes, which override other human signatures. The identifiability of cutmarks and impact fractures depends on the preservation of bones. Therefore, it is possible that the evidence of butchering is somewhat underestimated in the MP where the skeletal remains show a greater level of weathering (in this study and Niven, 2006). The frequency of processing marks is high in the BS assemblage of the MP (Table 6.18). At other sites, evidence of cutmarks and impact fractures ranges between 1.9-3.1% at VH, HF and GK. HS assemblage reveals the lowest rate of butchering traces at 0.1%. During the Aurignacian, VH assemblage indicate the greatest frequency of butchering, followed by HF (7.7%) and GK (4.3%), revealing a significant increase from the MP to the Aurignacian. Cutmarks and percussion marks are extremely low at HS and BS. Simple counts of modified specimens show intensified use of fauna by humans both in terms of butchering and burning across all sites except for HS.

Lithics

A simple count of lithics is direct evidence of hominin presence and a rough measure of occupational intensity. In the MP, the lithic assemblage is large at HS and BS. The assemblage of HF and GK includes debitage artifacts from waterscreened finds, which make the assemblage proportionally larger. There is a significant correlation between the number of lithics (Conard et al., 2012 and reference within) and the number of anthropogenically modified material during the MP. In the Aurignacian, the correlation is low, likely due to the inclusion of small artifacts at GK and HF, skewing the abundance of lithics. Nonetheless, the correlation of lithics and modified animal remains is highly significant. Therefore, it is likely that an increase of modified animal remains is a reflection of greater hominin use of the cave and thus a contribution to the faunal remains at the site.

Exploitation of cave bears

Exploitation of non-prey animals such as carnivores and bears is not a phenomenon that is readily observed in the Paleolithic. We see systematic hunting of carnivores only toward the later Upper Paleolithic when hunters began to pursue small carnivores, largely foxes, for their skin (Charles, 1997). In the Swabian Jura, exploitation of carnivores and cave bears is documented at several sites.

Cutmarks on few cave bear remains were identified on specimens from HS. While they are infrequent, their occurrence are nonetheless consistent with a hypothesis held by Münzel, who claims that modern humans began exploiting cave bear remains in the Swabian Jura (Münzel and Conard, 2004a). HF has yielded the most abundant evidence of ursid remains with anthropogenic modification. Cave bear specimens bear traces of both defleshing and skinning (Kitagawa et al., 2012). Further, some remains were modified into artifacts. Similar to discussions surrounding the question of mammoth hunting by hominins (Niven, 2006), little evidence directly attests to active hunting of the cave bears in the Aurignacian, although it is documented in the Gravettian (Münzel and Conard, 2004a). Due to the high mortality rate of cave bear in cave deposits, it is likely that humans encountered the remains as carcasses. More systematic taphonomic analysis of cave bear remains may falsify this statement.

Bear remains with anthropogenic traces do occur outside of the Swabian Jura, pointing to opportunistic exploitation of bears (Armand, 2006; Münzel and Conard, 2004a; Quiles, 2003). Some evidence extends back to the Middle Pleistocene (Quiles, 2003; Stiner, 2005) while there is documentation from recent periods such as the Mesolithic (Bar-Oz et al., 2009). Thus, the exploitation of bears is not exclusively attributed to modern humans. Such evidence is not geographically limited, occurring from Western Asia (Stiner, 2005) to Iberia (Martínez-Sánchez et al., 2011). Cave bears were more frequently targeted in the earlier phases of the Paleolithic and brown bear becomes common in the middle to later Upper Paleolithic

(Armand, 2006; Gernonpre and Sablin, 2001). While the data may not be representative of bear and hominin interaction in the past, it appears that the evidence of bear exploitation occurs more intensively in the Gravettian period, such as at HF (Münzel and Conard, 2004a) and Covolo Fortificato di Trene (Romandini and Nannini, 2012).

The extinction of cave bears occurred around 27.5 ka in the Swabian Jura and overall in Europe toward the end of the Gravettian period (Münzel et al., 2011; Pacher and Stuart, 2009). The extinction of mammals in the late Pleistocene has multiple causes, and is mainly attributed to climate change, humans, or a combination of both (Koch and Barnosky, 2006). In Eurasia, abrupt episodes of extinction are not documented, and instead, gradual contraction of animal populations occurred over an extended period of time. Studies of genetic diversity in cave bears also demonstrated that the declining population of cave bears preceded their final disappearance in the fossil record from the late Pleistocene (Stiller et al., 2010). The data reveal that there is a decrease in the genetic diversity of the females in the population, which is explained by the decrease in the number of cave bears. This gradual decrease does not appear to be correlated with climate changes.

The arrival of modern humans roughly corresponds to the beginning of the decrease in the cave bear population. Kurten was the first to argue for humans as the possible cause of the decline of cave bear populations (Kurten, 1958). This has also been suggested by Grayson and Delpech (2003) to explain the demise of cave bears at Grotte XVI in southwestern France. The decrease of cave bear does not necessarily signify that humans had a negative impact through hunting, but instead through intensified cave occupation that resulted in opportune shelters for winter hibernation (Kurten, 1958; Stiller et al., 2010). The relationship between the increase in the occupational intensity of humans during the Upper Paleolithic and the gradual decline in the diversity of cave bears needs to be investigated further, but the current view on the extinction of cave bears holds that humans may have had an adverse effect on the population dynamics of cave bears during the Upper Paleolithic. This phenomenon is also mirrored in the Swabian Jura, where there is intensified human occupation of caves and evidence of active exploitation of cave bears beginning from the Aurignacian and intensifying in the Gravettian (Münzel and Conard, 2004a).

Hohlenstein-Stadel in a regional context

The faunal assemblages support the notion that the function of the sites varied and that there are differences in the way sites were exploited in the Swabian Jura. In this context, past hunter-gatherers exploited preys differently at Hohlenstein-Stadel compared to the rest of the caves. The abundance of cave bears at GK and HF remains relatively high, but the growing presence of modern humans contrasts with the use of caves by Neanderthals.

The decisions made by hunter-gatherers to exploit sheltered areas are informed by the conditions of the cave, including the size of the cave, accessibility, the size of the opening of the cave, location (relative altitude, topography), terrain, visibility, as well as the distance to water sources and the favorable orientation with adequate sunlight (Garcia-Moreno, 2013a, b). Hohlenstein-Stadel, compared to other sites, is narrow, and although the surface area of the cave does not differ significantly, the cave was possibly unfavorable for long-term occupation or as an aggregation site for large groups.

The cave did not serve as a functional site for ‘regular’ settlement during the Aurignacian. The *Löwenmensch* was not found intermixed with other settlement debris. Few traces of human activities exist except for personal ornaments relative to other sites. Further, as noted before, the abundance of shed juveniles and/or female antlers has been interpreted as an intentional collection and deposit of antlers by humans. Kind and Wehrberger (2013) noted that it is possible that Hohlenstein-Stadel represents a “ritual cache area … reserved for cultic, totemic or shamanistic rituals with the mysterious lion man at their center” (159). This interpretation cannot be tested against the archaeological record and remains an open question.

However, given that there is a clear increase in the settlement intensity of modern humans in contrast to Neanderthals, scarce human presence at this site is an outlier to the pattern in the Swabian Jura. The regional pattern helps explain why traces of carnivores decrease, but not necessarily account for the decrease in anthropogenic activity at Hohlenstein-Stadel. Thus, it is possible that the role of the site differed from that of a habitation site such as Vogelherd with assemblages that point to intensified cave use.

Subsistence practice of Neanderthals and modern humans in the Swabian Jura

The subsistence practice of Neanderthals has been deeply embedded in the question of non-human predators and their roles in the contribution to the faunal remains of the caves in the Swabian Jura. Some MP deposits show clearer human signatures than others, the prominent example being Bocksteinschmiede III in the Bockstein complex. Horse was a preferred prey in the MP with the relative abundance of juvenile and adult remains in this assemblage. This possibly points to the tendency of Neanderthals to target family herds with many young. Other prey animals including reindeer and woolly rhinoceros were also targeted. *In situ* attrition and extensive weathering of prey remains unfortunately give us a limited view on the patterns of killing, transportation and processing of animal carcasses. The dominance of horse in other assemblages, such as HS, reflects the natural abundance of horses during the Pleistocene period. While this is evident in the Lone Valley, it is also reflected in the abundance of horse at Kogelstein in the Ach Valley. At other sites, the degree of carnivore involvement remains ambiguous and cannot be quantified. It is possible that like Hohlenstein-Stadel, many deposits represent a mixture of carnivore, cave bear and hominin activity.

Horses remain the most abundant herbivorous taxon in the Aurignacian assemblages both measured by NISP, with an exception of Bockstein. Equids are the highest ranked prey in both valleys, a pattern that does not alter from the MP. In terms of biomass, mammoth, rhinoceros, aurochs/bison and giant elk would be preferred over horses. However, the population density of preys varies significantly (Silva et al., 2001) and the encounter rate with larger preys was likely low. Thus, it appears that horses were selectively targeted by hunters over other ungulates and proboscideans due to their biomass and abundance on the landscape. The mortality profile of the horses reveals that the death assemblage represents a living structure with a slight predominance of prime adults. Such a pattern reflects non-selective mortality and hunting practiced by humans in VH and GK.

At the same time, the change in the abundance of reindeer signifies that it was also preferentially hunted during the Aurignacian. The contribution of reindeer grows across all sites, although less significantly at HS, which reflects the economic importance of this taxon. The increase of reindeer corresponds to the decrease of the horse NISP in the Lone Valley, expressed in AR values between the MP and the Aurignacian. In terms of biomass, the horse is roughly 60% heavier compared to reindeer and is energetically more beneficial as a target of prey. Nonetheless, the increase of reindeer indicates certain possibilities.

On the one hand, the population of reindeer likely grew in the Swabian Jura, which was triggered by environmental changes. While it is possible that the population density of horse fluctuated, their contribution to human diet does not alter significantly, and no other faunal or environmental data suggest any decrease in horse population during the early Upper Paleolithic. On the other hand, climatic deterioration evidenced by micromorphological analyses (Miller, 2009) and microfaunal study (Ziegler, in press) may have spurred growth among the local reindeer population. There is some evidence that link cooler climate with an increase in reindeer (Grayson and Delpech, 2005; Morin, 2008). Thus, greater contribution reflects natural abundance of the living population. Skeletal representation shows overrepresentation of appendicular parts including lower hindlimbs and metapodials. Therefore, Münzel (in press) suggests that reindeer remains, especially metatarsals, were also exploited for tool production.

Mammoth also gains considerable significance in the Aurignacian that is heavily represented at Vogelherd. Niven (2006) concludes that the selection and transportation of body parts were not based on meat utility but on non-nutritional importance, such as the use of fauna for architectural purpose, tool production and fuel for fire. Ivory becomes a prominent component of the Aurignacian assemblages, which is found in forms of artifacts and debitage (Münzel, in press; Wolf, 2013). Increased mammoth exploitation is better documented through the exploitation of non-nutritional elements than of elements with high caloric return for food.

Overall, there is little change in the subsistence behavior from the Middle Paleolithic to the early Upper Paleolithic. Continuity in hunting behavior has been documented outside of the Swabian Jura such as in France (Grayson and Delpech, 2006) or Caucasus (Adler et al., 2006). Specifically, study on large game animals, which comprise the majority of faunal assemblages, documents few notable shifts between the Middle Paleolithic and the early Upper Paleolithic (Stiner, 2013). Lack of change reflects the ecological principles such as optimal foraging models that govern the economic behavior regardless of the species and are more dependent on the environmental context. Local factors largely influenced what modern humans and Neanderthals foraged in their given territories, providing a complex picture that permits no generalization on economic behavior of the hominin species. Therefore, the notion that modern humans and Neanderthals behave differently on grounds of subsistence activities needs reconsideration.

The possibility of dietary diversification, often associated with modern humans (Hockett and Haws, 2003; Hockett and Haws, 2005) began to be explored in the Swabian Jura (Conard et al., 2013; Krönneck, in press; Owen et al., 2013). Studies on small game in other regions, many around the Mediterranean Basin, indicate that prey choice of small game shifted from slow-moving animals to fast-moving game due to hunting pressure (Stiner and

Munro, 2002; Starkovich, 2012; Stiner et al., 2002). Such shifts demonstrate that greater hunting pressure was driven by demographic changes of foragers, Neanderthals and modern humans (Stiner et al., 2002). This pattern remains to be tested in the Swabian Jura through systematic analysis of small mammalian remains as well as bird and fish remains.

Settlement pattern and interaction between hominins and animals

Conard and colleagues (Conard, 2011; Conard et al., 2012) discuss how Neanderthals had ‘low impact’ on the environment that allowed the coexistence of hominins and cave bears (Conard et al., 2012). The settlement pattern of Neanderthals in the region is mostly characterized by repetitive short-term occupations, an interpretation drawn from lithic analysis of Hohlenstein-Stadel that applies to most Middle Paleolithic deposits in the Swabian Jura (Beck, 1999). During the Aurignacian, there is a shift in the site occupation in the Lone valley from Bockstein to Vogelherd, and the Ach Valley shows greater anthropogenic input in the valley. Recent studies indicate that modern humans are represented by a higher artifact density than Neanderthals, calculated by the increased number of lithic and organic artifacts and greater intensity of combustion features relative to the volume of excavated sediment (Conard, 2011; Conard et al., 2012). While frequency is a rough measure, the increase in the quantity of artifacts represents relatively high population density or longer occupational periods.

The change in artifact density is a direct reflection of increased human presence. This pattern is mirrored in the faunal assemblages, represented in forms of increased anthropogenic modification on animal carcasses and input of prey animals by modern humans. While results of one or two deposits may be a localized phenomenon, the pattern observed in most sites of the Swabian Jura is a signal that speaks to changes in population density on a regional scale. Quantification of such intensity faces certain challenges, mostly due to intersite variability both geologically (i.e., depositional history) and archaeologically (i.e., site function). Nonetheless, this change is still significant on an ordinal scale and the difference in the intensity of site settlement between Middle Paleolithic and the Aurignacian is evident.

This trend attests to the increasing predominance of modern humans on the landscape and also correlates with the decrease of non-prey animals. Current data do not necessarily support the notion that the population of cave bear decreased in the Aurignacian period. Cave bears remained on the landscape until their demise in the Gravettian period. On the other hand, carnivores show a decline from the Middle Paleolithic to the Aurignacian. There is a notable decrease in the frequency of hyenas at most sites across the Swabian Jura. Further, the carnivore modification of animal remains also declines significantly at most sites. Therefore, these trends are indicative of the diminishing carnivore presence in the caves of the region. While direct causality cannot be inferred based on counts of animal abundance and modification, it is possible that modern humans may have outcompeted the carnivores for resources and habitation/denning sites.

7 Summary and Conclusions

The Swabian Jura is a geographically defined area with Paleolithic deposits and archaeological research in this region helps us understand the temporal trends of the past cultures and reconstruct hominin behavior in Central Europe. Hohlenstein-Stadel is one of the sites with the Middle and early Upper Paleolithic deposits and the analysis of the fauna helps to ‘fill the gap’ in understanding the site function on the one hand, and the nature of faunal assemblages on a regional scale on the other.

During the Middle Paleolithic, the number of sites exhibit clear overlap in the use of caves by carnivores and Neanderthals, documented by a decrease in carnivores as well as traces of non-anthropogenic modification on faunal remains. Bockstein is a possible exception to this pattern where greater frequency of prey and anthropogenically modified faunal material are recovered. Horse makes up a significant proportion of prey assemblages at all sites, while cervids, large bovids and woolly rhinoceros are found at lower frequency. Hohlenstein-Stadel confirms to the general pattern of faunal composition with short term occupation of Neanderthals, documented by burnt fauna and mortality profile of horse as well as carnivores, evidenced by carnivore remains, presence of juvenile hyena as well as high frequency of carnivore modification. Further, fauna accumulated by Neanderthals and carnivores are overlain by cave bears that occupied and died during the winter hibernation.

In the Aurignacian, faunal remains yield greater anthropogenic signal, with increased input of game animals and human-induced modification across most sites in the Swabian Jura. Persistence of horse and significant increase of reindeer characterize many prey assemblages. The increased abundance of reindeer in the Aurignacian is observed outside of the Swabian Jura. Grayson and Delpech (2006) observed similar pattern in France based on data over 200 assemblages dated to the Mousterian, Chatêlperronian and the Aurignacian period. This has also been demonstrated at St. Cesaire (Morin, 2008). The increase is attributed to environmental changes (Grayson and Delpech, 2005; Morin, 2008). Further, ivory fragments attest to the increase in the use of faunal remains for tool production and are likely collected by modern humans (Münzel, in press). To date, no clear evidence for active mammoth hunting is documented in the Swabian Jura (Niven, 2006).

In the early Upper Paleolithic, cave bears remain dominant at Hohlenstein-Stadel and overwhelm signals of other animals. Cave bears coexist with humans at other sites, and persist through the Aurignacian. No drastic fluctuation in the cave bear population is observed, although opportunistic exploitation of cave bear is documented (at Hohlenstein-Stadel and Hohle Fels). On the other hand, we observe change in the frequency of carnivores in sheltered contexts, notably hyenas, which decrease significantly at most sites. Further, the majority of sites show a decline in carnivore damage on skeletal remains. From this pattern, we infer that the decrease in carnivore presence correlates with increasing human presence in caves. Such increase is a rough measure of larger group sizes or longer residential times.

Hohlenstein-Stadel is distinct from other Aurignacian sites, many of which are characterized by high input of artifacts that signals long term human occupation. The site remains an outlier among other caves in that the representation of symbolic behavior in forms of mobiliary art occurred in a cave with low level of human activity. While this is not the case with other forms of symbolic representation such as rock painting or engraving (Clottes, 2003), Hohlenstein-Stadel is one of the few sites in which mobiliary art is recovered with sparse evidence of human presence.

There is a clear intention behind the production, transportation and deposition of *Löwenmensch* unlike other portable artifacts with symbolism such as bodily ornaments, which could be incorporated accidentally into the deposit, one due to its large size and another due to relatively low frequency of visits documented at the site. Therefore, Aurignacian people left the figurine and artifacts leaving little traces of other economic or functional activities. It appears that Hohlenstein-Stadel served a unique function unlike other sites with greater human presence.

On a larger scale, we observe trends in the faunal assemblages that reflect environmental changes and geographical variations. The zooarchaeological record of the Swabian Jura thus far indicates no clear shift in the subsistence practice between the Middle to early Upper Paleolithic. Change in the abundance of reindeer is likely caused by climatic shifts and greater input of ivory is driven by functional needs for raw material. Increase of ivory corresponds to the emergence of symbolic activity in the Aurignacian and reflects diversified use of faunal remains. Thus, no break between subsistence practice between Neanderthals and modern humans is evident from the dataset considered in this study. Continuity in the pattern of large game exploitation has been documented in areas with different geographic and environmental setting (Grayson and Delpech, 2003; Hoffecker, 2009; Stiner, 2013) and Swabian Jura fits to this general trend.

The difference between the Middle Paleolithic and the Aurignacian in the Swabian Jura pertains to changing intensity in the use of caves by Neanderthals and modern humans. The population density of two hominins has been inferred through various approaches including measures of artifact and site frequency (Conard et al., 2012; Mellars and French, 2011) and patterns in small game exploitation (Stiner, 2000; Stiner et al., 2012). Tracking demography in the past faces several issues (Dogandžić and McPherron, 2013), but analyses on an ordinal scale has the potential to shed light into a rough measure of population density over time. With some exceptions (Morin, 2008), it appears that the population density of modern human was significantly greater than Neanderthals.

This study alone cannot tackle the large question surrounding the mechanism behind the transition from the Middle to early Upper Paleolithic and the causes for the extinction of Neanderthals. Nonetheless, the study is one of the first attempts to understand the pattern of faunal assemblages from a regional perspective and to serve basis for comparison between modern humans and Neanderthals. Future study of the fauna from the Swabian Jura will continue to fill the gap in our understanding of Neanderthal and human behavior and to help us explore variability and similarity among *Homo* species of the past.

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