# Fauna from the Middle Paleolithic: Settlement, Dietary Patterns and Technology in the Swabian Jura

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## ABSTRACT

With 150 years of research on the Paleolithic of the Swabian Jura, the region offers one of the richest records of Neanderthal occupation. The faunal remains from the caves of the Ach and Lone valleys provide an important source of data from Central Europe. Sites in the Lauchert and Brenz valleys further augment the picture. The frequency of burned bone remains demonstrates inter-site variability in Neanderthal occupation and some sites show carnivore and cave bear activities, which spatially overlapped with that of hominins. The studies demonstrate that Bockstein was the most frequently visited site during the Middle Paleolithic (MP). Horse often dominates the faunal assemblages with additional exploitation of reindeer and bovids. The role of mammoth and woolly rhinoceros in MP subsistence is hotly debated, remaining an open-ended question, but megafauna were occasionally exploited albeit at a lower frequency than during the Aurignacian. In addition, retouchers were a common osseous tool type during the MP in the Swabian Jura. These data compliment the MP record of the Rhine region and help us better understand the adaptation of Neanderthals in Central Europe.

## RÉSUMÉ

Avec 150 ans de recherches sur le paléolithique du Jura souabe, la région offre l'un des plus riches témoignages de l'occupation néandertalienne.
Les restes de faune des grottes des vallées de l'Ach et de la Lone constituent une importante source de données d'Europe centrale. Les sites des vallées de Lauchert et de Brenz complètent l'image. La fréquence des restes d'os brûlés démontre la variabilité inter-sites de l'occupation néandertalienne dans l'occupation néandertalienne et certains sites montrent des activités de carnivores et d'ours des cavernes, qui se sont superposées dans l'espace à celles des hominines. Les études démontrent que Bockstein était le site le plus fréquenté au cours du Paléolithique moyen (PM). Outre l'ours des cavernes, le cheval domine généralement les assemblages de faune, avec une exploitation supplémentaire du renne et des bovidés. Le rôle du mammouth et du rhinocéros laineux dans la subsistance du PM est vivement débattu et reste une question ouverte, mais la méga-


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faune a été occasionnellement exploitée, bien qu'à une fréquence moindre que pendant l'Aurignacien. En outre, les retouchoirs étaient un type d'outil osseux fréquent pendant le MP dans le Jura souabe. Ces données complètent les archives du MP de la région rhénane et nous aident à mieux comprendre l'adaptation des Néandertaliens en Europe centrale.

## ZUSAMMENFASSUNG

Mit seiner 150-jährigen Paläolith-Forschung bietet die Region der Schwäbischen Alb eine der reichsten Nachweise für die Anwesenheit der Neanderthaler. Die faunistischen Hinterlassenschaften aus den Höhlen des Ach- und Lonetals liefern eine wichtige Datenquelle für Mitteleuropa. Fundstellen aus dem Lauchert- und Brenztal erweitern das Bild. Die Häufigkeit verbrannter Knochenreste weist auf eine Variabilität der Neanderthaler Besiedlung zwischen den Fundstellen hin und einige Fundstellen belegen auch Aktivitäten von Carnivoren und Höhlenbären, die sich räumlich mit denen der Menschen überlappen. Die Untersuchungen zeigen, dass der Bockstein die am häufigsten besuchte Fundstelle während des Mittelpaläolithikums war. Neben Höhlenbären, dominiert häufig Pferd die Fauna bei zusätzlicher Ausbeutung von Rentier und Boviden. Die Rolle, die Mammut und Wollhaariges Nashorn im Mittelpaläolithikum gespielt haben, wird heiß diskutiert und bleibt eine offene Frage, aber Megafauna wurde gelegentlich genutzt, jedoch weniger häufig als während des Aurignacien. Darüberhinaus, waren Retuscheure ein übliches Knochenwerkzeug während des Mittelpaläolithikums auf der Schwäbischen Alb. Diese Daten ergänzen die mittelpaläolithischen Funde der Rhein-Region und helfen uns die Anpassung des Neanderthalers in Mitteleuropa besser zu verstehen.

## INTRODUCTION

The Middle Paleolithic (MP) and Aurignacian in the Swabian Jura are well known and are represented by diverse tool assemblages that demonstrate the behavioral dynamics of Neanderthals and modern humans (Conard 2009, 2011; Conard et al. 2012; Conard et al. 2009; Posth et al. 2017). This cultural shift has long been central to the interests of Paleolithic archaeologists and points to two phenomena: the disappearance and extinction of Neanderthals as well as the westward spread of modern humans out of Africa through the Near East into Europe (Belfer-Cohen and Hovers 2010; Clark 2002; Finlayson et al. 2006; Hoffecker 2011; Hublin 2015; Riel-Salvatore 2010; Roebroeks 2008).

While our understanding of the early Upper Paleolithic represents a crucial key to gaining greater insight into the adaptation of *Homo sapiens* (Benazzi et al. 2015; Blades 1999; Conard 2003; Moreau et al. 2015; Teyssandier et al. 2010), the archaeological record from the MP helps us reconstruct the evolutionary trends of hunter-gatherers. In this chapter, we delve into the question of how Neanderthals occupied the Swabian landscape before the arrival of modern humans and how their dietary patterns differed from those of their successors. This study attempts to bring the MP of the Swabian Jura to the forefront, a period that is crucial for understanding continuity and changes over the span of the Paleolithic occupation in Central Europe.

In the history of Paleolithic research, the behavioral adaptations of Neanderthals were interpreted based on untested assumptions, which deemed them to be cognitively different from modern humans (Klein 2003; Mellars 1996; Wynn and Coolidge 2004). Currently, there is mounting evidence for behavioral parallels between the two hominin species (Grayson and Delpech 2006; Peresani et al. 2011; Soressi et al. 2013). A notable exception is the range and extent of symbolic behavior, which appears to be limited for Neanderthals (Conard 2013; Pettitt 2008). In addition, our prior understanding of Neanderthals and *Homo sapiens* as two distinct species has been refined by evidence of hybridization between the two populations based on ancient genetics (Fu et al. 2015; Green et al. 2010; Mafessoni and Prüfer 2017).

The Paleolithic faunal records reflect different aspects of Neanderthal adaptation, namely, subsistence, occupation patterns, and technology (Adler et al. 2006; Morin et al. 2014; Rendu et al. 2012; Starkovich 2017; Stiner and Munro 2002). We will consider the zooarchaeological assemblages from several caves of the Swabian Jura to interpret hunting and dietary strategies of the MP. In addition, we will investigate how the archaic humans exploited their living space. This study benefits from datasets of multiple sites, which are crucial when we consider inter-site variability and larger regional patterns.

We also assess the available published evidence of osseous artifacts (Münzel and Conard 2004b; Niven 2006; Wagner 1983), including bone retouchers (Toniato et al. 2018). The lack of a large-scale standardized production of organic artifacts during the MP goes hand in hand with the common difficulty in assessing the anthropogenic origin of tools that require minimal modification (Villa and D'Errico 2001). The occurrence of formal organic tools, characterized by specific production sequences and limited by chrono-geographic boundaries, is rare and sporadic (Soressi et al. 2013) and at present is not supported by the regional evidence from the Swabian Jura.

## BACKGROUND

The Swabian Jura represents the largest karst system in southwestern Germany. The topography is characterized by a dry upland plateau, which is bounded by the Upper Danube Valley that cuts through the Alpine Foreland to the south, the altitude ranging between 450-1000 m asl. The current river drainage system formed during the Riss Glacial Period (200-130 ka) and the Danube River fluctuated and meandered with the advances of the glaciers in the Alps (Abel et al. 2002).

Most archaeological deposits are concentrated in two valleys, those of the Lone and Ach, which are about 15 km apart (Fig. 1). For the discussion of organic tools, we also include materials from Schafstall I (Peters 1936), which is located in the Lauchert Valley, to the west of the Ach and Lone valleys. Archaeological sites take the form of either caves or rockshelters with little evidence of open-air occupation. Attempts have been

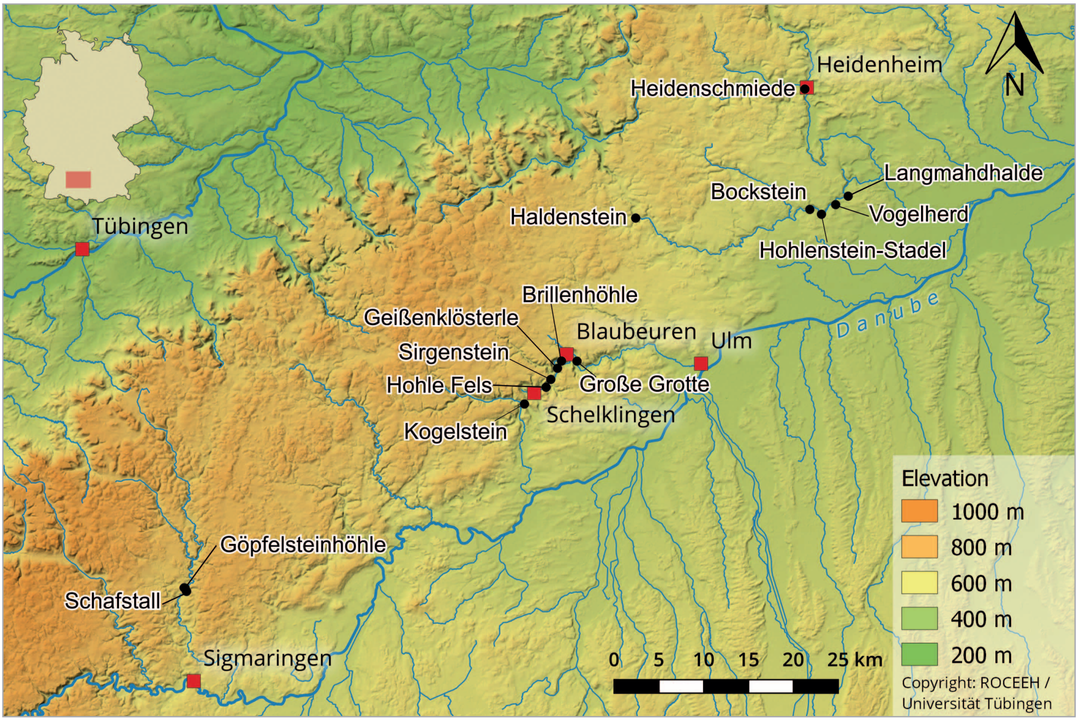


**Fig. 1.**
Map of the major Paleolithic sites in the Swabian Jura.
**Lone Valley**: 1. Vogelherd; 2. Hohlenstein-Stadel; 3. Bockstein; 4. Fohlenhaus; 5. Haldenstein.
**Ach Valley**: 6. Große Grotte; 7. Brillenhöhle; 8. Geißenklösterle; 9. Sirgenstein; 10. Hohle Fels 11. Kogelstein.
Lauchert Valley: 12. Schafstall; 13. Göpfelsteinhöhle.

made to document settlements in open-air contexts, including test pits and geological investigations in the valleys, but intact undisturbed stratigraphy remains elusive. This is partially explained by the meandering of the tributaries and the large input of Holocene sediments (Barbieri 2017; Bolus et al. 1999; Floss et al. 2017).

## CHRONOLOGY

Archaeologists have used several dating methods to reconstruct the chronology of Neanderthal occupation in the Swabian Jura. Researchers employ radiocarbon dating for the late MP while the earlier MP is temporally assigned to MIS stages and substages based on climatic signals. Recent ESR dating also provides greater insight into the chronological contexts, which go beyond the limits of radiocarbon dating. The association of straight-tusked elephant with MP lithics at Vogelherd suggests that the site was occupied by the Last Interglacial (MIS 5e) (Niven 2006). ESR dating places the lower Geißenklösterle horizon (AH VII) to MIS5 with a weighted mean age of 82 ± 9 ka, ranging between 94 ± 10 and 73 ± 9 ka (Richard et al. 2019). Radiocarbon dates provide a minimum age of 50,000-45,000 cal BP for the upper MP horizons of Hohlenstein-Stadel (Beutelspacher et al. 2011), which broadly fit the estimated ESR date of

~45 ka with some inconsistencies (Richard 2015). TL dating from the upper MP layer (IV) at Geißenklösterle produced a date of 43.3 ± 4 ka (Richter et al. 2000).

## NEANDERTHAL FOSSIL

The Neanderthal fossil from Hohlenstein-Stadel is one of the few known remains of Paleolithic hominins from the Swabian Jura. The paleoanthropological analysis identified a femur shaft with robust features and taphonomic observation revealed that it was gnawed on by a mid- to large-sized carnivore, a hyena being the most likely candidate (Camarós et al. 2016; Kitagawa 2014; Kunter and Wahl 1992). Mitochondrial DNA analysis demonstrates that this lineage diverged ~270 ka from other Neanderthals and that the diversity of their population was greater compared to the populations that existed later in the MP (Posth et al. 2017). Based on the calculated mutation rate, the molecular age is estimated at ~124 ka, making this one of the oldest Neanderthal fossils with genetic data. The stable isotopic analysis of the fossil and a red deer remain from the same layer suggests that the Neanderthal lived in a more forested environment. This temporally places the individual in MIS 5d-a and provides evidence of Neanderthal occupation after the interglacial phase (MIS 5e) in this region.

## MIDDLE PALEOLITHIC LITHIC INDUSTRY

The study of the Middle Paleolithic (MP) lithic industry is covered elsewhere here (Conard et al., this volume; Münzel and Çep, this volume). In this chapter, we provide a brief summary of the previous studies on lithic artifacts. The raw material is dominated by grey Jurassic chert and brown Bohnerz chert, nodules of which are found in the nearby river deposits (Burkert and Floss 2005; Çep 2013). The sourcing of raw materials demonstrates that local cherts were the dominant raw material used for lithic production, a pattern that continues throughout the MP. Local flints are fine grained and represent high quality raw materials.

The MP industry in the Swabian Jura is characterized by a Levallois technique with discoid cores, and bifacial and unifacial tools (Çep 2019). Sites such as Hohlenstein-Stadel, Sirgenstein, and Kogelstein have yielded a typical MP industry with reduced Levallois cores, but formal tools comprise a small portion of the assemblages (Beck 1999; Çep 2019; Conard 2011). The exception to this pattern is Bockstein and Heidenschmiede. At Bockstein, bifacial tools occur more frequently than other sites. In Horizon III of Bocksteinschmiede, *Keilmesser* is far more common than other bifacial tools including *Faustkeil* and *Blattspitzen*, which remain rare (Çep 2014; Çep and Krönneck 2015; Wetzel and Bosinski 1969). (See Münzel and Çep, this volume for Heidenschmiede). Recent studies help clarify the variability, definition and production sequence of *Keilmesser* in a larger geographic context (Frick and Herkert 2020; Frick et al. 2017) (Also see Frick et al., this volume).

## ENVIRONMENT

Local paleoenvironmental records provide insight into the past climatic conditions from MIS 5-3 (128 -40 kya) over the span of the MP. Archaeobotanical studies in the Swabian Jura are rare due to erosional processes that repeatedly affected the sedimentological history of the caves and open-air settings (Barbieri 2017; Heiri et al. 2014; Miller 2015).

At a regional level, pollen records are available from the cores of the Füramoos Lake, which is located in the Alpine foreland (Müller et al. 2003). Paleobotanical remains suggest that mild climates prevailed between >50,000-41,500 cal BP, spanning the shift from the MP to the Aurignacian. Another core record from Bergsee in the Black Forest informs us of the environmental conditions between 45-43,000 cal BP (Duprat-Oualid et al. 2017). The landscape alternated between a steppe landscape with some boreal forest, which was characterized by a high abundance of Poaceae (40% on average), *Betula* and *Pinus* (20%), and a more open boreal forest landscape, which was represented by a greater proportion of tree pollen (40-60%) (Duprat-Oualid et al. 2017). This finding corresponds well with other paleoenvironmental signals from similar geographic contexts in the mid-latitudes (de Beaulieu and Reille 1992).

Microfauna and avian fauna recovered from the archaeological sites provide a fine-grained picture of local climatic fluctuations. During the Late Pleistocene, the region was characterized by steppe tundra with a fluctuating abundance of woodlands. Species such as *Dicrostonyx* (collared lemming) are scarce during MIS 4 and the earlier stage of MIS 3 (60-50,000 BP), and the spectrum indicates that forests were more prominent in the milder climate of the MP periods. This environment is followed by an increase in tundra elements by 50 ka (Rhodes et al. 2018; Ziegler 2019). Similar fluctuation in the woodland element is documented at Hohle Fels (Rhodes et al. 2019). The avian fauna are represented by taxa that inhabit steppe-tundra, temperate steppe and coniferous forest in the vicinity of lakes (Böttcher et al. 2000; Krönneck 2019).

Micromorphological studies in the Ach Valley offer another picture of the past environment with some inter-site variability (Barbieri 2017; Goldberg et al. 2003; Miller 2015). At Geißenklösterle and Hohle Fels, the MP is marked by a mild and moderately humid climate evidenced by an abundance of phosphates (Miller 2015). Analysts have documented a similar climatic signal in Hohlenstein-Stadel (Barbieri 2017).

## PREVIOUS WORK

Previous zooarchaeological work has addressed topics that are of archaeological and paleobiological interest (Drucker et al. 2015; Kitagawa 2014; Kitagawa et al. 2012; Kitagawa et al. 2018; Krönneck et al. 2004; Münzel and Conard 2004a; Münzel 2019; Münzel and Conard 2004b; Niven 2006; Starkovich et al. n.d.). Many researchers discuss the subsistence patterns of Neanderthals and modern humans through the study of medium to large mammals (Krönneck et al. 2004; Münzel and Conard 2004a; Münzel 2019). Faunal studies have also explored the exploitation of small game (Conard et al. 2013). The interpretation of these analyses has been complicated by the lack of dry and water screening on the early excavations, and differential preservation between large and small bodied animals needs to be tested in future studies. Despite these limitations, previous studies suggest a low abundance and low diversity of small game including hares, birds and fish in the MP.

In addition, paleobiological studies on cave bears have provided important insight into the Pleistocene fauna and past ecological systems. Genetic analyses have demonstrated the existence of two different cave bear lineages (*Ursus spelaeus* and *Ursus ingressus*) in Central Europe. The latter replaced the former bear population by 31,272 ± 324 cal BP, which was followed by the local extinction of first *Ursus spelaeus* and later *Ursus ingressus* ~29,757 ± 531 cal BP (Hofreiter et al. 2007; Münzel et al. 2011; Stiller et al. 2019). Stable isotope analyses have helped reconstruct their plant-dominated diet and have revealed the existence of an ecological niche which remained separate from that of the coeval brown bears (Bocherens et al. 1994; Münzel et al. 2014; Münzel et al. 2011). The co-occurrence of cave bear remains and hominin occupations has allowed researchers to explore the nature of interactions, leading to hypotheses that suggest a possible anthropogenic cause for their extinction in the later Upper Paleolithic (Gretzinger et al. 2019; Münzel et al. 2011; Stiller et al. 2010). Other studies have focused on the relationship between hominins and other predators, reflecting possible interactions between the different species (Camarós et al. 2016; Kitagawa et al. 2012).

In this study, we address the taphonomic condition of the zooarchaeological record and assess the inter-site differences in site use. Taphonomic studies allow for a greater understanding of the impacts of non-human predators on faunal assemblages and provide insights into Neanderthal behavior when it comes to subsistence-related activities and site use.

## SITES AND METHODS

Faunal analyses have been conducted on several sites including Geißenklösterle (Münzel 2019), Hohle Fels (a sample of the complete assemblage is considered due to ongoing analyses) (Conard et al. 2013; Kitagawa et al. 2012), and Große Grotte (Weinstock 1999) in the Ach Valley and Bockstein (Krönneck 2012), Hohlenstein-Stadel (Kitagawa 2014), and Vogelherd (Niven 2006) in the Lone Valley (Table 1).

All four MP horizons in Vogelherd, which was excavated in 1931 by Riek, appear to be localized and are represented as thin deposits (Riek 1934). Horizons IX, VIII, and VI have produced small assemblages and the majority of the MP fauna from this site derive from Layer VII. Bockstein is a complex comprised of different cave niches and units, which were excavated in 1932–36 and 1953–56 by Wetzel. The excavations

| Site | MP cultural layers | Valley | Source |
|---|---|---|---|
| Hohlenstein-Stadel (HS) | VI-XI | Lone | Kitagawa 2014 |
| Vogelherd (VH) | VI-IX | Lone | Niven 2006 |
| Bockstein (BS) | Törle X, Schmiede III-IV | Lone | Krönneck 2012 |
| Hohle Fels (HF) | VI-IX | Ach | Conard et al. 2013, Münzel and Conard 2004, Münzel unpub |
| Geißenklösterle (GK) | IV-VIII | Ach | Münzel 2019 |
| Große Grotte (GG) | II–XI | Ach | Weinstock 1999 |

**Table 1.**
Sites, layers, location and respective sources of Swabian Jura sites.

yielded the largest faunal assemblage from Bocksteinschmiede (III-IV), in addition to Törle (X) (Krönneck 2012). These layers were recorded as discrete layers (Krönneck 2012). Hohlenstein-Stadel has produced a relatively long MP sequence, as deep as 3.85 m in parts of the cave. Excavations spanning 1935-39 and 1956-61 by Wetzel have yielded eight MP geological layers, which comprise three major MP units (Beck 1999; Kind 2019; Wetzel 1961). Recent work from 2009-2013 revealed similar stratigraphic profiles, and this study considers the two upper MP units to create a comparable sample size.

In the Ach Valley, excavations at Hohle Fels led by Hahn and Conard from 1977 to the present have produced four geological layers (VI-IX). The sediment of the layers has largely been characterized by karstic clays followed by phosphatized calcareous clays and silt aggregates (Miller 2015). Excavations at Geißenklösterle under the direction of Hahn and later Conard took place in 1973-1991 and 2001-2002, respectively, exposing five MP Layers IV-VIII (Goldberg et al. 2019; Miller 2015). The excavation of 2002 reached bedrock. The sedimentary matrices are similar to that of Hohle Fels, but loess was additionally introduced to the cave. Riek, excavating Grosse Grotte from 1960-1964, designated discrete cultural horizons (II-XI) to the MP. Layer II has yielded a possible *Blattspitzen* (Wagner 1983).

Some of the faunal material was recovered in the first half of 20th century, while the rest was excavated from the 1980s to the present. There are notable differences between the older excavations (Bockstein, Vogelherd, Große Grotte, and the larger part of Hohlenstein-Stadel) and recent excavations (Geißenklösterle, Hohle Fels, and part of Hohlenstein-Stadel) in terms of the recovery method used, i.e., the use of screening, which creates a bias toward small game and smaller skeletal elements. However, the piece-plotted remains from Geißenklösterle and Hohle Fels are the main focus of the study, so assemblages dominated by larger specimens (> 3 cm) from recent excavations are roughly comparable to the older collections. Thus, the data here are limited to mammalian taxa larger than lagomorphs.

In discussing the organic tools, Sirgenstein and Schafstall I are also considered. Located in the Ach Valley, Sirgenstein was excavated in 1906 by Schmidt who documented two MP layers (VII-VIII) (Schmidt 1910, 1912). Schafstall I is one of the few rockshelters found in the Lauchert

Valley. The site was excavated by Peters in 1935-1937 and 1943-1945 (Conard et al. 2016; Peters 1936) and lithics have mostly been attributed to the MP (Bosinski 1967; Peters 1936), but there are some doubts on this interpretation (Hahn 1977).

These studies follow standardized methods adopted by most zooarchaeologists, including the use of the number of identified specimens (NISP), which serves as the basic unit of quantification (Grayson 1984). The analyses involved macroscopic and microscopic observations of specimens under a 10x hand lens to examine structural alteration and the condition of the surface.

Different forms of non-biological (e.g., weathering), biological (e.g., rodent), and anthropogenic modification were considered. Some anthropogenic modifications are more susceptible to other post-depositional processes such as weathering, which can override human signatures on the fauna. Cutmarks, the most direct evidence of butchery, likely underestimate the extent to which Neanderthals impacted the animals. This is because no straightforward, measurable relationship between the presence of cutmarks and butchery intensity exists. In addition, fine cutmarks are likely obscured by carnivore gnawing or rounding due to chemical weathering (Kitagawa 2014; Niven 2006). We also document fracture patterns which may be attributed to marrow processing, although carnivores can cause fractures that closely resemble butchery (Stiner 1994). Despite these difficulties, we use the number of specimens with modifications to make comparable inferences from the different assemblages. This is used as a measure to compare the relative human input, which is discussed below.

Burnt faunal material is more complicated to interpret, but it is a rough measure of occupational intensity at cave sites. While it is not possible at this point to distinguish direct burning of bones (for cooking or as fuel) from indirect burning resulting from combustion features (Stiner et al. 1995), the remnants of burning are associated with Neanderthal presence at the caves. Both charred and calcified remains are quantified together. Lastly, organic tools are discussed separately.

## RESULTS

### Preservation

Table 2 lists the NISP values of crania and mandibles by teeth and bone remains to compare the state of preservation across sites. We considered the most common animals, ursid (cave bears as well as bears) for Hohlenstein-Stadel, Hohle Fels, Geißenklösterle, and Große Grotte, and horse for Bockstein and Vogelherd. Teeth generally preserve better than bony remains by at least a factor of two, if not more for most cases. Cranial remains are better represented than mandibular remains, but they generally show that teeth are overrepresented. This contrast between the preservation of teeth and bony remains is starker for horses. In an extreme case, no cranial bone were preserved at Vogelherd, despite the fact that maxil-

| Ursid NISP | Hohlenstein-Stadel | Hohle Fels | Geißen-klösterle | Große Grotte | Horse NISP | Bockstein | Vogelherd |
|---|---|---|---|---|---|---|---|
| cranium | 122 | 27 | 36 | 50 | cranium | 9 | 0 |
| maxillary tooth | 240 | 118 | 157 | 183 | maxillary tooth | 278 | 183 |
| total | 362 | 145 | 193 | 233 | total | 287 | 183 |
| bone/tooth | 0,51 | 0,23 | 0,23 | 0,27 | bone/tooth | 0,03 | 0,00 |
| mandible | 27 | 18 | 19 | 35 | mandible | 12 | 2 |
| mandibular tooth | 308 | 144 | 185 | 144 | mandibular tooth | 222 | 81 |
| total | 335 | 162 | 204 | 179 | total | 234 | 83 |
| bone/tooth | 0.09 | 0.12 | 0.10 | 0.24 | bone/tooth | 0.05 | 0.02 |

**Table 2.**
NISP values of crania and mandibles by teeth and bone remains.

lary teeth were present. These results signify that the faunal remains went through taphonomic processes such as attrition and thus, bony remains are underrepresented at all sites and, depending on the grade of fragmentation, less identifiable.

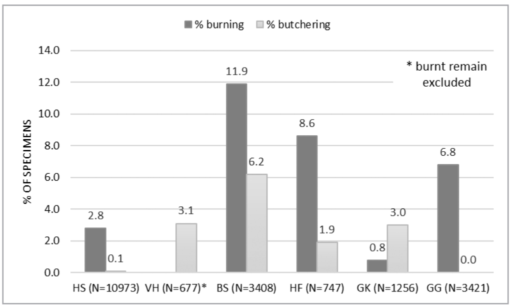


**Fig. 2.**
Percentage of specimens with anthropogenic modification per site (HS: Hohlenstein-Stadel, VH: Vogelherd, BS: Bockstein, GK: Geißenklösterle, HF: Hohle Fels, GG: Große Grotte).

## Anthropogenic modification

There is considerable variation in the frequency of anthropogenic modifications (Fig. 2). Processing marks and fractures provide a direct link between hunters and prey. Within all of the assemblages from the Swabian Jura, the frequency of cutmarks is highest at Bockstein (6.2%). Furthermore, the frequency of cutmarks and impact fractures ranges between 1.9 and 3.1% at Vogelherd, Hohle Fels and Geißenklösterle. Hohlenstein-Stadel and Große Grotte have yielded the smallest number of remains with tool marks or fracture patterns indicative of processing activities, ranging from 0 to 0.1%.

Recovery bias against small non-diagnostic remains at Vogelherd has likely led to the absence of burned material with little documentation (Riek 1934). Charred and calcined remains occur most frequently at Bockstein (11.9%) and Hohle Fels (8.6%), while they are encountered least frequently at Geißenklösterle (0.8%) and Hohlenstein-Stadel (2.8%). The low abundance of burned bones at Geißenklösterle is not explained by differences in excavation methods, but rather may indicate an infrequent use of fire in the excavated area, which was preserved after the roof collapse.

## Carnivore modification

We evaluated the degree to which carnivores affected the accumulation and modification of fauna (Table 3). The encounter rate of carnivore damage at Bockstein is presented as a range due to the uncertainty in the exact abundance of animal remains, which were affected by chemical rounding.

| | Lone Valley | | | Ach Valley | | |
|---|---|---|---|---|---|---|
| | Hohlenstein-Stadel | Vogelherd | Bockstein | Hohle Fels | Geißen-klösterle | Grosse Grotte |
| %total carnivore modification (including non indentifiable remains) | 8.7 | 21.6 | 5.19-11.1 | 6.6 | 7.9 | 10.1 |
| %herbivore with carnivore damage | 11.4 | 14.5 | 10.1 | 40.9 | 42.2 | 28.2 |
| %bear with carnivore damage | 3.8 | 14.8 | 3.6 | 7.5 | 7.9 | 8.9 |
| %carnivore with carnivore damage | 16.8 | 10.0 | 7.0 | 28.6 | 12.9 | 16.7 |
| commonly damaged animal groups | carnivore | herbivore/ bear | herbivore | herbivore | herbivore | herbivore |

**Table 3.**
% of carnivore damage for all remains,
% of damage on herbivores, bears and carnivores.

This type of modification can either result from the depositional environment or from the gastric acid in a predator's stomach (Barbieri 2017). This taphonomic modification was not differentiated at Bockstein (Krönneck 2012). Therefore, the most realistic proportion of remains affected by gnawing modification ranges between 5.2 and 11.1%. If we take the mean of 8.1%, it is comparable to Hohle Fels, Hohlenstein-Stadel, and Geißenklösterle. Based on the counts of all specimens with modification, damage is most frequently encountered at Vogelherd during the MP. Over 20% of remains bear carnivore modification, which is remarkable for an assemblage that was mainly accumulated by humans. In one MP layer (Level VII), over 79% of remains show gnawing marks made by middle- to large-sized predators (Niven 2006).

Herbivore, carnivore, and ursid remains were differentially affected (Table 3). During the MP, ungulates and proboscideans reveal the highest degrees of gnawing damage at Geißenklösterle, Hohle Fels and, to a lesser degree, at Große Grotte, all located in the Ach Valley. Twenty-eight to 42% of the faunal remains were affected, indicating a greater degree of transportation and modification of hunted prey by non-human predators. The rate of carnivore modification on herbivores, ranging between 10.1 and 14.5%, is comparable at Hohlenstein-Stadel, Bockstein, and Vogelherd. The Vogelherd assemblage is characterized by a greater number of bones bearing carnivore damages in the MP, but the fauna from caves in the Ach Valley (Hohle Fels, Geißenklösterle, and Große Grotte) are comprised of assemblages with greater carnivore damage on herbivores compared to sites in the Lone Valley (Bockstein, Hohlenstein-Stadel, and Vogelherd).

Given these data, the Bockstein fauna represent an assemblage with the smallest degree of impact by non-human predators, whereas the fauna of Hohlenstein-Stadel and Vogelherd exhibit slightly higher carnivore damage compared to Bockstein, but low in comparison to the caves of the Ach Valley. The degree and kinds of taphonomic damage as well as the taxonomic representation of carnivores (see below) indicate that the cursorial predators, namely hyenas, accumulated and modified faunal remains through hunting or scavenging.

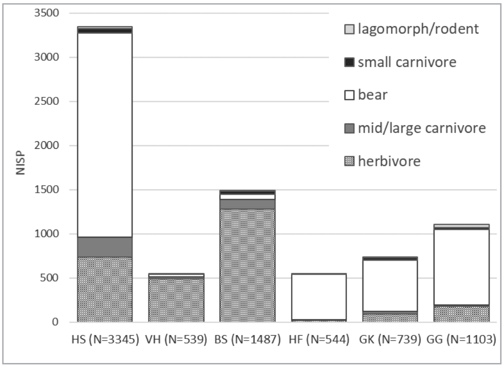


**Fig. 3.**
Animal groups by NISP per site (HS: Hohlenstein-Stadel, VH: Vogelherd, BS: Bockstein, GK: Geißenklösterle, HF: Hohle Fels, GG: Große Grotte).

## Animal groups

The relative abundance of animals reiterates some of the underlying patterns gleaned from the taphonomic data. There are two types of sites with different dominant animal groups (Fig. 3). The first set is characterized by a high proportion of cave bears and includes Hohlenstein-Stadel, Große Grotte, Geißenklösterle, and Hohle Fels. The NISP proportion of ursids is highest at Hohle Fels, making up 94% of the identified fauna. In the other three deposits, bear frequencies range between 69 and 78%. Herbivores comprise 4-22% of these assemblages. Cave bears are prominent in the faunal record throughout the MP with the exception of two sites, Vogelherd and Bockstein, where occupation by Neanderthals overlapped little with that of cave bears.

The second set of sites, Vogelherd and Bockstein, is characterized by relatively high proportions of herbivores, comprising 90% and 86% of the assemblages, respectively. The relative proportion of cave bears at Vogelherd and Bockstein is comparable, with 5% at Vogelherd and 3.8% at Bockstein. Besides the common animals, lagomorphs and rodents are scarce, which partially reflects the use of different recovery methods. Lastly, carnivore abundance varied from site to site. Bockstein is characterized by a higher proportion of medium and large carnivores (7.7%) and small carnivores (2.2%) compared to the proportional abundance in Hohlenstein-Stadel.

### Herbivores

Of all the sites, Bockstein has produced the largest assemblage of herbivore remains (Fig. 4). Here, more than half of the herbivores are horses (65.9%). They are followed in importance by reindeer (11%) and aurochs/bison (8.1%). The age profile of the equids based on teeth use wear shows that prime adults were primarily hunted (Fig. 5). Red deer are rare compared to reindeer. Furthermore, mammoth and woolly rhinoceros are less common relative to the other medium- to large-sized ungulates, as megafauna represent 5.1% and 7.3% of the assemblage.

In comparing the representation of herbivore species from other sites, we have excluded Hohle Fels from our discussion due to the small size of the assemblage. Horses are abundant at Hohlenstein-Stadel, Vogelherd, and Geißenklösterle, while ibex is more common at Große Grotte. At Vogelherd and Hohlenstein-Stadel, mammoth and woolly rhinoceros are the second most abundant taxa, respectively. Reindeer, aurochs/bison, and red deer occur at a lower frequency. Megafauna contributed to the Neanderthal diet to some degree, which is demonstrated in Vogelherd based on the age profiles of the rhinoceros (Niven 2006) and possibly Hohlenstein-Stadel, but it is not documented across all MP assemblages.

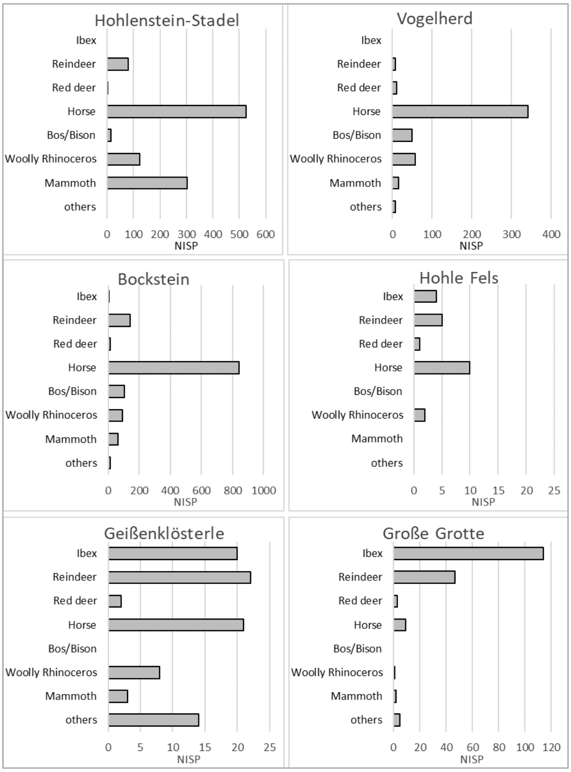


**Fig. 4. left**
NISP of herbivores by species per site (HS: Hohlenstein-Stadel, VH: Vogelherd, BS: Bockstein, GK: Geißenklösterle, HF: Hohle Fels, GG: Große Grotte).

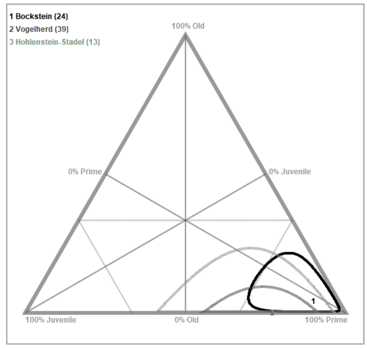


**Fig. 5. above**
Triangular plot indicating the age group abundance of horses from Bockstein, Vogelherd and Hohlenstein-Stadel (produced using Triangle Program from Weaver et al. 2011).

## Carnivores

The most common carnivores at Bockstein and Hohlenstein-Stadel are hyenas, as well as foxes at Geißenklösterle and Große Grotte, followed by wolves (Fig. 6). Many of the instances of gnawing and corrosive damage can be attributed to hyenas, although there is a strong but non-significant correlation between the number of predatory species and the frequency of carnivore modification (Pearson R=0.71, p-value=0.09). In addition, analysts have identified coprolites from medium to large carnivores in zooarchaeological and micromorphological studies at Hohle Fels, Geißenklösterle, and Hohlenstein-Stadel. Recent excavations of Hohlenstein-Stadel have yielded deciduous hyena teeth, thus supporting the hypothesis that the cave was used as a den by carnivores during the MP (Kitagawa 2014). The use of Bockstein Cave as a carnivore den is not clear given that no juveniles have been recovered on site (Krönneck 2012).

## Organic tools

According to previous work, formal organic tools were recovered at Vogelherd and Große Grotte (Münzel and Conard 2004b; Wagner 1983;

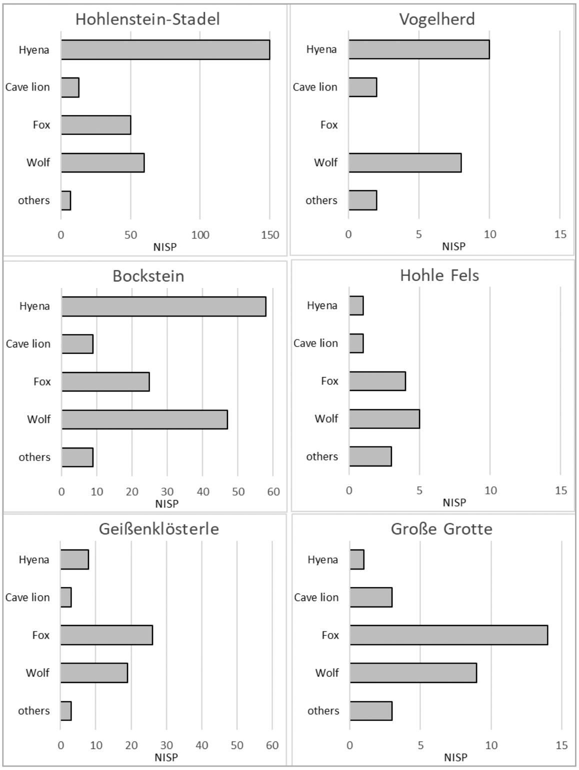


**Fig. 6.**
NISP of carnivores by species per site (HS: Hohlenstein-Stadel, VH: Vogelherd, BS: Bockstein, GK: Geißenklösterle, HF: Hohle Fels, GG: Große Grotte).

Weinstock 1999). MP Horizon II at Große Grotte has yielded a worked mammoth rib fragment, which was interpreted as a burnisher (Weinstock 1999), and an antler point (Wagner 1983). No dates are available for the organic tools or the layer, prompting us to be cautious regarding its assignment to the MP. Vogelherd has produced two organic artifacts, which were previously attributed to the MP (Horizon VI). The first is a mammoth rib with a pointed end (Fig. 7). However, another point from the same horizon has been directly dated to the Aurignacian 31,310 +240/-230 uncal years BP (Bolus and Conard 2006). Therefore, we cannot exclude the possibility that the other artifacts may be associated with the Aurignacian. Direct dating of the organic artifacts will help clarify whether formal organic tools existed in the Swabian Jura during the MP.

**Fig. 7.**
Modified mammoth rib from Layer VI, Vogelherd (photo modified from H. Jensen).

| Site (cultural layer) | N of specimens | Species/body class size | Skeletal element |
|---|---|---|---|
| **Hohlenstein Stadel (MP U)** | | | |
| | 3 | Horse/bear/large bovid size | Long bone |
| **Vogelherd (AH VI-VIII)** | | | |
| | 2 | *Equus ferus* | Radius |
| | 2 | Horse/bear size | Long bone |
| | 1 | Ungulate | Metapodium |
| **Bocksteinschmiede (AH III-IV)** | | | |
| | 1 | *Equus ferus* | Femur |
| | 1 | *Equus ferus* | Tibia |
| | 1 | Horse/bear size | Long bone |
| | 1 | Mammoth/rhinoceros size | Rib |
| **Sirgenstein (AH VII-VII)** | | | |
| | 3 | *Equus ferus* | Radius |
| | 2 | *Megaloceros giganteus* | Tibia |
| | 1 | Ungulate | Humerus |
| | 1 | Ungulate | Tibia |
| **Schafstall I** | | | |
| | 13 | Large bovid/giant deer size | Long bone |
| | 1 | Horse/bear size | Rib |
| | 1 | Mammal | Unknown |

**Table 4.**
Number of retouchers found with respective species/body class size and skeletal element.

Retouchers are the most common organic tool during the MP of the Swabian Jura and have been found at Hohlenstein-Stadel, Bockstein and Vogelherd in the Lone Valley, Sirgenstein in the Ach Valley, and Schafstall I in the Lauchert Valley (Table 4, Fig. 8) (Toniato et al. 2018) and Heidenschmiede in the Brenz Valley (see Münzel and Çep, this volume for details). They are characterized by marks such as linear scores with a V-shaped profile often associated with impact pits and striations (Mozota Holgueras 2013; Vincent 1993). Following Andrefsky (1994), these are expedient tools in that they are made of an abundant and easily accessible raw material, require minimal investment of time and effort in production, have unstandardized forms, and are generally discarded after use. The retouchers from the Swabian Jura fulfill all of these criteria. They are made of bone fragments from medium to large mammals, predominantly ungulates, and display irregular forms and variable dimensions.

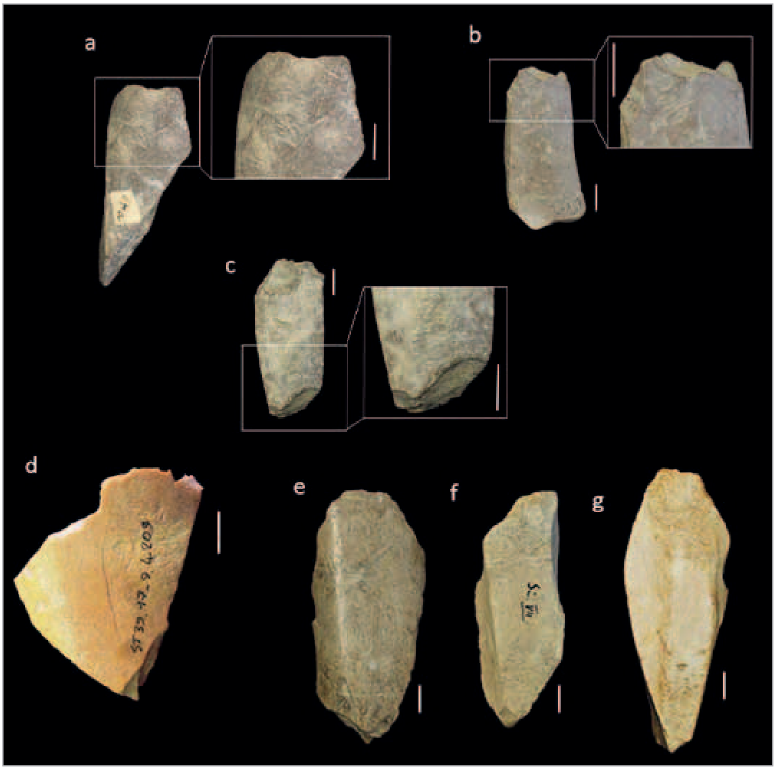


**Fig. 8.**
a-c) Schafstall: retouchers on large bovid/giant deer size bone shafts; d) Hohlenstein-Stadel: retoucher on large ungulate/bear size bone shaft; e-g) Sirgenstein: retoucher on horse radius (e) and on giant deer tibia (f,g). Scale is 1 cm.

## DISCUSSION

First, the greater abundance of teeth for common animals (ursids and horses) indicates that attrition shaped the nature of the faunal assemblages in the Swabian Jura. In particular, the comparison of bone and tooth remains from ursids are evidence of *in situ* destruction of animal remains that disproportionally affected the bony remains. Thus, the natural loss of bony remains does impact our overall understanding of the faunal assemblages.

This being said, our taphonomic study, combined with species representation, demonstrates that the faunal assemblages resulted from hominin occupations in addition to the activities of carnivores and cave bears. The abundance of cave bears reveals that they used the caves for winter hibernation. Furthermore, the frequency of carnivore damage on herbivore remains provides a direct link between predators and faunal remains, reflecting their role in the destruction and/or obscuring of patterns in the subsistence practices of Neanderthals. The intersection of carnivores and Neanderthals resulted in significant mixing of the anthropogenic and carnivore signals.

In reconstructing the intensity of carnivore impact on the faunal assemblages, several lines of evidence have proved useful including: iden-

| Site | carnivore | butchering | burning |
|---|---|---|---|
| **Bockstein** | low | high | high |
| **Hohlenstein-Stadel** | medium | low | low |
| **Vogelherd** | high | medium | - |
| **Hohle Fels** | medium-high | medium | medium |
| **Geißenklösterle** | high | medium | low |
| **Große Grotte** | medium | low | medium |

**Table 5.**
Summary for the impact of carnivores and anthropogenic input (burning/butchering).

tification of carnivore remains, taphonomic study of gnawing modification, presence of coprolites, and abundance of carnivore juveniles. In addition, micromorphological studies have arrived at a similar conclusion (Barbieri 2017; Miller 2015). This provides an interesting insight into the paleoecological system in which Neanderthals and other predators coexisted (Niven 2006).

The data (summarized in Table 5) indicate low input from carnivores and relatively high input from hominins at Bockstein, making this faunal assemblage one of the most reliable sources for reconstructing the subsistence behavior of Neanderthals (Çep and Krönneck 2015). This site reveals that horses, followed by reindeer, were the most common prey in the MP. Hohlenstein-Stadel has yielded an assemblage with relatively low input from Neanderthals and a medium degree of carnivore modification. No single explanation accounts for the high percentage of carnivore damage on carnivore remains at Hohlenstein-Stadel, but it suggests complex interactions among predatory species either resulting from intraspecific killing or scavenging. The pattern is in contrast to Hohle Fels, where the carnivore modification is medium to high, while the anthropogenic modifications are more abundant compared to most assemblages. The input from carnivores and Neanderthals at Große Grotte is indicative of mixed visits and occupations by both. The rate of predator damage appears to be higher at Vogelherd and Geißenklösterle, where it is intermixed with evidence of Neanderthal hunting.

The impact of carnivores makes the interpretation of the species abundance tentative, but horse appears to be the consistent species present in the Swabian Jura, reflecting the steppe-tundra landscape of the Late Pleistocene. Furthermore, no clear evidence for hunting and regular exploitation of megafauna has been recorded from the Swabian Jura with the exception of the site at Vogelherd. Thus, we still need to test in the future whether the hunting of woolly rhinoceros and/or mammoth was part of common subsistence practice in the region. The low abundance of megafauna at some sites may reflect the limited availability of large herbivores in the surrounding ecosystem or the high investment associated with hunting and transporting of carcasses. Ongoing excavation in Hohle Fels has the potential to contribute to this ongoing debate.

## THE RHINE REGION AND SWABIAN JURA

Neanderthals were mobile hunter-gatherers and their activity territories were likely not limited to the Swabian Jura. This is in part supported by the prevalence of MP stone tools such as *Keilmesser* (Bosinski 2008; Çep 2014; Frick and Floss 2017; Frick et al. 2017; Jöris 2006; Ruebens 2013). Due to the geographic proximity of the Rhine and Swabian Jura regions, respective MP populations were probably in contact and migrated between the areas. In what follows, we attempt to compare the Rhine region, which is highly interesting due to its abundance of open-air sites, and the Swabian Jura; comparisons between the two regions for the period from MIS 5e through to the end of the MP are particularly relevant.

The fauna from the Rhine region and the Swabian Jura share some broad similarities while also presenting some key differences. Cave bears comprise a large proportion of the Swabian faunal assemblage at several caves (Hohle Fels, Geißenklösterle, Große Grotte, and Hohlenstein-Stadel). This differs from open-air sites of the Rhine region where ungulates and megafauna are the predominant common prey (Conard and Prindiville 2000; Gaudzinski and Roebroeks 2000; Koehler et al. 2016) (Table 6). This difference is closely related to whether or not the sites are open-air or in closed contexts. The fauna from the Balver Cave, which is one of the few MP caves in the Rhine region, are similar to those of the Swabian caves, thus further supporting this observation (Kindler 2012).

There are additional differences in the spectrum of hunted prey. On the one hand, horses prevailed in the Swabian Jura (inarguably at Bockstein and to differing degrees at other sites) while the relative frequency of horse varies in the faunal assemblages of the Rhine region. Aurochs/bison and cervids are more common at Plaidter Hummerich (Street 2002), in addition to certain strata of Tönchesberg (Layer 2C and 2D) (Conard and Prindiville 2000) and Mutzig II (Layer 5, 7C1 and 2) (Koehler et al. 2016; Patou-Mathis 1997). At Wallertheim, the abundance of horse inversely correlates with that of bison; in Layers A, B, C and D, bison dominates while in Layers E and F, horse dominates. Sites with multi-layered occupations with strata exhibit temporal fluxes in the dominant species. At Mutzig II where occupation spans substages of MIS 5, reindeer is the most abundant fauna in all layers except 7A, in which mammoth predominated. In addition, Salzgitter-Lebenstedt represents one of the largest MP faunal assemblages, which is dominated by reindeer (Gaudzinski 2000). This species representation differs from Plaidter Hummerich where red deer comprises the majority of the assemblage.

The carnivore representation is different from that of the Swabian Jura. Many sites, including Plaidter Hummerich and Tönchesberg, have a relatively low abundance of medium- to large-sized carnivores as hyenas are infrequent. The most common carnivore at Wallertheim D is cave lion, but this is likely represented by one individual only (Conard and Prindiville 2000). Besides larger carnivores, foxes are also sporadically present. The data on carnivore modification are not available for all sites,

| Site | Plaidter Hummerich | Plaidter Hummerich | Tönchesberg | Tönchesberg | Tönchesberg | Mutzig I | Mutzig I | Mutzig I |
|---|---|---|---|---|---|---|---|---|
| Layer | C | D1 | 1B | 2B | 2C | 5 | 7A | 7C 1/2 |
| MIS (sub)stages/ date | 5d | 5b | 4-3 | | | 5d-c/90 ka | | |
| common species | Aurochs/ Bison | Aurochs/ Bison and Horse | Horse | Aurochs/ Bison | Red deer | Reindeer | Mammoth | Reindeer |
| reference | Street 2002 | Street 2002 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Koehler et al. 2016 | Koehler et al. 2016 | Koehler et al. 2016 |
| **Site** | **Wallertheim** | **Wallertheim** | **Wallertheim** | **Wallertheim** | **Wallertheim** | **Wallertheim** | **Balver Cave** | **Salzgitter-Lebenstedt** |
| Layer | A | B | C | D | E | F | II-IV | |
| MIS (sub)stages/ date | 5e | | | 5c | 5c | | 5-3 | 5-3 |
| common species | Aurochs/ Bison | Aurochs/ Bison | Aurochs/ Bison and Horse | Horse | Aurochs/ Bison and Horse | Horse | Cave bear | Reindeer |
| reference | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Conard and Prindiville 2000 | Kindler 2012 | Gaudzinski 2000 |

**Table 6.**
Summary of Rhine sites and common fauna.

but given the low density of carnivores in the Rhine open-air sites, it is likely that non-human predators had little impact on the fauna, and this marks a striking contrast with most sites in the Swabian Jura. This pattern is also explained by the physical nature of the sites. Caves and rockshelters display a greater overlap of carnivore and human activities than open-air occupations. This suggests that the differences in the faunal remains are tied to the physical setting of the Neanderthal occupations.

As noted before, the faunal assemblage from the Balver Cave resembles that of the Swabian Jura (Kindler 2012). Cave bears comprise more than 76% and other common animals include mammoths and horses. The main difference between the Balver Cave and Swabian sites is the occurrence of cave lions in the former. The rate of anthropogenic modification is 7.7% (13.2% on herbivores only) while carnivore modifications on herbivores are low (4.1%) (Kindler 2012). This may be attributed to the rare presence of hyenas and wolves, which leave heavier impacts on their prey compared to cave lions.

The zooarchaeological record from the Swabian Jura and the Rhine region is marked by differences despite sharing a similar environmental setting. Inter-site variability among settlements in the Rhine region is also significant, partially reflecting a diachronic fluctuation in the availability, abundance, and access to prey for Neanderthals. Overall, the pattern of animal species recovered from open-air sites shows that prey game, such as aurochs/bison and red deer, were also important for the MP subsistence in addition to horse. Mammoth hunting is documented in Layer 7A at Mutzig (Koehler et al. 2016) but this is a unique pattern among other open-air sites.

The organic tools present in the Rhine region are broadly similar to those found in the Swabian Jura, and the industry is mostly characterized by the production of retouchers and formal tools made from megafauna. Analysts have documented retouchers at Mutzig (Layer 5) (Sévêque and Auguste 2018), Salzgitter-Lebenstedt (Staesche 2017), and the Balver Cave (Kindler 2012). The latter cave appears to be rich in retouchers, many of which are manufactured from long bone fragments of bear/large ungulates. Of the identifiable remains, horses and cave bears are the common species exploited by Neanderthals to manufacture expedient tools, though hominins also occasionally used mammoth and/or rhinoceros. The taxonomic representation of bone tools mirrors the larger faunal assemblages, indicating that Neanderthals were not selective in the species they used for bone tools.

Salzgitter-Lebenstedt has also produced a corpus of organic artifacts besides retouchers (Gaudzinski 1999). The artifact assemblage consists of modified mammoth ribs and one bone fragment of megafauna. The Balver Cave also yielded one worked bone manufactured from a mammoth rib; the flat surface of the rib has been worked through scraping of the surface and finds parallels in modified ribs from Salzgitter-Lebenstedt (Kindler 2012). These mammoth ribs are also similar to the worked mammoth ribs from Vogelherd and Grosse Grotte, suggesting a similar technological repertoire for organic tools in both regions. We argue that Neanderthals opportunistically used mammoths as a source for organic artifacts, which provides an additional consideration for the debate on the exploitation of megafauna.

In addition, the abundance of red deer correlates well with a high concentration of shed antlers at Tönchesberg (Layer 2B) and Plaidter Hummerich (Layer D1). Many shed antlers are recovered with the base intact, but analysis thus far shows no clear patterns in breakage patterns and there is no clear use wear at Tönchesberg (Conard 1992). Nonetheless, the antlers are clearly associated with Neanderthals as they served as a possible raw material for the production of expedient tools. The intentional gathering and transport of antlers, which are not related to subsistence activities driven by nutritional gains, need to be investigated for general taphonomic analyses and possible use wear.

## CONCLUSION

In order to understand the subsistence strategies of Neanderthals, we must first determine the extent to which non-human predators were involved in the accumulation of faunal remains. Some MP deposits show greater impacts of hominin behavior than others, Bockstein being the prominent example. The preferred prey of Neanderthals in the Swabian Jura was prime aged adult horses. Other prey animals such as reindeer, aurochs/bison, woolly rhinoceros, and mammoth were targeted at lower rates, and it is still unclear whether megafauna were regularly hunted or not. The dominance of horse in other assemblages, such as at Hohlenstein-

Stadel, reflects the natural abundance of equids during the Pleistocene, some of which were targeted by non-human predators. It is likely that many of the cave deposits in the Swabian Jura represent a mixture of carnivore, cave bear, and hominin activity.

The MP of the Swabian Jura has yielded evidence for MP osseous artifacts, although they are few in number. On the one hand, retouchers are the most frequent tool type encountered. They are unelaborate expedient tools, mostly made from long bone fragments of medium to large mammals, and they show less variability in skeletal element choice than those attributed to the Aurignacian (Toniato et al. 2018). On the other hand, the evidence for formal organic tools is scarce and limited to few single finds; these tools display the use of a similar selection of raw materials.

Neanderthal occupation in the Rhine region and on the Swabian Jura over the last interglacial until the arrival of modern humans was by no means homogeneous or static. The Swabian faunal signature differs considerably from that of the Rhine region, though this is most likely a product of the predominant site type. Specifically, the intersection of carnivores, cave bears, and hominins is more common in the caves, suggesting that the spatial overlap of predator activities is a phenomenon frequent in closed contexts, but it is not a prevalent form of interaction between Neanderthals and other potential competitors in the open landscape. At the same time, we can trace the production of certain tool types at multiple sites and observe technological behaviors of Neanderthals in both regions. As we see more faunal studies from these regions in the future, the zooarchaeological record from the two settlement areas of Central Europe in the MP will continue to provide rich grounds to discuss common characteristics and variability of Neanderthal behavior and adaptations.

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