Human Paleoecology during the Magdalenian in the Swabian Jura of Southwestern Germany

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Table of Contents

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Abbreviations

LGM – Last Glacial Maximum

cal yr BP – calibrated years Before Present

uncal yr BP – uncalibrated years Before Present

NGRIP – North Greenland Ice Core Project

GI – Greenland Interstadial

GS – Greenland Stadial

AH – Archaeological Horizon

GH – Geological Horizon

NISP – Number of Identified Specimens

%NISP – percent Number of Identified Specimens

MNI – Minimum Number of Individuals

MAU – Minimum Animal Units

%MAU – percent Minimum Animal Units

MNE – Minimum Number of Elements

BA – Bioclimatic Analysis

CRI – Climate Restriction Index

BC – Bioclimatic Component

Summary

The Swabian Jura is well-known as an important region for the study of Paleolithic archaeology. The Magdalenian, though, has received little attention in this region compared to other periods of the Paleolithic. Open questions, therefore, remain regarding regional subsistence strategies, settlement patterns, and environmental conditions during this time. There have been, for example, almost no modern, quantitative studies of environmental conditions during the Magdalenian that are specific to the Swabian Jura. In this dissertation, I use remains from Langmahdhalde, a rock shelter in the Lone Valley that is one of the first archaeological sites in the Swabian Jura with intact Magdalenian remains to have been discovered in decades.

I use the faunal remains from the site to explore trends in human subsistence behavior, use of the rock shelter, local environmental conditions, and the resettlement of the Swabian Jura during the Late Glacial. To do so, I take four methodological approaches. First, I use traditional zooarchaeological analysis to understand human behavior. Second, I conduct stable isotope analyses on bone collagen of horse (*Equus ferus*) and reindeer (*Rangifer tarandus*) from the site. Third, I apply a model for reconstructing past environments, called the Bioclimatic Analysis (Hernández Fernández, 2001a, 2001b; Hernández Fernández and Peláez-Campomanes, 2005, 2003), to the microfaunal assemblage. Finally, I do a taphonomic analysis of the microfaunal assemblage.

My results regarding human behavior during the Magdalenian in the Swabian Jura are consistent with current understandings of the Central European Magdalenian. The primary taxa at the site are hare (genus *Lepus*), small carnivores, reindeer, horse, and medium birds. There is evidence of butchery, marrow extraction, antler working, skinning, and needle making at the site. The results of the stable isotope analyses show that Late Glacial horses were more adaptable to local environments than reindeer and that their $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values are better indicators of local environments than those of reindeer. Further, I document evidence of the loss of the preferred habitat of reindeer in the region.

The Bioclimatic Analysis demonstrates that Late Glacial environments surrounding Langmahdhalde were generally open tundra but with more precipitation, warmer and shorter winters, and longer vegetative activity periods than modern tundra environments. The models also suggest that the landscape was mosaic in nature and likely even had stands of trees, indicating that the region was more heterogeneous than previously thought. This heterogeneity probably means that there was a higher diversity of plant and animal species on the landscape than in modern tundra regions. Finally, my taphonomic analysis of the microfauna indicates that in the majority of the horizons at Langmahdhalde, several predators, mostly species of owl, deposited the microfaunal remains. These predators include both opportunistic feeders and specialists who prefer specific prey. The microfaunal assemblage can, therefore, most accurately provide reconstructions of paleoenvironments when the presence or absence of taxa, not taxonomic abundance, is used in analyses. As the Bioclimatic Analysis uses presence/absence data, this suggests that the paleoenvironmental interpretations from the site are robust. Further, the hunting ranges of the predators responsible for the assemblage suggest that my paleoenvironmental interpretations apply to the Lone Valley and its surroundings.

I end by arguing that the Swabian Jura (at least the Lone Valley) offered Magdalenian hunter-gatherers a greater diversity of resources than other regions, even those to the west, during this time. It is possible that this is one of the reasons that the resettlement of the Swabian Jura during the Late Glacial was successful.

Zusammenfassung

Die schwäbische Alb ist seit langem als Schlüsselregion zur Erforschung der älteren Steinzeit bekannt. Im Vergleich zu anderen Abschnitten des Paläolithikums wurde das Magdalénien dieser Region allerdings bislang weniger intensiv untersucht. Fragen nach regionalen Subsistenzstrategien, Landnutzungsmustern oder Umweltbedingungen während des Magdalénien blieben daher lange Zeit offen. Moderne, quantitative Untersuchungen zu den Umweltbedingungen dieser Zeit in der Schwäbischen Alb liegen zudem kaum vor.

Die vorliegende Arbeit beruht auf Analysen an Material aus der Langmahdhalde, einem Abri im Lonetal, das eine der wenigen Fundstellen darstellt, in denen in den vergangenen Jahrzehnten ungestörte Magdalenienschichten entdeckt werden konnten. Anhand der Faunenreste dieser Fundstelle lassen sich Rückschlüsse auf das Subsistenzverhalten, die Nutzung des Abris selbst, lokale Umweltbedingungen, sowie die Wiederbesiedlung der Schwäbischen Alb während des Spätglazials ziehen.

Zu diesem Zweck wurden verschiedene methodologische Ansätze gewählt. Zum einen die traditionelle archäozoologische Analyse, um Hinweise auf das Jagdverhalten der Menschen zu gewinnen. Weiterhin wurden Untersuchungen an stabilen Isotopen an Collagen von Pferde- bzw. Rentierknochen aus der Langmahdhalde durchgeführt. Zudem wurde das Modell „ Bioclimatic Analysis“ zur Rekonstruktion vergangener Umweltbedingungen auf die Ergebnisse der Mikrofaunenanalyse angewandt. Abgerundet wurden die Untersuchungen durch eine taphonomische Untersuchung der Mikrofaunenreste.

Die Ergebnisse der hier vorgestellten Methoden zeigen, dass das Verhalten der Menschen in der Langmahdhalde sich gut in das Bild einfügt, dass den derzeitigen Forschungsstand zum Mitteleuropäischen Magdalénien widerspiegelt. Die bevorzugte Jagdbeute während des Magdalénien besteht aus Hase (genus *Lepus*), kleineren Carnivoren, Rentier, Pferd und mittelgroßen Vögeln. Zudem konnte die Zerteilung der Karkassen, Gewinnung von Knochenmark, Verarbeitung von Geweih, die Häutung der Tiere, sowie die Herstellung von Knochennadeln vor Ort belegt werden. Die Analyse der stabilen Isotope verweist auf eine höhere Anpassungsfähigkeit von Wildpferden auf lokale Umweltbedingungen hin als bei Rentieren. Die $\delta^{13}C_{coll}$ und $\delta^{15}N_{coll}$ Werte der Wildpferde eignen sich daher besser als Indikatoren für lokale Umweltbedingungen als die der Rentiere. Zudem konnte festgestellt

werden, dass sich die regionalen Umweltfaktoren entgegen des von Rentieren bevorzugten Habitats verändert haben.

Die bioklimatische Analyse belegt eine eher offene Tundrenlandschaft in der Umgebung der Langmahdhalde zur Zeit des Spätglazials, jedoch unter dem Einfluss häufigerer Niederschläge, sowie kürzere und wärmere Winter und längere Wuchsperioden der Vegetation als es aus heutigen Tundrengebieten bekannt ist. Das Modell suggeriert jedoch auch ein mosaikartiges Muster in der Vegetation. Stellenweise ist auch von Bewaldung auszugehen, was auf eine heterogenere Landschaft schließen lässt, als bislang angenommen. Diese Heterogenität könnte auf eine höhere Diversität im Artenspektrum von Flora und Fauna hinweisen, als sie uns aus modernen Tundrenlandschaften bekannt ist.

Die taphonomische Analyse der Mikrofaunenreste aus der Langmahdhalde lässt auf eine Einbringung überwiegende durch verschiedene Raubtiere bzw. -vögel, allen voran die Eule, schließen. Diese Raubtiere bzw. -vögel umfassen sowohl opportunistische als auch auf bestimmte Beutetiere spezialisierte Jäger. Die Mikrofauna aus der Langmahdhalde kann daher hauptsächlich dann zur stichhaltigen Rekonstruktion der Paläoumwelt herangezogen werden, wenn die Präsenz bzw. Absenz bestimmter Spezies als Parameter zur Umweltrekonstruktion dient und nicht etwa die Häufigkeit, mit der bestimmte Taxa vorkommen. Da die bioklimatische Analyse mit der Präsenz bzw. Absenz arbeitet, können die dadurch gewonnen Daten zur Umweltrekonstruktion als verlässlich angesehen werden. Weiterhin lassen die Jagdgebiete der Raubtiere bzw. -vögel, die in der Langmahdhalde nachgewiesen werden konnten, den Schluss zu, dass die hier gewonnenen Ergebnisse ebenso für das Lonetal und die angrenzenden Gebiete Gültigkeit besitzen.

Zusammenfassend kann davon ausgegangen werden, dass die Jäger und Sammler des Magdalenien im Schwäbische Jura (bzw. im Lonetal) tendenziell eine größere Vielfalt an verfügbaren Ressourcen ausschöpfen konnten, als in anderen Regionen, insbesondere auch westlich des Schwäbischen Jura. Dies könnte unter Anderem den Grund für eine erfolgreiche Wiederbesiedlung im Spätglazial darstellen.

List of Publications

Published articles:

Wong, Gillian L., B. M. Starkovich, and N. J. Conard. 2017. Human subsistence and environment during the Magdalenian at Langmahdhalde: evidence from a new rock shelter in the Lone Valley, southwest Germany. *Mitteilungen der Gesellschaft für Urgeschichte* 26: 103-123. (Appendix 1)

Wong, Gillian L., D. G. Drucker, B. M. Starkovich, N. J. Conard. 2020. Latest Pleistocene paleoenvironmental reconstructions from the Swabian Jura, southwestern Germany: evidence from stable isotope analysis and micromammal remains. *Palaeogeography, Palaeoclimatology, Palaeoecology* 540: 109527. https://doi.org/10.1016/j.palaeo.2019.109527 (Appendix 2)

Submitted manuscript:

Wong, Gillian L., B. M. Starkovich, D. G. Drucker, N. J. Conard. New perspectives on human subsistence during the Magdalenian in the Swabian Jura, Germany. Accepted in: *Archaeological and Anthropological Sciences*, special issue "Post-glacial human subsistence and settlement patterns: insights from bones." (Appendix 3)

Personal Contribution

Below is a description of the extent and significance of my personal contribution to all collaborative works in this dissertation, according to § 6,2 of the Doctoral Degree Regulations of the Faculty of Science at the University Tübingen.

I was the primary writer and the first and corresponding author of all manuscripts. I developed the project, implemented the methodology, and conducted the research for all three papers. Britt Starkovich provided editorial input, assisted in writing the manuscripts, including the development of some interpretations, and supervised the studies for all papers. She also provided help with taxonomic identifications and implementation of the macrofaunal methods for the first and third papers and sourced funding for the isotopic analyses of the second paper. Nicholas Conard provided editorial input, assisted in writing the manuscripts, supervised the studies, and is the director of excavations and principal investigator of the Lone Valley project. He also sourced funding for the isotopic analyses of the second paper. For the second and third papers, Dorothée Drucker provided editorial input, assisted in writing the manuscript, advised on stable isotope methods and results, helped develop some of the interpretations, provided further isotopic data, and sourced funding for the isotopic analysis.

Chapter 1: Introduction

The Magdalenian cultural period has been well-studied since its definition in Gabriel de Mortillet's (1869) chronology of the Paleolithic. Despite the large distribution of the Magdalenian across much of continental Europe, distinct regional groups existed during this time (Kretschmer, 2015; Maier, 2015; Straus et al., 2012). Several regions, particularly in southwestern France where the Magdalenian was originally defined, have archaeological sites with well-documented sequences of Magdalenian remains, allowing for an understanding of regional-scale cultural, behavioral, and economic variations in Magdalenian populations. In the Swabian Jura of southwestern Germany, though, an area with a long history of Paleolithic research, the Magdalenian has not been the focus of the majority of the archaeological research. This is partially because the record of the early Upper Paleolithic in the Swabian Jura, especially the Aurignacian, is large, well-preserved, and has provided evidence of some of the earliest art in the world. In contrast, Magdalenian remains from this region are often poorly preserved, affected by severe taphonomic processes, or found in poorly stratified deposits. This has left unanswered questions regarding human behavior during this period in the Swabian Jura that can only be answered by modern data obtained from newly discovered, well-stratified, Magdalenian sites. Further, there exist few local-scale reconstructions of environments during the Late Glacial (~18,000 to 11,600 cal yr BP) in the Swabian Jura that use modern quantitative methods. Our understanding of the ecological context within which Magdalenian peoples lived in this region, therefore, is limited.

This dissertation seeks to address human paleoecology during the Magdalenian in the Swabian Jura using faunal remains from a recently discovered archaeological site, called Langmahdhalde. Langmahdhalde is a rock shelter located in the Lone Valley of the Swabian Jura that has intact, well-stratified Magdalenian horizons with associated lithic artifacts, faunal remains, and combustion features. I analyze the faunal remains from the site using three primary methods. First, I use traditional zooarchaeological analysis to discuss human behavior at the site. Second, I conduct stable isotope analyses of bone collagen from reindeer and horse remains from the site in order to reconstruct past environments and obtain ecological information associated with these species. Finally, I use the microfaunal remains to reconstruct the environment and several climate variables, such as temperature and precipitation. I then bring the results together to address the following research questions:

- What trends in human subsistence during the Magdalenian are visible in the faunal assemblage from Langmahdhalde?
- What information can the faunal assemblage of Langmahdhalde provide about human use of the rock shelter during the Magdalenian?
- What local environmental conditions did Magdalenian hunter-gatherers in the Swabian Jura face?
- What implications do these environmental reconstructions from Langmahdhalde have for the resettlement of the Swabian Jura during the Late Glacial and for hunter-gatherer behavior during this time in general?

1.1 The Magdalenian in Central Europe

The Magdalenian is a cultural period of the Upper Paleolithic in Europe that existed from approximately 20,000 cal yr BP until the advent of the Late Paleolithic at the end of the Late Glacial. The Magdalenian record in Central Europe begins later than that of other parts of Europe because this region was largely uninhabited during the Last Glacial Maximum (LGM; 27,200 to 23,500 cal yr BP; Sanchez Goñi and Harrison, 2010) and it was not until about 16,500 cal yr BP that much of Central Europe was resettled (Kretschmer, 2015). After the recolonization of Central Europe, the Magdalenian covered a large portion of continental Europe, stretching from the Iberian Peninsula to eastern Europe (Wiśniewski et al., 2012). Within this large distribution, distinct regional differences in tool types, settlement patterns, raw material procurement, and artifact assemblages are visible (Maier, 2015; Straus et al., 2012).

Gabriel de Mortillet (1869) named this cultural period the Magdalenian (or *Magdalénien* in French) in his revision of Lartet's (1861) chronology of the Paleolithic. In this work, de Mortillet named Le Madeleine, a rock shelter in the Vézère Valley of southwestern France, the type site for the Magdalenian. In 1912, the chronology of the Paleolithic was again revised by Henry Breuil who, in his work *Les subdivisions du Paléolithique supérieur et leur signification*, divided the Paleolithic into two periods: the Lower and Upper Paleolithic. In this work, he defined six phases of the Upper Paleolithic that have been refined over time and remain in use today. This system includes several phases of the Magdalenian that are defined based on lithic tool technology and organic artifacts, and are set within the context of climatic change. The recolonization of Central Europe is generally associated with phases IV and V of this chronology (Adaileh, 2017; Jochim et al., 1999).

Lartet's (1861) original chronology of the Paleolithic was based on the presence of extinct fauna and one of the periods he defined was "*L'Âge du Renne*," or the Reindeer Age. It is this period that later became de Mortillet's Magdalenian. As this name suggests, reindeer (*Rangifer tarandus*) are common in Magdalenian faunal assemblages and were an important part of human subsistence during this period. However, this does not necessarily mean that Magdalenian peoples were reindeer "specialists." Over the years, it has become clear that reindeer is not the dominate taxon at all Magdalenian sites (e.g. see summaries of Central European Magdalenian faunal representation in Eriksen, 1996, Gaudzinski and Street, 2003, and Maier, 2015) and assuming specialization based on taxonomic abundance in the archaeological record can ignore the complexity of variables affecting human subsistence decisions (e.g. Enloe, 1999; Grayson et al., 2001).

In Central Europe, reindeer and horse are generally the most common animals found in Magdalenian archaeological assemblages, although their relative abundances vary by site (Maier, 2015). Reindeer have high caloric values, especially when it comes to their marrow, which can have up to 13 times more calories than Equid marrow (Binford, 1978; Blumenschine and Madrigal, 1993; Enloe, 2003). This species is not only valuable as a food source but also for its antler, raw material that was used by Paleolithic peoples to make tools. Further, reindeer herds have predictable seasonal movements and life histories that make them easy to exploit, as do horses, although they move at the regional scale while reindeer move over much larger distances. Other species common in Magdalenian assemblages of Central Europe include ibex (*Capra ibex*), ptarmigan (*Lagopus lagopus*), hare (genus *Lepus*), and fox (genus *Vulpes*; Eriksen, 1996; Gaudzinski and Street, 2003; Maier, 2015; Weniger, 1982).

1.2 The Swabian Jura

The Swabian Jura is a karstic system located in southwestern Germany between the Swiss Jura and the Franconian Jura. It is bordered by the upper Neckar valley in the north, the Ries Crater in the east, the Danube River in the South, and the Black Forest in the southwest. It is approximately 220 km in length and ranges in elevation from approximately 450 to 1000 m above sea level. Several caves and rock shelters are present in the large outcrops of limestone of the Swabian Jura, many of which have *in situ* archaeological remains dating to the Paleolithic.

There is a long history of systematic archaeological research in this region that began in the mid-1860s with excavations by Oscar Fraas at the open air site Schussenquelle (Fraas, 1867; Schuler, 1994), near the Federsee, and the cave site Bärenhöhle (part of the Hohlenstein complex) in the Lone Valley. In the early 1900s, Robert Rudolf Schmidt worked on several excavations in the region and published the first detailed summary of the German Paleolithic in the monograph *Die diluviale Vorzeit Deutschlands* (The Diluvial Prehistory of Germany; Schmidt, 1912). This monograph placed the archaeological record from southwestern Germany, including Schmidt's fieldwork in the Swabian Jura, within the context of European prehistory (Bolus and Conard, 2012). After Schmidt, work by Gustav Riek, Robert Wetzel, and Eduard Peters in the Swabian Jura during the 1930s continued to establish the region as important for Paleolithic research. Riek and Wetzel excavated in the Swabian Jura until the 1960s and, beginning in the 1970s, Joachim Hahn began working in the region. Hahn's work in the Swabian Jura, especially his long-term excavations in Geißenklösterle and Hohle Fels caves, set the modern standard for excavation at the University of Tübingen and established the caves of the region as important for understanding the European Upper Paleolithic (Bolus, 2015).

The Lone Valley is a wide, 44 km long, valley located in the northeastern part of the Swabian Jura (Figure 1). The first systematic excavations of the Lone Valley were those conducted by Fraas at Bärenhöhle in 1866. During these excavations, he found cave bear remains in association with Paleolithic artifacts that he had initially overlooked in his earlier studies of the site. Later, in the 1880s, Ludwig Bürger conducted excavations in the valley at Bockstein, a cave with primarily Aurignacian finds. In the first half of the 20th century, between the world wars, Elsbeth Soergel-Reith excavated at Kleine Scheuer in the Hohlenstein complex and wrote one of the first studies of microfaunal remains in the Swabian Jura that reconstructed paleoenvironments during the Pleistocene-Holocene transition (Soergel-Rieth, 2011). Besides Soergel-Reith's work, Riek and Wetzel both conducted field work in the Lone during this time. Riek famously excavated the Aurignacian cave site Vogelherd in 1931, and Wetzel spent the 1930s excavating at the Hohlenstein complex and in Bockstein. It was on the last day of Wetzel's excavations at Hohlenstein-Stadel in 1939 that his team found the worked ivory pieces that would later be refitted and identified as the famous lion man statue. After World War II, Wetzel returned to the Lone Valley and continued his work there until his death in the early 1960s.

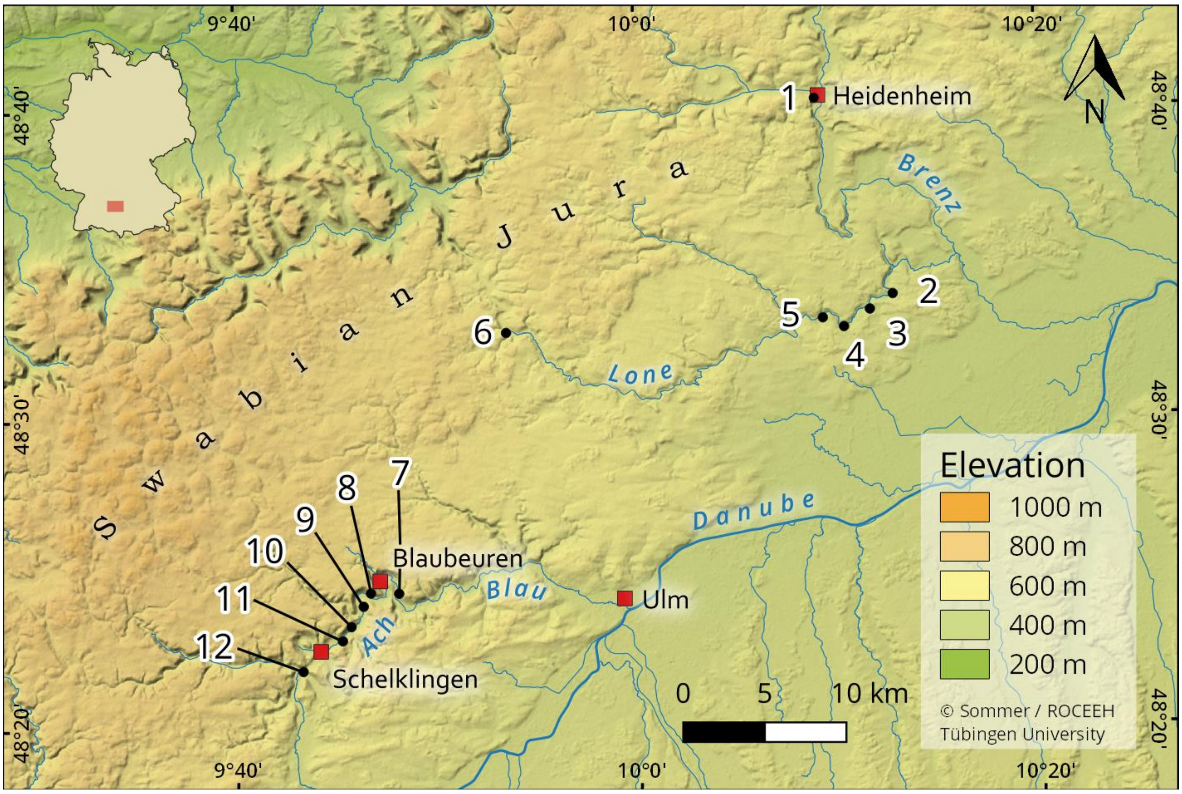

Figure 1. Map of the Swabian Jura showing important archaeological sites dating to the Paleolithic. 1 = Heidenschmiede, 2 = Langmahdhalde, 3 = Vogelherd, 4 = Hohlenstein-Stadel, 5 = Bockstein, 6 = Haldenstein, 7 = Große Grotte, 8 = Brillenhöhle, 9 = Geißenklösterle, 10 = Sirgenstein, 11 = Hohle Fels, 12 = Kogelstein. Map created by C. Sommer with site coordinates collected by M. Malina, G. Toniato, and the ROAD Database. Elevation data are from SRTM V3, hydrological raw data are from LUBW, and the country boundaries are from Natural Earth. https://doi.org/10.5281/zenodo. 3460300.

More recently, Nicholas Conard, of the University of Tübingen, led new excavations at Vogelherd cave. This work, which ran from 2005 to 2012, was a re-excavation of the back dirt from Riek's excavation of the cave and led to numerous new lithic, bone, and artwork finds (Boger et al., 2014; Conard et al., 2013, 2010, 2009, 2008; Conard and Malina, 2007; Conard and Zeidi, 2012, 2011). Additionally, from 2008 to 2013, Claus-Joachim Kind led new excavations at Hohlenstein-Stadel that revealed further fragments of the lion man figurine (Beutelspacher et al., 2011; Beutelspacher and Kind, 2012).

Excavations at Langmahdhalde are part of a recent project in the Lone Valley led by Conard that seeks to increase field work in the valley after the re-excavation of Vogelherd. Within the framework of this project, several caves were identified as having potential for archaeological deposits through survey of the region by Friedrich Seeberger and Herman Glatzle (2012). Prior to work at Langmahdhalde, Fetzershalden Cave, Linden Cave, and Wolftal Cave were excavated as part of this project (Conard et al., 2016, 2015b; Conard and Zeidi, 2014), but none yielded well-stratified archaeological horizons that merited long-term excavations.

Relatively new radiocarbon dates on finds from the cave site Hohle Fels in the Ach Valley indicate that Magdalenian peoples from the west recolonized the Swabian Jura (Maier, 2017, 2015; Taller et al., 2014) by 16,300 cal yr BP (Taller et al., 2014), placing the recolonization of this region within the late Pleniglacial, or GS-2 on the NGRIP record (see Figure 2; Litt et al., 2001; Lowe et al., 2008). As this means people moved into the region before the onset of an interstadial, Taller et al. (2014) argue that this resettlement was not driven by ameliorating climates but by population growth and these peoples' adaptation to specific environmental conditions.

Schussenquelle, Brillenhöhle, and Felsställe are archaeological sites in the Swabian Jura that have large Magdalenian assemblages that have been well-studied. The remains from these sites (Fraas, 1867; Kind, 1987; Riek, 1973a; Schuler, 1994), as well as more recent studies of the Magdalenian remains from Hohle Fels cave (Napierala et al., 2014; Taller, 2014), Helga Abri rock shelter (Hess, 2019), and open air sites in Baden-Württemberg (Floss, 2019), have shown that the Magdalenian of the Swabian Jura is similar to that represented in most of Central Europe. Lithic assemblages are composed primarily of backed blades and bladelets, burins, and end-scrapers (Bolus, 2012; Conard et al., 2015a; Hahn, 1991; Taller, 2014). Bone tools, reindeer antler, some pieces of ivory, and art objects made on bone, antler, and stone have been recovered from Magdalenian contexts in the Swabian Jura (Conard et al., 2015a; Conard and Malina, 2011, 2010; Eriksen, 1991; Maier, 2015; Schmidt, 1912; Taller, 2014). Further, Magdalenian hunter-gatherers seem to have primarily hunted reindeer and horse in the Swabian Jura, although, like other regions of Central Europe, ibex, hare, fox, and ptarmigan remains are also common in the faunal assemblages from this region (Eriksen, 1996; Gaudzinski and Street, 2003; Maier, 2015; Napierala et al., 2014; Riek, 1973b).

To date, settlement patterns during the Magdalenian for this region have been best studied by Weniger (1989, 1987). In his review of archaeological assemblages across Central Europe, he classifies the archaeological sites of southwestern Germany as small, medium, or large based on their artifact assemblages and features. He states that at large sites, Magdalenian peoples aggregated in large groups in the lowlands during the winter where they prepared skins and food and primarily hunted reindeer. He classifies medium sites as "residential camps of local groups." These sites were occupied during spring and summer, are found in both the lowlands and hills, have hearths, and approximately equal amounts of horse and reindeer remains. Finally, his small sites are located in the hills and occupied during the spring and summer

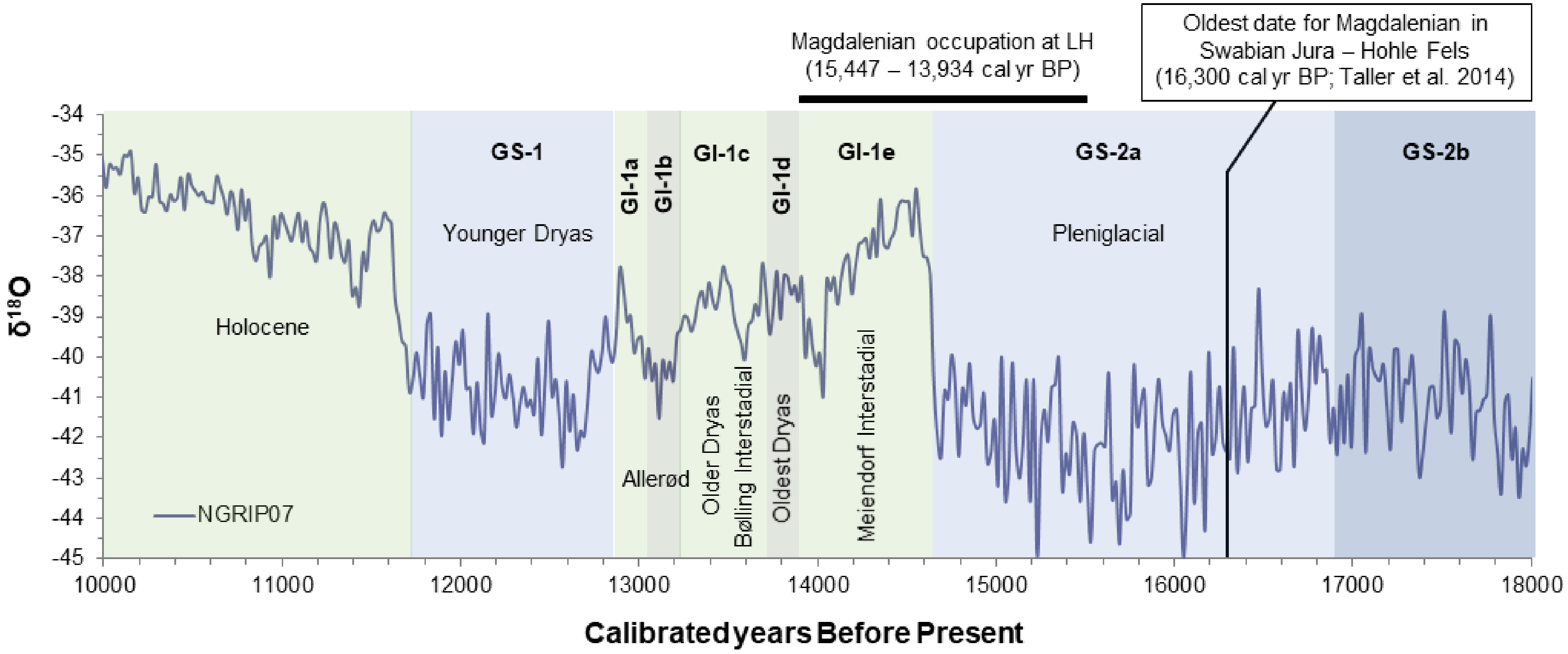

Figure 2. The NGRIP curve (Andersen et al., 2006; Lowe et al., 2008; Svensson et al., 2006) associated with GI and GS events, as well as climatic events defined by the vegetative record of central Europe (i.e. Meiendorf, Bølling, Dryas). The correlation of these datasets is taken from Litt et al. (2001), Litt et al. (2007), and Lowe et al. (2008). The distribution of the radiocarbon dates from the Magdalenian occupation of Langmahdhalde and the earliest date associated with the Magdalenian in the Swabian Jura are both indicated on the figure. NGRIP data downloaded from National Oceanic and Atmospheric Administration (eftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/greenland/summit/ngrip/gicc05-60ka-20yr.txt).

months by smaller bands who primarily hunted horse and ibex. He refers to these small sites as “short-term field camps.” I would argue that classifying archaeological sites into only three categories can oversimplify hunter-gatherer behavior and settlement patterns, but the nature of the archaeological record often necessitates making such categories. Here, I present faunal analyses that contribute to building models of landscape use during the Magdalenian that are based on a finer scale of ecological data than has been available in the past.

1.3 Environments During the Late Glacial

In this dissertation, I use the NGRIP (North Greenland Ice Core Project; Andersen et al., 2006; Lowe et al., 2008; Svensson et al., 2006) oxygen isotope record when I discuss climatic periods. Litt et al. (2007, 2001) have correlated the GRIP record to Central European varved lake sediment records, making it easier to compare studies that discuss, for example, the “Oldest Dryas” and “Allerød” to studies that discuss Greenland Stadial (GS) and Interstadial (GI) events. In Figure 2, I have used this work, as well as Lowe et al.'s (2008) comparison of the NGRIP and GRIP records, to roughly correlate the NGRIP record to the Central European vegetative record and place Langmahdhalde and the Magdalenian of the Swabian Jura within this context.

In general, the Late Glacial in Central Europe has been characterized as relatively unstable climatically as “climatic shifts occurred within a matter of decades” during this period (Lowe et al., 2008). The glaciers of the Last Glacial Maximum were retreating during this time, temperatures were warming, and forested regions and grasslands eventually developed (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989), but these trends were not continuous. Instead the period includes both interstadial and stadial events that reflect large-scale changes in temperature (Litt et al., 2001; Lowe et al., 2008; Figure 2). In Central Europe, this period was generally drier and colder than today and included steppe and tundra environments (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989).

There have been several studies of paleoenvironments during the Middle and early Upper Paleolithic in the Swabian Jura using geoarchaeology, zooarchaeology, archaeobotany, geochemistry, and palynology (Drucker et al., 2016; Krönneck, 2012, 2008; Miller, 2015; Rhodes et al., 2019, 2018; Riehl et al., 2014; Schmidt, 1912; Weniger, 1982). However, as mentioned above, there exist no modern quantitative studies of environments during the Late Glacial in the Swabian Jura, except a few stable isotope studies (Drucker et al., 2011; Immel et al., 2015). In order to understand the complexity past of environments, which are often not fully comparable to any modern environment (i.e. the Mammoth Steppe; Guthrie, 2001, 1982), proxy data from several different sources are necessary.

When discussing past human behavior, the spatial scale of environmental and climatic reconstructions is relevant. Due to the nature of many proxy data sources, most paleoenvironmental and climatic reconstructions that researchers use to discuss Paleolithic humans are applicable at a large scale. For example, the NGRIP record (Andersen et al., 2006; Lowe et al., 2008; Svensson et al., 2006; Figure 2) is applicable to the northern Atlantic. Smaller scale reconstructions, though, are more relevant to studies of hunter-gatherer behavior in the past because these people likely traveled only a few hundred kilometers per year (Weniger, 1991). Palynological and botanical proxy records have the ability to reconstruct more local signatures and there are some pollen records from southwestern Germany that provide information on what the vegetation was like during the Late Glacial in this region (e.g. Duprat-Oualid et al., 2017; Firbas, 1935). The closest of these records to the Swabian Jura is a lake core from the Bergsee in the Black Forest of Germany that provides vegetative data for the period 45,000 to 14,700 cal yr BP (Duprat-Oualid et al., 2017). This study finds that from 30,000 to 14,700 cal yr BP vegetation is steppe during GS phases and boreal during GI phases and documents an increase in birch (genus *Betula*) at the end of the record (Duprat-Oualid et al., 2017).

Another source of local scale paleoenvironmental reconstructions is microfaunal remains. These are the bones and teeth of small animals like rodents, insectivores, fish, amphibians, and reptiles that are found in archaeological and paleontological contexts and are almost always deposited by avian and mammalian predators (Fernández-Jalvo et al., 2016). Rodents and insectivores, for example, have relatively short lifespans, reproduce quickly, and have large litter sizes, meaning that they respond to environmental changes more rapidly than other species. This makes these taxa particularly appropriate for environmental and climatic reconstructions of the past (Grayson 1981, 1984; Terry 2010; Broughton and Miller 2016: 95). Amphibians, reptiles, and fish are often adapted to specific habitats and can, therefore, also provide information on past environments (Blain et al. 2009; Broughton and Miller 2016: 18). In most of the cave and rock shelter sites in the Swabian Jura, microfaunal remains have been found in association with archaeological artifacts, making them incredibly useful for interpretations of human behavior within the context of local environmental conditions.

The power of microfaunal assemblages in paleontological and archaeological contexts to interpret past environments and biochronology has long been acknowledged in Germany (e.g. Böhme, 2007; Schmidt, 1912; Soergel-Rieth, 2011; Ziegler and Dean, 1998). Most of this past work has relied on the indicator taxon method, in which the presence or absence of species known to be associated with specific environmental conditions today is used to reconstruct past environmental conditions (for a review of the use of faunal remains in paleoenvironmental reconstructions, see Andrews, 1996, 1995 and Lyman, 2017). Recently, though, new, more quantitative models have been developed that build on the indicator taxon method and are able reconstruct climate variables, such as temperature and precipitation, and environment type more accurately and at a finer scale than before (e.g. Agustí et al., 2009; Blain et al., 2009; Hernández Fernández, 2001a; Hernández Fernández and Peláez-Campomanes, 2005, 2003). This more local scale is particularly relevant in the Swabian Jura, where the geography of the individual river valleys varies greatly, suggesting that Paleolithic hunter-gatherers did not move through or use these valleys in the same way.

Chapter 2: Langmahdhalde Rock Shelter

Excavations began at Langmahdhalde in 2016 with two 2 x 1 m trenches located in different sections of the rock shelter. Trench 1, which was located in the more southern section of the rock shelter, yielded few archaeological remains and no identifiable archaeological horizons and was closed. Trench 2, located about 6 m north of trench 1 along the rock face, yielded bone and lithic artifacts that were later dated to the Magdalenian. The primary area of excavation and research at the site is, therefore, Trench 2, which has been expanded significantly. We have returned to Langmahdhalde for excavations annually since 2016. Figure 3 shows a view of the rock shelter from the Lone Valley and excavators working at the site in 2019.

From 2016 to 2019, our work at the site revealed 10 geological and archaeological horizons (GHs and AHs) from the Holocene and Pleistocene (Appendix 2, Figure 2). This dissertation uses remains from the 2016 to 2018 excavations from which there are seven horizons: GH1/AHI, GH2/AHII, GH2a/AHIIa, GH3/AHIII, GH4/AHIV, GH5/AHV, and GH6/AHVI. Radiocarbon dates have been taken from most of the horizons from the site and are presented in Table 1. GH1/AHI is a modern humus layer. GH2/AHII has ceramics and lithics from several periods including the Neolithic, metal ages, and early middle ages and has been dated to the Holocene (Table 1; Conard et al., 2017; Wong et al., 2020). The dates from GH2a/AHIIa are mixed but all fall within the Holocene (Table 1). The lithics from this horizon appear to be Mesolithic. GH3/AHIII has very few lithic or faunal remains and a date from the bottom of this layer indicates that it is from the Late Glacial (Table 1; Conard et al. 2017; Wong et al. 2020).

GH4/AHIV through GH6/AHVI have overlapping radiocarbon dates that range from 15,447 – 13,934 cal yr BP, falling at the end of the GS-2a event and within the GI-1e event in the NGRIP record (Lowe et al., 2008) during the Late Glacial (Table 1; Conard et al., 2019, 2018, 2017; Wong et al., 2020). These dates correspond to the Magdalenian cultural period in the region (Gaudzinski and Street, 2003; Hahn, 1995; Housley et al., 1997; Kind, 2003; Taller et al., 2014). GH4/AHIV to GH6/AHVI have higher numbers of lithic and faunal remains compared to the horizons above. Lithic refits have been observed between these three horizons during excavation, but the lithic assemblage has yet to be systematically studied. GH5/AHV has six combustion features that are associated with charcoal and burnt limestone features. In Appendix 1, Figure 4 shows the largest of these features, Feature 1, as well as

Figure 3. Top: view of Langmahdhalde rock shelter from the Lone Valley (the rock face is visible through the trees on the left side of the photo). Bottom: excavations at Langmahdhalde during the 2019 field season, photo taken facing northeast.

Features 2 and 3. In this figure, you can see the dark sediment and charcoal associated with these features and the burnt limestone rocks that are common in this horizon.

Langmahdhalde is excavated following the University of Tübingen excavation system which uses quadrants measuring 1 x 1 m and four sub-quadrants within these quadrants that measure 50 x 50 cm. The quadrants of the site are named based on the coordinates of their southwestern corner. Figure 4 shows the quadrant system for Langmahdhalde as of the 2019 excavations. Each horizon is excavated by sub-layers that are two to three centimeters deep and follow the geology of the horizon. Only GH5/AHV and GH6/AHVI were excavated using sub-layers. During excavation, all sediment is kept and later water-screened through 1 x 1 mm mesh with the exception of GH3/AHIII. Because GH3/AHIII is almost anthropogenically sterile, only the southwestern sub-quadrant of each quadrant was water-screened from this horizon. This may create a sampling bias in the remains of this horizon.

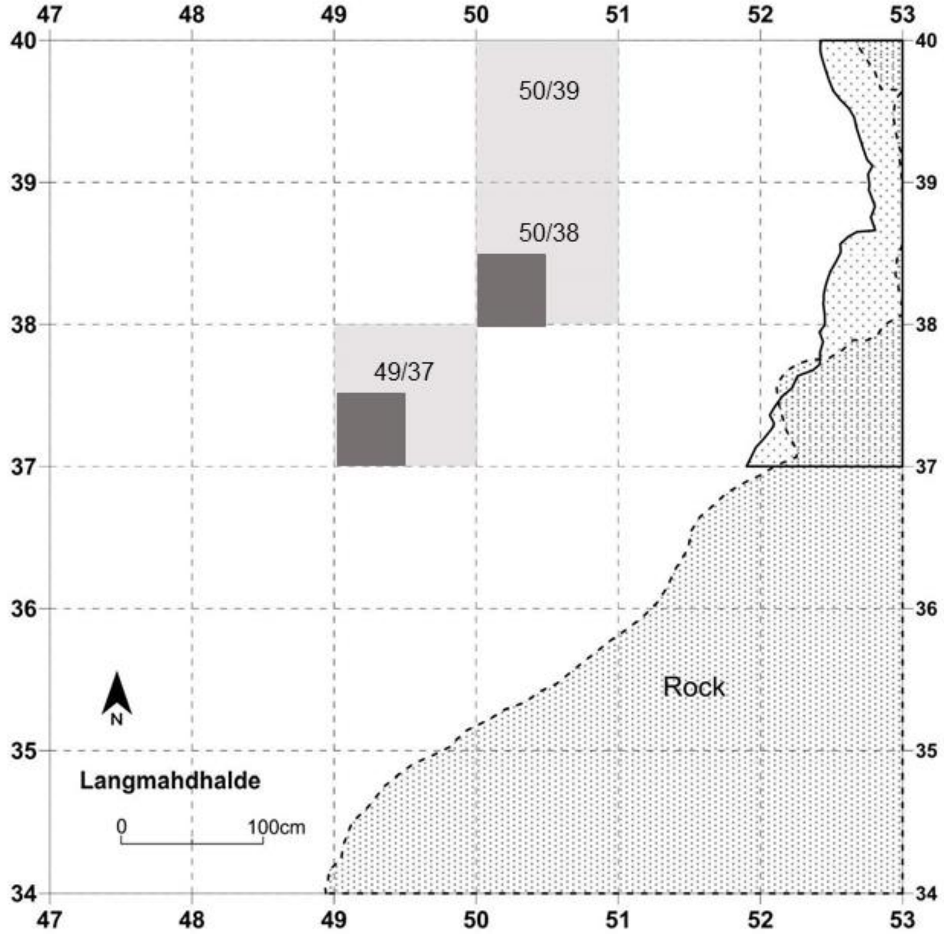

Figure 4. Plan view of the quadrant system at Langmahdhalde rock shelter with quadrants used in the microfaunal analysis highlighted. I used microfauna from the light gray quadrants (49/37, 50/38, and 50/39) for the taxonomic analysis and microfauna from the dark gray sub-quadrants for the taphonomic analysis. Figure by M. Zeidi.

Lab Number	Quadrant	Find Number	GH	AH	Sub-Layer	Feature	Material	Modifications	Date ^{14}C (yr uncal BP)	Date ^{14}C (yr cal BP)	Source
ETH-74893	51/38	43	2	II	-		pig distal tibia		2418 ± 24	2680 - 2354	1
ETH-94572	49/36	31	2a	IIa	-		pig distal humerus		4569 ± 23	5437 - 5071	3
ETH-94574	50/36	65	2a	IIa	-		roe deer radius fragment		5636 ± 24	6483 - 6322	3
ETH-74894	51/39	170	3	III	-		Charcoal	-	12295 ± 63	14653 - 14034	1
ETH-749895	50/38	201	4	IV	-	1	Charcoal	-	12784 ± 37	15381 - 15090	1
ETH-94573	49/36	146	5	V	2		deer femur fragment		12159 ± 31	14164 - 13934	4
ETH-83806	50/37	170	5	V	1	2	Charcoal	-	12221 ± 58	14376 - 13928	4
ETH-84042	48/38	170	5	V	1		horse humerus fragment	cutmarks	12636 ± 47	15210 - 14765	2
ETH-84040	51/38	409	5	V	3	1	large mammal long bone shaft fragment		12714 ± 48	15313 - 14936	2
ETH-84039	51/37	166	5	V	1	2	large ungulate long bone shaft fragment	cutmarks	12732 ± 48	15335 - 14979	2
ETH-84041	50/37	218	5	V	3	3	medium mammal long bone shaft fragment		12794 ± 48	15447 - 15084	2
ETH-94575	52/37	90	6	VI	2		horse proximal third metatarsal	cutmarks & cone fracture	12476 ± 32	14981 - 14305	4

Table 1. Radiocarbon dates from Langmahdhalde. Dates were calibrated using OxCal v4.3.2 (Bronk Ramsey, 2017, 2009) and IntCal13 atmospheric curve (Reimer et al., 2013). GH = Geological Horizon; AH = Archaeological Horizon. The sources for the previously published dates are as follows: 1 = Conard et al. 2017; 2 = Conard et al. 2018; 3 = Conard et al. 2019; 4 = Wong et al. 2020. Table adapted from Wong et al. (2020; Appendix 2).

Chapter 3: Methods

The taxonomic classifications in this dissertation follow Wilson and Reeder (2005), with the exception of the order Eulipotyphla which is the most recent version of the order that includes shrews, moles, and hedgehogs (Douady et al., 2002; Waddell et al., 1999).

For this dissertation, I analyzed both the macrofauna and microfauna from the Langmahdhalde rock shelter. I define macrofauna as specimens that have implications for human and large carnivore behavior and use of the rock shelter. In the Upper Paleolithic of Central Europe, then, macrofauna could include animals such as deer, horse, and small game, such as hare or medium-sized birds. Microfauna, on the other hand, are small animals that belong to taxonomic categories that have strong potential to reconstruct past environments and climates at the local scale. For the purposes of this dissertation, microfauna includes the mammalian Orders Rodentia and Eulipotyphla (I refer to members of the Order Eulipotyphla as “insectivores” throughout the text). As discussed above, fish, amphibians, and reptiles can also be used to reconstruct past environments (Blain et al., 2009; Broughton and Miller, 2016), but the sample sizes for these taxa at Langmahdhalde are relatively small, especially compared to those of rodents and insectivores. Microfaunal remains are very rarely deposited by humans and their accumulations in cave and rock shelter sites around the world are usually the result of avian or small mammalian predator activity (Fernández-Jalvo et al., 2016).

3.1 Macrofauna

As the goals of my dissertation focus on reconstructing human behavior during the Magdalenian, my analysis of the macrofaunal remains from Langmahdhalde includes only specimens from GH3/AHIII through GH6/AHVI. I identified the macrofauna specimens using several osteological atlases (e.g. Gilbert, 1990; Gilbert et al., 2006; Hillson, 2005; Pales and Lambert, 1971; Schmid, 1972) and the vertebrate comparative collection housed at the Institute for Archaeological Sciences at the University of Tübingen. I identified all specimens to the lowest taxonomic level possible and recorded them using Stiner's (2005) coding system with modifications for Late Glacial taxa in Central Europe. If specimens were not identifiable to a specific taxon, I assigned them to broader categories, such as “medium ungulate” or “small mammal.” I define small ungulates as ungulates weighing between approximately 10 and 23 kg, medium ungulates between 40 and 250 kg, and large ungulates between 250 and 1,000 kg. For the mammalian size classes, I define small mammals as those mammals weighing less than 10 kg, medium mammals as those weighing between 10 and 250 kg, and large mammals as those weighing over 250 kg. The category “large deer” includes the genera *Cervus* and *Rangifer*.

I based the species-level identifications of hare remains on tooth morphology (Callou, 1997; Donard, 1982; Niethammer and Krapp, 2003) and post-cranial measurements (Donard, 1982; Pelletier et al., 2015) and used measurements of teeth to identify fox specimens to the species-level (Baumann, 2016). For each taxonomic category, I calculated the number of identified specimens (NISP; Grayson, 1984; Lyman, 2008) and for each specific taxonomic category (i.e. species-level identifications), I calculated the minimum number of individuals (MNI; Grayson, 1984; Lyman, 2008). My calculations of MNI are based on the most common element and take side into account when possible. I assigned an NISP value of 1 to specimens that articulate and included long bone shaft fragments in the NISP calculations. I did not include small unidentifiable fragments of ungulate tooth in the calculations of NISP because these would have greatly overinflated the values.

For each specimen, I recorded taphonomic signatures, such as burning (Stiner et al., 1995), weathering (Behrensmeyer, 1978), mineral staining, breakage, tooth marks, and any human modifications (Fernández-Jalvo and Andrews, 2016; Lyman, 1994). When possible, I also recorded indicators of age, such as epiphyseal fusion, tooth eruption, and tooth wear (Hufthammer, 1995; Levine, 1982, 1979; Miller, 1974; Payne, 1973; Severinghaus, 1949; Silver, 1969). For reindeer (*Rangifer tarandus*) remains, I used tooth wear stages from Miller (1974) and Severinghaus (1949) and epiphyseal fusion information from Hufthammer (1995). Further, I follow the age categories defined for reindeer by Miller (1974) and define juveniles as 0 to 25 months old, subadults as 27 to 39 months old, and adults as 41 months or older. For horse specimens, I used tooth eruption and long bone fusion information from Silver (1969) and incisor wear information from Levine (1982, 1979). I follow the age categories for horse used by Turner (2002) and define juvenile horses as 0 to 2 years old, prime adults as 3 to 6 years old, and old horses as 7 years old or older.

Body part representation in archaeofaunal assemblages can provide information on carcass transport or selection of animal parts based on utility. It is necessary, however, to explore whether body part representation was affected by processes other than human behavior (Lyman, 1994). Differences in the structural density of different bones, for example, affects the probability of a specimen being preserved in the fossil record (Lyman, 1994). In order to examine whether density-mediated attrition possibly affected skeletal element representation in the Langmahdhalde macrofaunal assemblage, I used two methods.

First, for each horizon, I compared bone density to survivorship (percent minimum animal units or %MAU). MAU was originally developed by Binford (1984, 1978) to explore the representation of different body parts in assemblages and essentially standardizes the frequencies of "anatomical units" in a sample based on the frequency of these units in one animal. It is calculated by dividing MNE by the number of times the element occurs in the skeleton (Binford, 1984, 1978). To compare bone density and %MAU, I conducted a Spearman's rank-order correlation using the stats package in RStudio version 1.2.1335. A significant positive correlation between bone density and survivorship would indicate that more dense parts of the skeleton are more commonly represented in the assemblage. Due to sample size, I conducted this analysis for only hare (specimens identified to mountain hare, *Lepus timidus*, European hare, *Lepus europaeus,* and the genus *Lepus*) and medium ungulates at Langmahdhalde. The medium ungulate category includes specimens assigned to ibex (*Capra ibex*), red deer (*Cervus elaphus*), reindeer, large deer, and medium ungulate. For the bone density of hare, I used data on snowshoe hare (*Lepus canadensis*) from Pavao and Stahl (1999) and for the bone density of medium ungulates, I used the reindeer data without corrections for marrow cavities from Lam et al. (1999; called "BMD_1"), as variations in relative bone density across different taxa are low enough to allow for accurate interpretations using density data from similar species (Lam et al., 1999).

Second, I examined the ratio of teeth to cranial bone (cranial bone elements and mandibles) for each horizon for specimens identified to horse, hare, and medium ungulate. In general, we can assume that when hunter-gatherers transported animal carcasses to the rock shelter, the teeth of the carcass remained in the skull, therefore, teeth and cranial bone arrived at the site together. Because they arrived together, teeth and cranial bones would thus have the same values for minimum number of elements (MNE; Lyman, 1994). Compared to bone, tooth enamel is more likely to preserve in archaeological sites because it has a higher mineral content (Hillson, 2005; Lyman, 1994). Therefore, finding a ratio of tooth MNE to cranial bone MNE higher than one suggests that density mediated attrition affected the assemblage.

I examined body part representation for the major taxonomic groups in the Langmahdhalde macrofaunal assemblage: hare, fox, horse, and medium ungulates. The categories of "hare" and "medium ungulate" are defined above. The fox category includes specimens identified to arctic fox (*Vulpes lagopus*) and the genus *Vulpes*. Based on Stiner (1991), I divided the skeleton into nine anatomical regions (Table 2) and calculated the MAU for each region by horizon.

Region Number	Region Name	Elements
1	Horn	Antler (shed & unshed), Horn
2	Head	Mandible, Cranial Bones
3	Neck	Atlas, Axis, Cervical Vertebrae
4	Axial	Thoracic Vertebrae, Lumbar Vertebrae, Sacral Vertebrae, Innominate, Ribs
5	Upper Front	Scapula, Humerus
6	Lower Front	Radius, Ulna, Metacarpals
7	Upper Hind	Femur
8	Lower Hind	Tibia, Calcaneus, Astragalus, Metatarsals
9	Feet	Phalanges

Table 2. The anatomical regions of the body, following Stiner (1991).

3.2 Stable Isotope Analysis

I conducted stable isotope analysis on bone collagen from five horse and six reindeer specimens from GH4/AHIV and GH5/AHV (Table 3). I chose these specimens based on their age (adult specimens were preferred), the presence of cortical bone, their preservation, and element. Six of the specimens have green fractures and two of the horse specimens have cutmarks, indicating that these two specimens were deposited by human activity. One of the horse specimens has been directly dated using radiocarbon dating to 15,210 to 14,765 cal yr BP (reference number ETH-84042; see Table 1; Conard et al., 2018).

I extracted the collagen from these specimens in the laboratory of the Biogeology Working Group in the Department of Geosciences at the University of Tübingen following protocol based on Longin (1971) and modified by Bocherens et al. (1997). This extraction procedure includes demineralization of the sample in HCl 1M, soaking the sample in 0.125M NaOH, and solubilization of the sample in acidified water (pH = 2). After these steps, the sample is freeze-dried. Before extraction, an elemental analysis (C_{coll} and N_{coll}) was conducted at the

Department of Geosciences at the University of Tübingen. The Laboratory of Chronology in the Finnish Museum of Natural History at the University of Helsinki conducted the isotopic analysis ($\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$) of the bone collagen using an NC 2500 elemental analyzer coupled to a DeltaPlusAdvantage or a DeltaVPlus isotope ratio mass spectrometer. The following known values of international reference materials were used to calibrate the measurement data for $\delta^{13}C$ and $\delta^{15}N$: USGS-40 ($\delta^{13}C$ = -26.39 ‰, $\delta^{15}N$ = -4.5 ‰) and USGS-41 ($\delta^{13}C$ = +37.63 ‰, $\delta^{15}N$ = +47.6 ‰). Based on multiple measurements of matrix matched in-house reference materials (modern camel and European elk/moose bone), there is an external reproducibility (1σ) of ±0.19 ‰ for $\delta^{13}C$, ±0.24 ‰ for $\delta^{15}N$ values. The error in the reproducibility for the amounts of C and N was better than 4%. Measuring the chemical composition of collagen can establish the reliability of the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values, with C:N_{coll} atomic ratio ranging from 2.9 to 3.6 (DeNiro, 1985) and percentage of C_{coll} above 8% and percentage N_{coll} above 3% (Ambrose, 1990).

Lab Number	Element	Find Number	Horizon	Notes
Reindeer				
LGN-6	tibia R	LH 47/37_156	GH5/AHV sub-layer 2	
LGN-9	metatarsal	LH 48/39_129	GH4/AHIV	
LGN-10	mandible R	LH 50/38_297	GH5/AHV sub-layer 3	
LGN-12	mandible R	LH 51/37_201	GH5/AHV sub-layer 2	
LGN-13	metatarsal	LH 52/38_100	GH5/AHV sub-layer 1	
LGN-14	metatarsal	LH 50/39_133	GH4/AHIV	
Horse				
LGN-4	humerus R	LH 48/38_170	GH5/AHV sub-layer 1	14C Date: ETH-84042; 15210 – 14765 cal yr BP (Conard et al. 2018)
LGN-5	metatarsal R	LH 47/37_124	GH4/AHIV	
LGN-7	metatarsal R	LH 47/38_129	GH4/AHIV	
LGN-8	metacarpal	LH 47/38_142	GH5/AHV sub-layer 1	
LGN-11	radius	LH 50/39_171	GH5/AHV sub-layer 1	

Table 3. Information for the specimens I conducted stable isotope analysis on from Langmahdhalde. For more information on the dated specimen see Table 1.

3.3 Microfauna

Langmahdhalde has a large microfaunal assemblage that I estimate has over 400,000 specimens. Consequently, I used a sample of these remains for this dissertation. My work with the microfaunal remains can be broken into two different components: the taxonomic analysis and the taphonomic analysis. The taxonomic analysis, which I used to reconstruct paleoenvironments, includes specimens from quadrants 49/37, 50/38, and 50/39, and the taphonomic analysis includes specimens from the southwestern sub-quadrant of 50/38 (Figure 4). There is one exception to this: in GH3/AHIII, no sediment was water-screened from 50/38. I, therefore, used the southwestern sub-quadrant of 49/37 for the taphonomic analysis of GH3/AHIII (Figure 4). Although this dissertation focuses on the Late Glacial, I also include analyses of the microfauna from GH2/AHII and GH2a/AHIIa to provide context for GH3/AHIII through GH6/AHVI.

3.3.1 Paleoenvironmental Reconstructions

3.3.1.1 Taxonomic Identifications

Paleoenvironmental analyses that are based on microfaunal remains require lower levels of taxonomic identification because it is generally at the genus- or species-level that these animals have specific habitat preferences. For these identifications, I used the vertebrate comparative collection housed at the Institute for Archaeological Sciences at the University of Tübingen and several identification guides (e.g. Agadjanian et al., 1977; Nadachowski, 1982; Niethammer and Krapp, 1990, 1982, 1978; Repenning, 1967; von Koenigswald et al., 1974). I calculated NISP and MNI values for each taxonomic category (Grayson, 1984; Lyman, 2008).

In this work, I only include specimens within the genus *Microtus* that are identifiable to the species-level because at a higher taxonomic category, they do not provide specific environmental information. There are two exceptions to this: specimens identified to the Terricola group (genus *Microtus*; see Niethammer and Krapp, 1982 and Wilson and Reeder, 2005 for discussions on the taxonomy of this group) and specimens identified as common or field voles (*Microtus arvalis* or *agrestis*). Common and field voles are differentiable based on metrics (Luzi, 2018; Nadachowski, 1984) and morphological characteristics (Borodin and Markova, 2015; Chaline, 1974; Dienske, 1969; Luzi, 2018; Luzi et al., 2017; Nadachowski, 1982). Historically, though, researchers in Germany did not differentiate between the common and field vole in studies of fossil assemblages because little work had been done demonstrating that these species have specific environmental preferences. Initially, therefore, I did not separate these species from each other in my taxonomic identifications. Current research, though, indicates that differentiating between these two species can have important implications for paleoenvironmental reconstructions (Luzi, 2018; Luzi et al., 2019, 2017; Luzi and López-García, 2017). With this in mind, I sampled a portion of the specimens identified to common or field vole in each horizon and sub-layer to determine whether both species were present.

In the Langmahdhalde assemblage, teeth are the most common element identifiable to lower taxonomic categories, such as species or genus, although some insectivore mandibles and forelimbs identifiable to this level are also present in the assemblage (Niethammer and Krapp, 1990; Repenning, 1967). I identified certain specimens from the genera *Talpa*, *Sorex*, and *Apodemus* to the species level using measurements (Figure 5). To identify humeri belonging to the genus *Talpa* to the species-level, I used measurements from Maul (2001) and von Koenigswald (1985). In the case of specimens identified to the genus *Sorex*, I followed the measurements presented by Maul (2001) and Ziegler (1995) of mandibles and lower premolars and molars in order to identify specimens to the species-level. I used length measurements of lower and upper first molars belonging to the genus *Apodemus* in order to identify them to either yellow-necked mouse (*Apodemus flavicollis*) or wood mouse (*A. sylvaticus*; Niethammer and Krapp 1978: 326, 338, 361). I took all measurements at the Institute of Archaeological Sciences at the University of Tübingen using a Keyence Digital Microscope VHX-500F.

3.3.1.2 Diversity

I use Simpson's Diversity Index (Simpson, 1949) to evaluate ecological diversity within the microfaunal assemblage of Langmahdhalde. This index measures the distribution of specimens across taxonomic categories and predicts the probability of picking two taxa at random that are different species. It, therefore, measures "evenness." An "even" sample means that all taxa represented in the sample are abundant in similar numbers, while an "uneven" sample would have one or a few dominate taxa. The result of the calculation of Simpson's Diversity Index, the value D, decreases as evenness increases, which can make D confusing to interpret. I, thus, present values as 1/D, or as the reciprocal of Simpson's Index, as is common in zooarchaeological analysis (Lyman, 2008). Larger 1/D values indicate greater evenness in the sample. I use the following equation to calculate D, originally

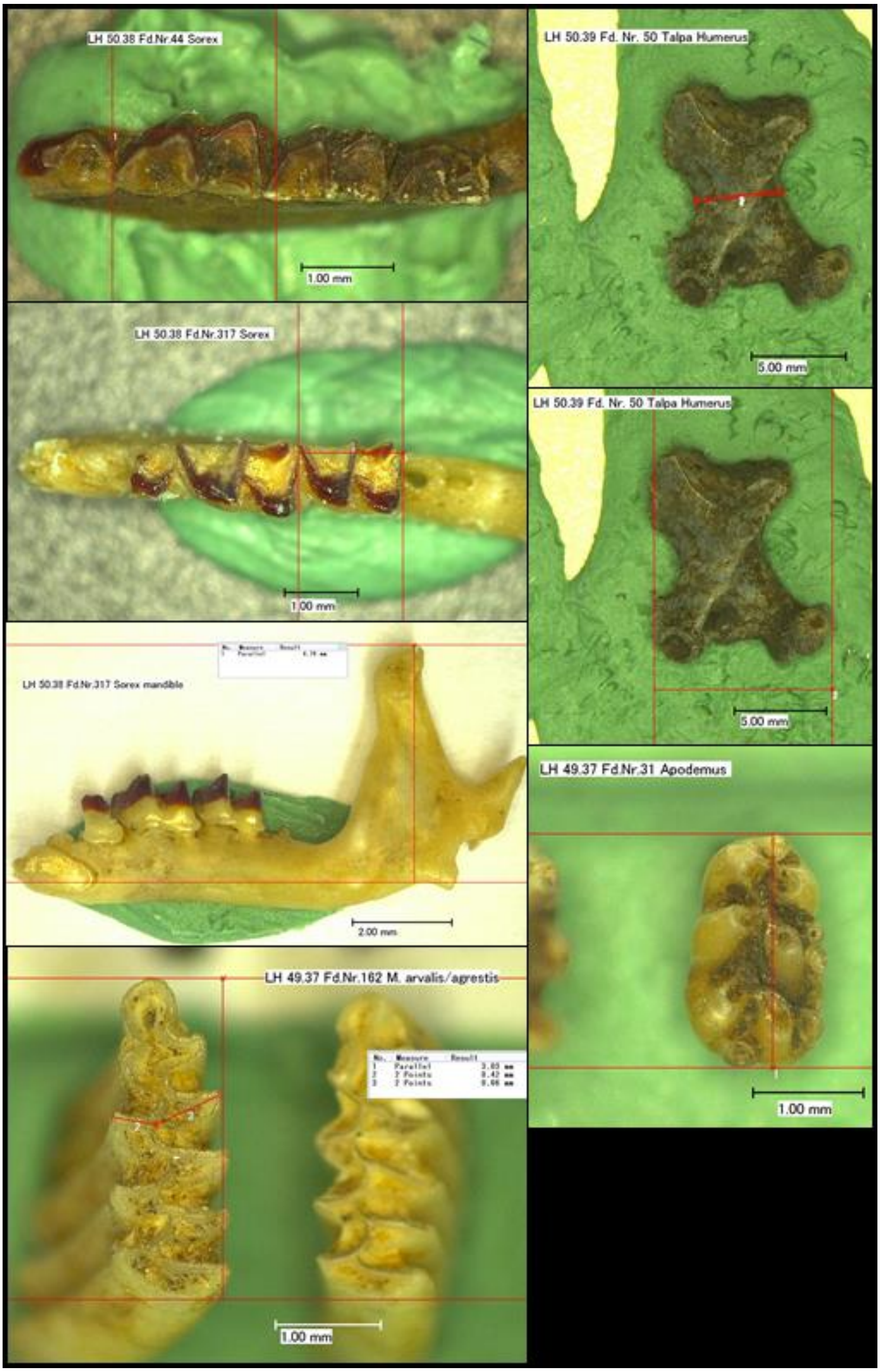

Figure 5. Examples of measurements taken on microfaunal remains. Scales and specimen numbers given in photos. Left column (top to bottom): length of *Sorex* lower first molar, length of *Sorex* lower second molar, height of *Sorex* coronoid process, measurements of *Microtus arvalis/agrestis* lower first molar (length, width of fourth triangle, width of fifth triangle). Right column (top to bottom): width of diaphysis of *Talpa* humerus, width of distal epiphysis of *Talpa* humerus, length of *Apodemus* lower first molar. Photos taken with Keyence Digital Microscope VHX-500F.

proposed by (Pielou, 1969) as an unbiased way of estimating finite samples, like those from fossil assemblages:

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

where n_i is the MNI of taxon i and N is the total MNI of the horizon or sub-layer.

In general, I only included specimens identified to the genus-level or below in these calculations. If there were specimens in a horizon or sub-layer that were identified to the genus *Talpa* and to the common mole (*Talpa europaea*) or to the genus *Sorex* and to the common shrew (*Sorex araneus*), these specimens were grouped together by genus for the calculations. I included certain insectivore specimens identified to Soricidae and Soricinae in the diversity calculations for GH6/AHVI sub-layers 1 and 2 so that the presence of insectivores in these sub-layers would be represented. In this case, I grouped the MNI values of these specimens together to represent one taxon in the calculations.

3.3.1.3 Bioclimatic Analysis

In order to reconstruct past environments and climates, I applied the Bioclimatic Analysis (BA; Hernández Fernández, 2001a, 2001b; Hernández Fernández and Peláez-Campomanes, 2005, 2003) to the microfaunal assemblage from Langmahdhalde. This analysis uses a modified version of Walter's (1970) climate zone nomenclature (Table 4) and includes a qualitative model and several quantitative models. The qualitative model of the BA predicts the most probable climate zone that existed in a locality, while the quantitative models predict specific climate variables for the locality.

The BA is based on the presence or absence of mammalian taxa in a locality and was built using modern data from 50 localities around the world. Hernández Fernández (2001a) tested the accuracy of the models of the BA using different groups of mammalian taxa, such as all mammals ("whole fauna"), carnivores, bats, and rodents. I used the rodent models, and, therefore, the results are based only on the rodent remains from Langmahdhalde. The qualitative models based on rodents provide some of the most accurate results for the qualitative models (Hernández Fernández, 2001a) and classify 94% of the localities in the modern dataset to the correct climatic zone (Hernández Fernández and Peláez-Campomanes, 2003). For the quantitative models, Hernández Fernández and Peláez-Campomanes (2005) find that using rodent faunas is, on average, better at reconstructing climate variables than other groups of mammalian taxa, especially when it comes to predicting precipitation.

To apply the BA to a fossil assemblage, the researcher makes a species-to-climate zone matrix for each locality (or, in this case, horizon or sub-layer) based on the modern occurrence of each species in Walter's (1970) climate zones. If the species does not exist in the climate zone, the researcher gives a value of 0 for that climate zone. The researcher assigns a value to each of the climate zones that the species does exist in that is equal to 1/n, n being the total number of climate zones the species exists in. The values assigned to a species for each climate zone are, together, referred to as the Climate Restriction Index (CRI).

Zone	Climate	Vegetation Type
I	Equatorial	Evergreen tropical rain forest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semi-arid	Savanna
III	Subtropical arid	Sub-tropical desert
IV	Subtropical with winter rains and summer drought	Sclerophyllous woodland-shrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Polar	Tundra

Table 4. Climate and vegetation zones from (Walter, 1970) with updated terminology from (Hernández Fernández et al., 2007). This terminology is used in the Bioclimatic Analysis.

I took CRI values for each species from Hernández Fernández (2001b). Hernández Fernández (2001b), however, does not provide CRI values for the narrow-headed vole (*Microtus gregalis*), a common species in microfaunal assemblages from the Late Pleistocene in Central Europe. I, therefore, used the criteria explained in Hernández Fernández (2001a) and information on the modern distribution of the narrow-headed vole from the International Union for Conservation of Nature’s Red List (Batsaikhan et al., 2016) to assign this species to climate zones VII, VIII, and IX. For specimens identified to the genus *Lemmus*, I used CRI values for brown lemming (*Lemmus sibiricus*; Hernández Fernández, 2001b).

After creating the species-to-climate matrix, the researcher uses this and the CRI values to calculate the Bioclimatic Component (BC) for each climate zone in that horizon or sub-layer. The formula for the BC is as follows:

$$BC_i = (\Sigma CRI_i)100/S$$

where i is the climate zone, CRI is defined above, and S represents the number of species in the horizon or sub-layer. For each horizon or sub-layer, the BC value of a climate zone represents the percentage of the species in that horizon or sub-layer that are present in that climate zone and together, the BC values of one horizon or sub-layer are called the bioclimatic spectra.

To apply this to the qualitative model of the BA, the researcher runs the BC values through a discriminant function analysis. This discriminant function analysis was constructed by Hernández Fernández and Peláez-Campomanes (2003) using the above-mentioned 50 modern localities to predict the most probable climate zone. I ran the linear discriminant function analysis in R Studio version 1.2.1335 (see Supplementary Materials 4 in Appendix 2 for the complete R code).

For the quantitative models of the BA, the researcher applies the bioclimatic spectra to a multiple linear regression unique to each climate variable (Appendix 2, Supplementary Materials 1). Hernández Fernández and Peláez-Campomanes (2005) developed these multiple linear regressions for 13 different climatic variables. I use only nine of these climatic variables in this study: mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, the thermicity index, winter length, vegetative activity period, free vegetative activity period, annual total precipitation, and drought length. Table 5 presents the details for each of these variables, including the determination coefficient and the standard error of the model for each variable.

3.3.2 Taphonomy

The taphonomic analysis I conducted on the microfauna from Langmahdhalde follows the methodology established by Andrews (1990). Different avian and mammalian predators create microfaunal assemblages with predictable patterns of taxonomic representation, breakage, digestion, and skeletal element representation (Andrews, 1990; Andrews and Evans, 1983; Dodson and Wexlar, 1979; Korth, 1979; Stewart et al., 1999). Andrews (1990) assigns

Abbreviation	**Climate Variable**	**Description**	**Units**	**r^2**	**SE**
MAT	Mean Annual Temperature	average of the mean monthly temperature	ºC	0.930	3.6
MTW	Mean Temperature of the Warmest Month		ºC	0.746	4.8
MTC	Mean Temperature of the Coldest Month		ºC	0.932	5.1
It	Thermicity Index	measures the intensity of winter (It = 10(MAT+2MTC))	0.1ºC	0.938	130.6
W	Winter Length	number of months in which the mean monthly temperature is < 0ºC	months	0.920	1.0
VAP	Vegetative Activity Period	number of months in which mean monthly temp is >7ºC; estimates the length of plant winter dormancy and spring-summer growing periods	months	0.955	0.9
FVAP	Free Vegetative Activity Period	gives the number of months in which both temperature and humidity allow the normal growing of vegetation (FVAP=VAP-D)	months	0.918	1.3
P	Annual Total Precipitation		mm	0.746	471
D	Drought Length	estimates the length of the dry period or period in which P<2MAT	months	0.926	1.3

Table 5. Climate variables reported in this study using the Bioclimatic Analysis for rodents. Information from Hernández Fernández and Peláez-Campomanes (2005). r^2 is the determination coefficient and SE is the standard error.

predators to five categories based on the amount of modification, in terms of breakage and digestion, made on microfaunal assemblages. A category 1 predator modifies the remains of their prey very little, meaning the assemblages they leave behind have low amounts of breakage and light or no evidence of digestion. Predators assigned to category 2 leave intermediate levels of modification on microfaunal assemblages. Category 3 predators modify prey assemblages moderately. Predators in category 4 greatly modify microfaunal remains and predators in category 5 leave high levels of modification (extensive breakage and extreme levels of digestion) on microfaunal remains.

In order to identify the predator(s) most likely responsible for depositing the microfaunal assemblages in each horizon and sub-layer of Langmahdhalde, I recorded information regarding skeletal element representation, breakage, and digestion in the material. I calculated the relative abundance of each skeletal element by horizon and sub-layer using all rodent and insectivore remains as a whole, not by individual taxon. The percent relative abundance of each skeletal element is equal to the actual number of the element in the horizon or sub-layer multiplied by 100 and divided by the number of that element that would be expected based on the total MNI of the horizon or sub-layer (Andrews, 1990: 46-47). For example, if the MNI of a horizon is 15, we would expect 30 humeri to be present in the assemblage because each individual rodent and insectivore has two humeri in their body. Like Andrews (1990), I report the relative abundance of vertebrae combined, excluding caudal vertebrae and set the expected number of vertebrae for one individual as 32.

Using Kendall’s tau b (following Rhodes et al., 2018), I compared the relative abundance of skeletal elements in the horizons and sub-layers of Langmahdhalde to the relative abundance of skeletal elements reported in modern studies of prey assemblages deposited by a known predator and summarized in Appendix Tables 12 and 13 of Andrews (1990). I only compared the Langmahdhalde data to predators relevant to Late Glacial and Holocene assemblages in Europe. In Kendall’s tau b, the correlation coefficient, called tau, ranges from -1 to 1. Tau values close to zero indicate a lack of relationship while values close to -1 or 1 indicate a complete negative or positive relationship. I used the stats package in RStudio version 1.2.1335 to run these correlations.

I recorded digestion on molars, incisors, distal humeri, proximal ulnae, and proximal femora using the levels of digestion defined by Andrews (1990) – light, moderate, heavy, and extreme – as well as the categories light/moderate and moderate/heavy (following Rhodes et al., 2019, 2018). I only recorded digestion on long bones that are fully fused. I present information on molar digestion only for taxa belonging to the family Arvicolidae, excluding lemmings (in this case, the genera *Lemmus* and *Dicrostonyx*). I excluded lemmings because there is no enamel on the buccal and lingual tips of the triangles of their molars, which makes categorizing the level of digestion on these teeth difficult and comparisons with other taxa biased. I excluded insectivores, Murids, and Glirids because light and moderate levels of digestion are either difficult to identify or invisible on the molars of these taxa (Fernández-Jalvo et al., 2016; Fernández-Jalvo and Andrews, 2016: 241).

I quantified breakage of individual bone specimens using the long bone portions and categories of mandible and maxilla breakage defined by Andrews (1990: 51-56). To further examine breakage in mandibles and maxillae, I calculated the relative proportion of isolated molars and incisors for each horizon and sub-layer of the assemblage. The proportion of isolated molars and incisors is calculated using the following formulas:

$$\frac{100 * (number\ of\ isolated\ teeth)}{number\ of\ teeth\ missing}$$

where the number of teeth missing is equal to

$$(expected\ number\ of\ teeth) - (number\ of\ in\ situ\ molars\ or\ incisors)$$

where the expected number of teeth is based on the number of maxillae or mandibles in the horizons. For example, if there are five mandibles in the horizon, the expected number of incisors would be five and the expected number of molars would be 15. It can be assumed that avian and mammalian predators brought prey to the rock shelter with their teeth still inside the alveolar sockets. When the relative abundance of isolated teeth is higher than 100%, there are more isolated molars or incisors in the assemblage than would be expected based on the number of preserved sockets in mandibles and maxillae. Thus, values higher than 100% indicate breakage of the maxillae and mandibles.

I also calculated the percentage of tooth loss to quantify breakage in these elements. The percentage of tooth loss is calculated using the following equation:

$$\frac{100 * (tooth\ loss)}{(expected\ number\ of\ teeth)}$$

where tooth loss is the number of empty alveolar sockets in mandibles or maxillae and the expected number of teeth is defined above. This calculation is done separately for molars and incisors as the anterior portion of mandibles and maxillae are usually broken first and incisors are usually lost first.

Chapter 4: Results

4.1 Macrofauna

4.1.1 Density Mediated Attrition

In Table 3 of Appendix 3, I report the results of the Spearman's rank-order correlation between bone density values and survivorship (%MAU) for hare and medium ungulates at Langmahdhalde. The MNI values I used to calculate survivorship for each horizon can be found in Supplementary Table 1 of Appendix 3. There are no significant *p*-values for any of these correlations. In Table 4 of Appendix 3, I report the ratio between tooth and bone MNE for horse, medium ungulates, and hare, as well as the ratio of all of these taxa summed for each horizon. GH3/AHIII has small sample sizes for these values but for all taxonomic categories, the ratio of tooth to bone MNE is one. In GH4/AHIV, tooth MNE is higher than bone MNE for all three taxonomic categories, suggesting that teeth are better preserved than bone in this horizon. For horse and medium ungulate remains in GH5/AHV there are the same MNE values for tooth and bone, but, for hare, tooth MNE is larger than bone MNE. Finally, in GH6/AHVI, sample sizes are small but medium ungulate tooth and bone MNE values are equal (there are no horse tooth or cranial bone specimens and no hare cranial bone specimens for this horizon). In general, I find evidence that only in GH4/AHIV is the skeletal element representation affected by density mediated attrition.

4.1.2 Taxonomic Representation

In Appendix 3, Table 2 shows the NISP and MNI values of the mammalian specimens in the macrofauna from GH3/AHIII to GH6/AHVI at Langmahdhalde. GH3/AHIII has the fewest and GH4/AHIV has the most mammalian remains, although GH4/AHIV and GH5/AHV have very similar amounts. The relative abundances of each taxonomic category are similar across GH4/AHIV through GH6/AHVI. Hare, small carnivores, reindeer, and horse are the most common taxa represented throughout all horizons of the assemblage. I identified both mountain hare (*Lepus timidus*) and European hare (*Lepus europaeus*) remains in GH4/AHIV to GH6/AHVI. I made all of these identifications based on tooth morphology except one innominate from GH4/AHIV that I identified to mountain hare based on measurements (diameter of transverse condyle = 12.6 mm; maximum diameter of anterior-posterior condyle = 13.1 mm; Donard, 1982; Pelletier et al., 2015). Within small carnivores, foxes and mustelids are the most common. I could identify only one fox specimen to the species level; I assigned it to arctic fox based on tooth measurements (medial-distal = 14.2 mm; buccal-lingual = 5.4 mm; Baumann, 2016). GH3/AHIII lacks mustelid remains completely.

After small carnivores, ungulates are the most common mammals in the macrofaunal assemblage. These include reindeer, horse, red deer, chamois (*Rupicapra rupicapra*), ibex, wild cattle or bison (*Bos*/*Bison* sp.), one European elk/moose (*Alces alces*), and one roe deer (*Capreolus capreolus*). Reindeer and horse are the most common ungulates identifiable to the species-level. Reindeer specimens at site include bone, antler, and teeth. One antler fragment (Figure 6B) has an intact base, indicating that it was collected after shedding and not as a result of hunting, while another antler fragment is still attached to the braincase (Figure 6A). Horse remains include a nearly complete left mandible with *in situ* premolars and molars and a nearly complete pelvis (Figure 6C and 6D). Both of the above-mentioned antlers and the horse mandible are from GH5/AHV. The horse pelvis is from GH4/AHIV.

The mammoth (*Mammuthus primigenius*) remains at the site consist of three pieces of ivory, one from GH5/AHV and two from GH6/AHVI. There are no large carnivore remains at the site except for nine cave lion (*Panthera spelea*) specimens spread across GH3/AHIII to GH5/AHV. In all horizons, I identified most specimens to the larger body size categories of mammal, such as “small mammal.” The NISP values of these categories are primarily driven by long bone shaft fragments. For example, in GH3/AHIII, GH4/AHIV, and GH5/AHV, long bone shaft fragments make up over 80% of the NISP values for small mammals, medium mammals, and large mammals, and in GH6/AHVI long bone shaft fragments make up between 50% and 65% of the specimens.

The bird remains from the site are presented in Table 2 of Appendix 3. Again, GH4/AHIV has the largest sample size. Most of the specimens could only be identified to body size (small, medium, or large bird). The specimens that could be identified to a specific taxon are most commonly ptarmigan in GH4/AHIV through GH6/AHVI. In GH3/AHIII there are very few bird remains compared to the other horizons. As in the mammal assemblage, GH6/AHVI has at least half the number of remains as GH4/AHIV and GH5/AHV. Compared to the other horizons, GH4/AHIV has the most bird specimens that were identifiable to a specific taxon and most of these specimens are medium-sized birds such as grouse, ducks, or phasianids but there are also two stork specimens. This horizon also has the highest numbers of small birds and Passeriforms in the assemblage. In GH4/AHIV and GH5/AHV, most specimens assigned to a specific taxon are ptarmigan. Both horizons also have relatively high numbers of specimens assigned to the category “small bird.” In GH6/AHVI, four of the bird specimens are raptors: one specimen belongs to the genus *Bubo*, two are tawny owls (*Strix aluco*), and one is in the family Accipitridae. Across GH4/AHIV, GH5/AHV, and GH6/AHVI, the medium bird category has the most specimens.

Figure 6. Notable reindeer and horse specimens from Langmahdhalde. All specimens are from GH5/AHV except the horse pelvis (D), which is from GH4/AHIV. A: Reindeer antler attached to the cranium and notched at its base, the scales in the magnified photos are 1 cm long in total, figure by A. Blanco Lapaz and replicated from Wong et al. (in review; Appendix 3 (LH48/34_134). B: Reindeer antler with intact base, replicated from Wong et al. (2017; Appendix 1; LH50/39_260). C: Nearly complete left horse mandible (LH48/37_254). D: Nearly complete horse pelvis, image replicated from Wong et al. (2017; Appendix 1; LH51/37_159).

4.1.3 Taphonomy

I summarize the recorded taphonomic modifications on the macrofaunal assemblage in Table 5 of Appendix 3. Several macrofaunal specimens from GH4/AHIV, GH5/AHV, and GH6/AHVI have intensive root etching or chemical weathering visible on their surfaces, making identifications of other surface marks, such as cut marks, difficult. Root etching is more common than chemical weathering and occurs on 16.7% to 19.5% of the macrofaunal specimens, depending on horizon (Appendix 3, Table 5). Cut marks appear on less than 2% of the specimens from all horizons. I observed four cone fractures in the assemblage, two from GH4/AHIV and two from GH6/AHVI, as well as two bone negatives from cone fractures (one from GH4/AHIV and one from GH5/AHV). Spiral fractures are most common in GH3/AHIII where approximately 7% of the macrofaunal specimens have spiral fractures. In the other horizons, I observed spiral fractures on approximately 3% to 4% of the remains. There is no evidence of carnivore modification in GH3/AHIII, but bite marks are present on specimens in the other horizons (<1%), and I observed three specimens in GH6/AHVI with evidence of digestion.

Notable human modifications to reindeer and horse specimens include the nearly complete horse pelvis mentioned above (Figure 6D) that has a hack mark on the pubis, the reindeer antler attached to the braincase that has been notched near the base (Figure 6A), and a small piece of antler that has been grooved (Figure 7). There is also a left fox mandible in the assemblage with parallel cut marks on its buccal side (Figure 8) and a distal humerus of a goose (*Anser* sp.) that has blanks removed from its shaft, liking for needle-making (Figure 8).

Overall, few specimens are burned. Despite the fact that GH5/AHV has five combustion features, it is GH3/AHIII that has the highest percentage of burned specimens (9.5%). Approximately 3% of the diagnostic specimens in GH4/AHIV are burned, less than 1% are in GH5/AHV, and there are no diagnostic specimens that are burned in GH6/AHVI. The combustion features in GH5/AHV have few burned bones associated with them and most of the burned bones that are associated with the features are not diagnostic, and, therefore, I did not include them in the NISP values. In Table 6 of Appendix 3, I show the number of specimens (NSP; Lyman, 2008: 27) and the NISP of burned bones for each feature.

4.1.4 Age at Death Information

In Supplementary Table 2 of Appendix 3, I list the specimens in the macrofaunal remains that provide information on the age of death, the approximate age of these specimens, the age category, and the source I used for the age estimate. There are a few small mammal and bird specimens in this table: six juvenile hare specimens, six juvenile fox specimens, and 12 medium bird specimens with unfused bones. In GH3/AHIII, I identified a fetal pelvis, both the left and right sides, that is likely ungulate. The majority of specimens that provide aging information are reindeer or horse. I was able to assign nine of these to specific age categories. In GH4/AHIV, there are two juvenile and one adult reindeer and one old horse, and in GH6/AHVI, there is one juvenile reindeer.

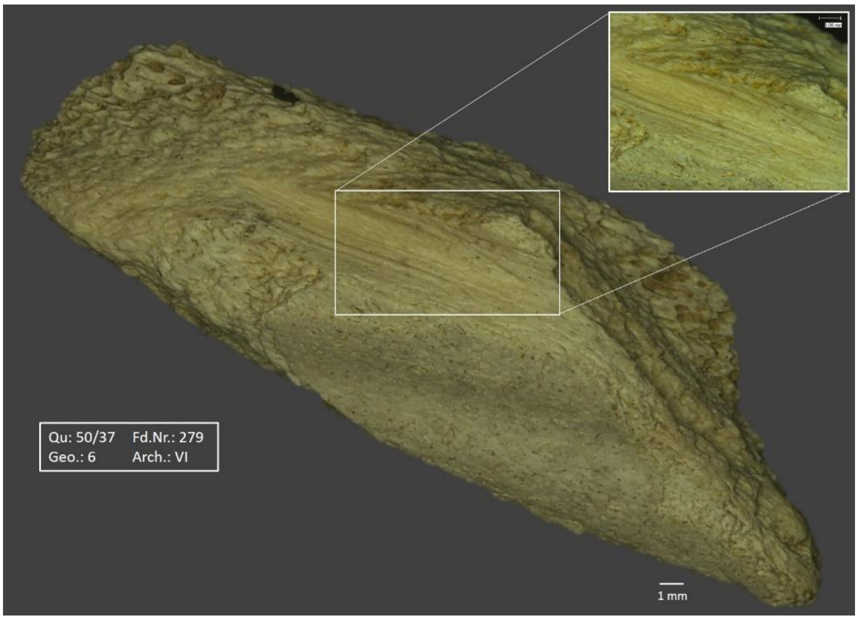

Figure 7. Antler fragment that has been grooved from GH6/AHVI (LH50/37_279). Figure by A. Blanco Lapaz.

Figure 8. Left: goose (*Anser* sp.) distal humerus with evidence of blank removable for needle production from GH4/AHIV (LH50/37_139). Right: fox (*Vulpes* sp.) left mandible with two cutmarks on the buccal side from GH4/AHIV (LH47/38_125).

4.1.5 Skeletal Element Representation

In Figure 4 of Appendix 3, I present the skeletal element representation for hare, fox, horse, reindeer, and medium ungulate for each horizon at Langmahdhalde. Note that region one is only present in the reindeer and medium ungulates, as it is horn and antler. Again, GH3/AHIII has many fewer specimens in this analysis than the other horizons. In GH4/AHIV and GH5/AHV almost all regions of hare are present in the assemblage but elements from the upper front limbs are the most common. Foxes are almost completely absent from GH3/AHIII and GH5/AHV, although in all horizons fox feet are present. In all four horizons, horse is represented by only specific elements. Lower hind elements of reindeer are always present in the macrofaunal assemblage and reindeer antler and cranial elements are present in every horizon but GH3/AHIII. In GH4/AHIV to GH6/AHVI, medium ungulates are represented by almost all anatomical regions, but neck elements are never present in the assemblage and axial elements are rare.

4.2 Stable Isotopes

I present the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ results from the horse and reindeer specimens from Langmahdhalde in Table 6 and Figure 6 of Appendix 2. The horse specimens range in $\delta^{13}C_{coll}$ values from –21.0 ‰ to –20.7 ‰ and the reindeer specimens range from –20.1 ‰ to –19.4 ‰. The $\delta^{15}N_{coll}$ values for horse range from +2.1 ‰ to +3.1 ‰ and for reindeer from +1.6 ‰ to +2.5 ‰.

Lab Number	**Coll Yield (mg/g)**	**C_{coll} (%)**	**N_{coll} (%)**	**C/N_{coll}**	**$\delta^{13}C_{coll}$ (‰)**	**$\delta^{15}N_{coll}$ (‰)**
Reindeer						
LGN-6	77.8	42.5	14.9	3.3	-19.4	1.6
LGN-9	33.4	37.3	13.1	3.3	-19.9	2.0
LGN-10	46.8	38.2	13.5	3.3	-19.9	1.8
LGN-12	89.1	40.6	14.4	3.3	-19.8	2.0
LGN-13	45.5	36.5	12.9	3.3	-19.8	2.0
LGN-14	125.8	42.1	14.8	3.3	-20.1	2.5
Horse						
LGN-4	17.1	39.0	13.8	3.3	-20.9	3.1
LGN-5	16.9	38.0	13.5	3.3	-20.7	2.3
LGN-7	45.2	35.6	12.5	3.3	-20.9	2.1
LGN-8	5.7	31.8	11.5	3.2	-20.8	2.4
LGN-11	65.2	36.8	13.1	3.3	-21.0	2.7

Table 6. Measured $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values for horse and reindeer specimens from Langmahdhalde. Further information on these specimens and their context can be found in Table 3.

4.3 Microfauna

4.3.1 Paleoenvironmental Reconstructions

There are a total of 5,144 specimens in this analysis. I present the taxonomic identifications of the microfaunal specimens from Langmahdhalde in Table 5 of Appendix 2 and Figure 4 of Appendix 2 provides photos of specimens from the assemblage belonging to the taxa that are most commonly represented. I have provided a complete description of the Langmahdhalde microfaunal assemblage in Supplementary Materials 2 of Appendix 2. This document includes further photos, habitat information, identification criteria, and lists of specimens for each taxon represented in the assemblage. I reviewed a sample of specimens that I identified as “common/field vole” and found that both species are present in every horizon and sub-layer. Common/field voles, red-backed voles (*Myodes glareolus*), narrow-headed voles (*Lasiopodomys gregalis*), and collared lemmings (*Dicrostonyx* sp.) are the most commonly represented species at the rock shelter. Common/field voles have the highest or second highest MNI values in all horizons. Red-backed voles are primarily found in GH2/AHII and GH2a/AHIIa but are present in small numbers in other horizons. Narrow-headed voles are most common in GH4/AHIV to GH6/AHVI but there is one specimen in GH3/AHIII. Collared lemmings are usually the most common species in GH3/AHIII to GH6/AHVI, only in GH4/AHIV and GH5/AHV sub-layer 1 do common/field voles have higher MNI values than collared lemmings. There is one collared lemming specimen in GH2/AHII but, as this is a Pleistocene species, I assume that this specimen is intrusive.

4.3.1.1 Species Diversity

In Table 6 of Appendix 2, I show the results of my calculations of the reciprocal of Simpson’s Diversity Index. The Holocene horizons (GH2/AHII and GH2a/AHIIa) have higher evenness values than the Pleistocene horizons, except GH3/AHIII which has the highest evenness values at Langmahdhalde. This high value in GH3/AHIII should be interpreted carefully as it may be a result of the sampling bias in this horizon and not of actual evenness values.

4.3.1.2 Bioclimatic Analysis

I report the Bioclimatic Spectra for each horizon and sub-layer at Langmahdhalde in Supplementary Materials 3 of Appendix 2. The results of the quantitative models are in Table 6 of Appendix 2 and Figure 5 of Appendix 2, while the results of the qualitative model are in Table 7 of Appendix 2. When I performed the discriminant function analysis for the qualitative model, I was not able to replicate Hernández Fernández and Peláez-Campomanes' (2003) coefficients for their rodent model (which they report in their Appendix 2.2), but I was able to confirm that the discriminant function analysis I ran in R works. The R code used to do this discriminant function analysis and further discussion of this analysis compared to that of Hernández Fernández and Peláez-Campomanes (2003) can be found in Supplementary Materials 4 of Appendix 2. It is likely that the discrepancies between my analysis and the original lie either in potential differences in the method with which data was normalized or the algorithms of SPSS (the software used for the original model), which are not publicly available.

The results of the qualitative model indicate that throughout the occupation of Langmahdhalde, climate zones VI (typical temperate climate with nemoral broadleaf-deciduous forest vegetation) and IX (polar climate with tundra vegetation) were the most common. The quantitative models show a distinct difference between Holocene (GH2/AHII and GH2a/AHIIa) and Late Glacial values (GH4/AHIV through GH6/AHVI). This is particularly visible in Figure 5 of Appendix 2. In general, I find that Holocene temperatures were warmer, winters were shorter, vegetative activity periods were longer by two to four months, and annual precipitation was higher than in the Late Glacial.

In the Late Glacial, I reconstructed mean annual temperatures between -3.2 °C and 0.3 °C, with mean temperatures of the warmest month as high as 12 °C and mean temperatures of the coldest months as low as -12 °C or -13 °C. Further, I find that Late Glacial winters lasted between three and five months, a third or more of the year, and vegetative activity periods lasted between approximately three and four months of the year. Finally, during the Late Glacial, I find that annual precipitation ranged from about 800 to 1000 mm per year. Across the Late Glacial horizons and sub-layers the quantitative models reconstruct similar climate variables, with some exceptions. GH4/AHIV has the warmest temperatures, the shortest and least intense winter, and the highest vegetative activity periods for the Late Glacial horizons and sub-layers. Further, GH6/AHVI sub-layer 1 has the lowest value for precipitation and the only non-negative value for drought.

4.3.2 Taphonomy

The taphonomic analysis of the microfauna from Langmahdhalde includes 7,861 specimens, which I present in Table 7 of Appendix 3 organized by element and horizon. This table also includes the total MNI for each horizon. I did not observe any microfaunal specimens identifiable to element in GH5/AHV sub-layer 1. This sub-layer is, therefore, absent from all tables in this section and discussions of microfaunal taphonomy. I show the number of specimens that are burned or have oxide staining in Table 8 of Appendix 3. Very few specimens are burned in the sample, only three upper molars. Oxide staining, though, is much more common and is present on 13% to 40% of the specimens, depending on the horizon. GH4/AHIV exhibits the highest amount of oxide staining (40.4%).

4.3.2.1 Skeletal Element Abundance

In Table 7 of Appendix 3, I include the relative abundance of each element by horizon and sub-layer. Based on the results of the Kendall's tau b correlations between the Langmahdhalde relative abundance data and the relative abundance data from modern predator assemblages (from Andrews, 1990: 213), I found that each horizon and sub-layer is significantly correlated with several predators. The results of all of these correlations can be found in Supplementary Table 3 of Appendix 3, while in Table 9 of Appendix 3, I report only the predator with the highest correlation coefficient from each horizon and sub-layer. Overall, the most common predators listed in Table 9 of Appendix 3 are owls, including little owls (*Athene noctua*), Eurasian eagle owls (*Bubo bubo*), short-eared owls (*Asio flammeus*), and great grey owls (*Strix nebulosa*). GH2/AHII, though, is most strongly correlated with hen harrier (*Circus cyaneus*), and three other horizons are most strongly correlated with small carnivores: red fox (*Vulpes vulpes*; GH3/AHIII and GH5/AHV sub-layer 2) and pine marten (*Martes martes*; GH2a/AHIIa).

4.3.2.2 Breakage

I provide the representation of long bone portions in the microfauna in Table 10 of Appendix 3. There are few complete specimens in the sample and none in GH3/AHIII. The highest percentage of complete long bones comes from the humeri in GH5/AHV sub-layer 2 (20% of the sample). In the Holocene horizons (GH2/AHII and GH2a/AHIIa), distal portions are the most common, while proximal portions are the most common in GH3/AHIII. In the remaining horizons, proximal and distal ends are similarly represented and make up approximately 30% to 45% of the long bones.

Table 11 of Appendix 3 reports information on maxilla and mandible breakage including breakage categories, tooth loss, and the relative proportion of isolated teeth. There are also few complete mandibles and maxillae in the sample. Most mandibles have broken inferior borders and are missing their ascending rami. Maxillae are particularly highly fragmented across all horizons and sub-layers; most are missing their zygomatic arch, and none are present in skulls. Molar and incisor loss are low (almost all values are below 50%), reflecting that few alveolar sockets are preserved. Further, in all horizons but GH4/AHIV, the relative proportion of isolated molars is above 100%, indicating that in most horizons and sub-layers there is substantial tooth row breakage. This is particularly true for GH2/AHII, which has the highest relative proportion of isolated molars: 308.3%. My results also demonstrate that a considerable number of mandibles and maxillae in the sample have anterior breakage. All horizons have relative proportions of isolated incisors over 11%. The highest values are in GH6/AHVI sub-layers 1 and 2 (428.6% and 339.1% respectively).

4.3.2.3 Digestion

In Figure 9, I provide photographs of some examples of digestion on microfauna specimens from Langmahdhalde. I quantify the amount of digestion in the microfaunal sample in the following tables of Appendix 3: Table 12 has information on long bone digestion, Table 13 has information on incisor digestion, and Table 14 has information on molar digestion. The majority of the long bones, incisors, and molars in the sample are not digested. The only exception is in GH2/AHII where the most common level of digestion is moderate in the long bones. In GH2a/AHIIa, only two long bones are digested, although the sample size is small in this horizon. I observed no digestion on any long bone specimens from GH3/AHIII. In all horizons and sub-layers from GH4/AHIV to GH6/AHVI, there are long bone specimens with light, medium, and heavy digestion, except in GH5/AHV sub-layer 2. Approximately 40% of the long bones from GH4/AHIV are digested, light and medium digestion are the most common. GH5/AHV and GH6/AHVI have long bones with similar proportions of digestion-level categories (light to extreme); light digestion is the most common, followed by medium. The majority of the teeth in the sample are not digested. If they are digested, they usually have light digestion. No *in situ* incisors are digested. There are four isolated incisors (one from GH4/AHIV and three from GH5/AHV sub-layer 6) and three molars (from GH5/AHV sub-layers 4 and 6 and GH6/AHVI sub-layer 2) in the sample that are extremely digested. I observed very few *in situ* molars and, as a result, I can say little regarding digestion on *in situ* versus isolated molars.

Figure 9. Examples of microfaunal specimens from Langmahdhalde that have been digested. Specimen numbers and scales are specified in each photo. A: proximal ulna with light digestion and “etching of the epiphyseal line” visible. B: three distal humeri with various levels of digestion, specimen on the left and in the middle have moderate digestion (and breakage) and the specimen on the right has light digestion (and breakage). C: proximal femur with moderate digestion. D: incisors with light digestion. E: *M. arvalis/agrestis* right lower first molar with light digestion (lingual side). F: *M. arvalis/agrestis* right lower first molar with moderate digestion (lingual side). Photos taken with Zeiss SteREO Discovery V8.

Chapter 5: Discussion

5.1 Human Use of Langmahdhalde

This dissertation represents one of the first analyses in decades of newly excavated archaeological material from the Swabian Jura that is dated to the Magdalenian. The macrofaunal remains from Langmahdhalde reinforce our current understanding of human subsistence behavior during the Magdalenian in southwestern Germany. I find that people using the rock shelter primarily hunted horse and reindeer, large, migratory animals that travel in herds. My work also demonstrates, through the identification of collected and worked antler at the site, that reindeer were a source of raw material as well as food. Smaller game, like hare, fox, and ptarmigan, are also present at the site. Based on the placement of the cutmarks on the fox mandible, it is likely that the people occupying Langmahdhalde skinned foxes as a source of fur (Binford, 1981). The faunal remains indicate that butchering and marrow extraction occurred at the site, as well as other non-subsistence practices such as antler preparation and needle-making.

The faunal remains and other artifacts at Langmahdhalde seem to suggest that the site was not occupied by large groups of people or for long periods of time. The site is reminiscent of Weniger's (1989, 1987) medium site category, or a “residential camp of local groups,” as it has evidence of antler and needle working, similar amounts of reindeer and horse remains, and combustion features. Further, Weniger (1987) states that medium sites usually have between 30 and 50 cores and several hundred lithic tools. At Langmahdhalde, excavators have recovered approximately 30 cores and 170 stone tools. Although, as I mentioned in the introduction, I find these categories useful for discussing the archaeological record but less useful for interpretations of human behavior. Weniger’s system, therefore, benefits from more detailed discussions of local ecological conditions, such as those below.

I find little evidence for the season of occupation at the site except the fetal pelvis in GH3/AHIII, which suggests a late winter or spring occupation, as most ungulates give birth in spring or summer. Although sample sizes for the MAU values are small in my examination of skeletal part representation of the macrofaunal remains, it is possible that the people using the rock shelter transported only certain parts of fox, horse, and reindeer back to the site. Hares, on the other hand, appear to have been transported to the site whole. Larger sample sizes are necessary in order to make meaningful interpretations of selective hunting from these results. It is also likely that the results from GH4/AHIV reflect the differential preservation of more dense elements, not human decision-making. Finally, I find that, at least during the occupations represented by GH4/AHIV and GH6/AHVI, hunters took juvenile horse and reindeer individuals. There is also evidence that they took adult and old individuals.

GH4/AHIV and GH5/AHV potentially represent the most intensive period of use of Langmahdhalde, as all combustion features and most worked bone, cut marks, and cone fractures and negatives come from these horizons. However, my results cannot speak to whether this means occupation for longer periods of time or more repeated use of the rock shelter. GH3/AHIII, which represents the end of the Late Glacial sequence at the site, has the smallest sample sizes in the macro- and microfaunal analyses that I present here. In terms of the microfauna and remains of smaller animals and elements, this is probably a reflection of the sampling bias in the water screening of this horizon. The near absence of archaeological remains from this horizon, though, suggests that it could represent a decline or end in the use of the rock shelter by Late Glacial humans. Geoarchaeological assessments of the site are necessary, though, to establish whether natural processes, such as erosion or increased sedimentation, are the cause of this decrease in artifacts.

5.2 Accumulators of the microfaunal remains

Below, I discuss, by horizon and sub-layer, which predator likely deposited the microfaunal remains at Langmahdhalde. To do so, I rely on the summary of predator modifications on micromammalian assemblages in Andrews (1990: 88-90) and Table 12 of Rhodes et al. (2019), which summarizes the predator categories based on digestive etching.

The results of the taphonomic analysis of the Langmahdhalde microfauna indicate that more than one predator likely deposited the remains of each horizon and sub-layer at the site. The correlations between the relative abundance of skeletal elements from known predator assemblages and the Langmahdhalde material showed that each horizon was significantly correlated with more than one predator. Further, in all horizons and sub-layers, except GH2/AHII, most of the remains were not digested, suggesting that a category 1 predator was responsible for the microfaunal accumulations at the rock shelter. However, this does not explain the high levels of breakage in the assemblage or the presence of a few specimens with extreme levels of digestion. I cannot eliminate the possibility that breakage could be a result of trampling or water screening, so my discussion below focuses more on digestion than levels of breakage.

In GH2/AHII, the analysis suggests that both a category 2 and category 3 predator are responsible for the assemblage. The percentage of incisors that are digested and the prevalence of moderate levels of digestion on long bones falls in line with a category 2 predator, but the percentage of molars and long bones digested indicate a category 3 predator. Although the relative abundance of skeletal elements for this horizon is correlated most strongly with hen harrier, a category 4 predator, the data overwhelmingly suggest that the microfauna from this horizon was deposited by an Eurasian eagle owl, tawny owl, snowy owl, short-eared owl, or barn owl. Most of these owls feed preferentially on Arvicolids and have hunting ranges within a maximum of 10 km from their nesting sites (Andrews 1990: 178-193). The tawny owl and Eurasian eagle owl, though, are both opportunistic feeders whose prey remains reflect the natural environment quite well (Andrews 1990: 188-193). Therefore, Arvicolids are likely overrepresented in this horizon compared to their abundances on the landscape but, because of the contribution of the opportunistic feeds, the presence or absence of microfauna taxa in the assemblage is likely a good indicator of their presence or absence on the natural landscape.

In both GH2a/AHIIa and GH5/AHV sub-layer 5, the percentage of incisors digested and the percentage of long bones digested suggest a category 2 predator, while the percentage of molars digested suggest a category 3 predator. Further, the majority of the molars, incisors, and long bones in both show no evidence of digestion. I, therefore, conclude that owls such as the long-eared owl, great grey owl, Eurasian eagle owl, tawny owl, barn owl, short-eared owl, and snowy owl most likely deposited the microfaunal assemblages of GH2a/AHIIa and GH5/AHV sub-layer 5. This is similar to GH2/AHII, but with the addition of the long-eared owl, a selective hunter that prefers Arvicolid prey and has a large hunting range of ten times that of the tawny owl (Andrews 1990: 182-184). Like in GH2/AHII, then, Arvicolids may be overrepresented in the assemblages of these two horizons compared to their relative abundance on the landscape, but presence/absence data for the taxa in these assemblages likely accurately reflect the present/absence of the taxa on the landscape.

GH3/AHIII and GH6/AHVI sub-layer 2 have similar results in terms of the category of predator suggested by the levels of digestion on the microfaunal remains. Both show low percentages of digestion on incisors and long bones, suggesting a category 1 predator and higher percentages of molar digestion (30% to 40%) that are more characteristic of a category 3 or 4 predator. These horizons, therefore, appear to be similar to the three discussed above. However, GH6/AHVI sub-layer 2 also has one molar that I categorized as having extreme digestion, indicating that a category 5 predator, such as a mammalian carnivore or hen harrier, also contributed to the microfaunal assemblage in this sub-layer. Possibly, then, in GH6/AHVI sub-layer 2, it is the contribution of a high-category predator that drove the higher percentage of molars digested and a category 1 predator was responsible for the rest of the assemblage. In this case, a high-modifying predator, such as a mammalian carnivore or hen harrier, and a low-modifying predator, such as a barn owl, snowy old, long-eared owl, great grey owl, or short-eared owl likely deposited the assemblage. As mentioned above, these owls preferentially prey on Arvicolids, although studies have found that the great grey owl may prey on enough other taxa that the presence/absence of taxa in its prey remains can reflect the natural composition of the environment (Andrews 1990: 178-185, 189-191). Small mammalian predators and hen harriers do not generally create assemblages that are a good reflection of prey available on the landscape (Andrews 1990: 196, 206-208). For GH6/AHVI sub-layer 2, then, taxa that were present on the landscape may be missing from the microfaunal assemblage.

In both GH4/AHIV and GH5/AHV sub-layer 4, the most common digestion category and the percentage of incisors digested suggests a category 1 predator, while the percentage of molars and long bones digested suggests a category 2 predator. The relative abundance of skeletal elements for both GH4/AHIV and GH5/AHV sub-layer 4 are also highly correlated with that of little owls. These assemblages, then, like GH2/AHII and GH2a/AHIIa were likely deposited by owls that are both generalists and specialists. In both GH4/AHIV and GH5/AHV sub-layer 4, there is one tooth with extreme digestion so it is likely that a mammalian predator or hen harrier was also involved in accumulating the microfaunal remains. Again, in these horizons, presence/absence data in the microfaunal assemblage more accurately reflect the natural environment than abundance data.

GH5/AHV sub-layer 2 seems to have been deposited by a mix of category 1 predators, based on the most common level of digestion, and category 2 predators, based on the percentage of digestion on teeth and long bones. Suggesting that, like in GH6/AHVI sub-layer 2, owls such as long-eared owls, great grey owls, snowy owls, barn owls, and short-eared owls accumulated these rodent and insectivore remains. Again, these birds prefer to prey on Arvicolids. Additionally, the relative abundance of skeletal elements in this sub-layer is most strongly correlated with assemblages deposited by red foxes, whose prey assemblages rarely reflect natural abundances of prey taxa (Andrews, 1990: 206-207).

Finally, there are four sub-layers with microfaunal remains that have similar taphonomic patterns: GH5/AHV sub-layers 3 and 6 and GH6/AHVI sub-layers 1 and 3. In these sub-layers, the percentage of incisors digested and the most common level of digestion are most consistent with a category 1 predator, while the percentage of molar digestion is more characteristic of a category 3 predator and the percentage of long bones digested is more characteristic of a category 2 predator. These sub-layers are, thus, like most of the other horizons and seem to have been deposited by both specialist hunters, such as barn and short-eared owls, and opportunistic hunters, such as tawny and Eurasian eagle owls. In GH5/AHV sub-layer 6, there are three molars that are extremely digested, suggesting that a category 5 predator also contributed to this assemblage.

The diets of several of the above-mentioned predators include birds (e.g. long-eared owls, short-eared owls, and tawny owls) and several of the owls, such as the Eurasian eagle owl, hunt Lagomorphs (Andrews, 1990). Therefore, it is possible that avian or mammalian predators, not humans, deposited the small birds and young small mammals at the rock shelter. No small birds or young small mammals are burned or have evidence of human modification in the assemblage, but there are five hare specimens that have bite or puncture marks.

In conclusion, it seems that in all horizons and sub-layers of Langmahdhalde, except GH5/AHV sub-layer 2 and GH6/AHVI sub-layer 2, analyses that rely on the presence or absence of taxa are more accurate than those based on taxonomic abundance. As the BA uses the presence or absence of mammalian species in fossil assemblages to reconstruct past environments, my taphonomic analysis of the microfauna suggests that the interpretive power of these reconstructions is high. For GH5/AHV sub-layer 2 and GH6/AHVI sub-layer 2, though, I find that rodents and insectivores that were present on the landscape are likely missing from the remains of these sub-layers. Indeed, GH6/AHVI sub-layer 2 has the lowest amount of taxonomic diversity at the site, although taxonomic diversity in GH5/AHV sub-layer 2 is similar to those of the other sub-layers of GH5/AHV and GH6/AHVI and that of GH4/AHIV (Appendix 2, Table 5). Therefore, the paleoenvironmental reconstructions from these sub-layers are probably not as accurate as those from the rest of the site.

Finally, the taphonomic analysis of the microfauna has implications for the spatial scale of the paleoenvironmental reconstructions. Long-eared owls, great grey owls, and small mammals, such as foxes and pine martens, have large territory and hunting range sizes. Long-eared owl territories can be as large as 750 hectares, while pine martens have territories 30 km^2 in size (Andrews 1990: 182-184, 206-208). Great grey owls have ranges between 50 and 70 km^2 (Bull et al., 1988; Chang and Wiebe, 2018). Further, tawny owls, short-eared owls, Eurasian eagle owls, and hen harriers, likely accumulators for most of the horizons and sub-layers, have ranges of less than 15 km^2 from their nesting site (Village 1987; Bull et al. 1988; Andrews 1990: 178-197). This suggests that the paleoenvironmental reconstructions from horizons and sub-layers associated with long-eared owls or mammalian carnivores (GH2a/AHIIa, GH4/AHIV, GH5/AHV sub-layers 4 to 6, and GH6/AHVI sub-layer 2) apply to within 30 km^2 of the rock shelter, while reconstructions from the other horizons and sub-layers of the site apply to within 70 km^2.

5.3 Late Glacial Paleoecology in the Lone Valley

5.3.1 Environments in the Lone Valley

One of the reasons the BA is more powerful than the indicator taxon method is that it allows researchers to compare their reconstructed climatic variables to modern climatic variables. In Figure 5 of Appendix 2, I have added modern temperature and precipitation data to the graphs of the results of the quantitative models. These data are from a weather station in Hermaringen, approximately 6 km northeast from Langmahdhalde (station "Hermaringen-Allewind," ID# 7331), and are based on temperature and precipitation from the past ten years (from 2009 to 2018; data downloaded on 8 November 2019 from the Deutscher Wetterdienst, Climate Data Center version 2.0.v1907). Comparing the Langmahdhalde results to these data, I find that temperatures today are generally warmer than those I have reconstructed from Langmahdhalde, the only exception being the mean temperature of the coldest month from GH2/AHII. This comparison also shows that modern precipitation in the region is lower than any that I have reconstructed from Langmahdhalde.

In order to explore whether the Late Glacial environments of the Lone Valley are similar to modern environments, I also compare the climate variables from those horizons and sub-layers assigned to zone IX (polar climates and tundra vegetation; GH3/AHIII, GH5/AHV sub-layers 5 and 6, and GH6/AHVI sub-layers 2 and 3) to those same climate variables from today's polar regions. In general, the temperatures that I reconstruct using the BA for these horizons and sub-layers fall within the range of modern polar climates, except for the mean temperature of the coldest month. Today winter temperatures can average approximately -34°C in polar regions ("The Tundra Biome," 2004), 20°C colder than the values reconstructed for these horizons and sub-layers at Langmahdhalde. Further, I find that vegetative activity periods in modern polar regions are much shorter, only about two to two and a half months (Woodward, 2012), than those I report here for the Late Glacial. This short growing season in modern polar environments is partially responsible for the treeless landscape in these regions (Grace et al., 2002; Payer et al., 2013) so it may be that the longer vegetative activity periods in the Lone Valley promoted tree growth during the Late Glacial.

The precipitation values from the Late Glacial horizons and sub-layers at Langmahdhalde are much higher than those of the modern tundra, which receive less than 127 mm of precipitation per year (Woodward, 2012). But the multiple linear regression used to reconstruct precipitation in the BA has an r^2 and standard error value that suggest it is not as reliable as the other multiple linear regression models (see Appendix 2, Supplementary Materials 1). Taking all my data into account, though, it is likely that there were higher amounts of precipitation during the Late Glacial in the Lone Valley. This is reflected in the results of the qualitative model of the BA, which suggests that the environment was not uniform and may have even included forests. Additionally, the standard error for the multiple linear regression for precipitation is 471 mm, which indicates that the precipitation values from Langmahdhalde could have actually been about half of what I predict. This would still be more precipitation than in modern tundra environments, which, along with the evidence for longer vegetative activity periods and the results of the qualitative model, supports the presence of trees and/or more densely vegetated areas on the landscape.

I expected the qualitative model to predict zones VII, VIII, or IX for the horizons and sub-layers that are dated to the Late Glacial because this time period in Central Europe has generally been characterized as steppe or tundra (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989). This is the case for GH3, two sub-layers of GH5, and two sub-layers of GH6, but the model assigned the remaining horizon and sub-layers to zone VI, nemoral broadleaf-deciduous forest. The qualitative model, therefore, does not predict one continuous climate in the Lone Valley during the Late Glacial and even suggests that temperature forests were present. These results could be interpreted as change over time, but, as I discussed in the introduction, the climatic changes during the Late Glacial were not continuous, and I argue that it is more likely that these results suggest that a mosaic of environments existed across the landscape that allowed temperate mammalian fauna to occasionally enter the region.

Upon initial inspection, the similarity of the values from the quantitative models and the reciprocal of Simpson’s Diversity index across GH4/AHIV, GH5/AHV, and GH6/AHVI seem to indicate that the environment was uniform. Further, the reindeer and horse $\delta^{13}C_{coll}$ values from Langmahdhalde support the idea that the environment was open, as they are all higher than –21‰ (Table 6; Bocherens, 2003; Drucker et al., 2008). But when we take scale into account, a more complex environmental reconstruction emerges. The quantitative models of the BA predict climate variables at the annual scale, making interpretations of seasonal climatic variables, like precipitation, difficult. Further, the stable isotope results from bone collagen are time-averaged over the lifetime of the individual, and thus do not operate at the same spatial or temporal scale as the microfaunal results. Together, the results of the stable isotope analysis and quantitative models suggest what past studies have found: Central Europe had a polar climate, low faunal diversity, and an open environment. But my dissertation also takes all of these data from one site, considers them together, and adds the qualitative model of the BA. Combined, my results suggest that the landscape of the Lone Valley during the Late Glacial was more heterogenous than today’s polar regions.

Hernández Fernández (2006) also found discrepancies between the quantitative and qualitative results of the BA that he applied to rodent remains from eastern France. He discusses two possible explanations for this: (1) the presence of birch trees (*Betula* sp.) in the environment and (2) different concentrations of atmospheric CO_2 in the past. Birch can provoke vegetative growth similar to that in nemoral forests when it is abundant. This may have some explanatory power for the conditions in the Late Glacial of the Swabian Jura as pollen records from southwest Germany demonstrate that birch was present (Maier, 2015: 69) and even increasing in some areas (Duprat-Oualid et al., 2017) during the time of occupation at Langmahdhalde. In regard to atmospheric CO_2, broadleaf-deciduous forests can develop even if temperatures are colder than those that are normally associated with this type of vegetation. When atmospheric levels of CO_2 are lower, the optimal temperature for photosynthesis in C3 plants is also lower (Cowling and Sykes, 1999), which could allow deciduous forests to be present in regions with colder temperatures. This situation is plausible, as Figge and White (1995) find a decrease in atmospheric CO_2 levels at about 12,200 uncal yr BP (~14,183 to 14,003 cal yr BP; Bronk Ramsey, 2017, 2009; Reimer et al., 2013).

5.3.2 Ungulates on the landscape

The above environmental reconstruction helps to explain the presence of a European elk/moose phalanx in the Langmahdhalde assemblage. Modern European elk/moose prefer deciduous and mixed forests, but can penetrate deep into the tundra in the summer (Nygrén, 1986). The more heterogeneous environments in the Lone Valley may have allowed some individuals of this species to occupy the region, at least seasonally. There is also a roe deer specimen in GH3/AHIII. Today, this species prefers to live in agricultural areas or wooded areas that provide some cover (Stubbe, 1999; Walker, 1968: 1404), and they are “very selective feeders” that prefer energy-rich food which has a high water content (Sempere et al., 1996). They are, therefore, rare in Central European assemblages dating to the Magdalenian as there were no large forests and not enough of their preferred food during this time. It is possible that this specimen is younger than the date from GH3/AHIII as it is in a different area of the site, where the stratigraphy is less clear and it is located at the top of this horizon while the date was taken at the bottom.

The $\delta^{13}C_{coll}$ values from Late Glacial reindeer seem to be tracking a transition in the diets of these animals in southern Central Europe (Drucker et al., 2012). There appears to be a decrease in lichens in their diets as more vascular plants expand into the region. The $\delta^{13}C_{coll}$ values from reindeer at Langmahdhalde, the results of the qualitative model of the BA, and the longer vegetative activity periods and higher precipitation values I reconstruct with the quantitative models of the BA further support the idea that there was a slow loss of preferred habitat for this species.

My results from the stable isotope analysis of bone collagen from reindeer and horse at Langmahdhalde also provide insight into large ungulate ecology in different regions during the Late Glacial. In Figure 6 of Appendix 2, I present the Langmahdhalde results compared to stable isotope values of horse and reindeer from other sites in the Swabian Jura and Switzerland, all dated to the same period of time. The other sites include Petersfels, Schussenquelle, Felsställe, and Geißenklösterle from the Swabian Jura and Kesslerloch and Champréveyres from Switzerland (see Figure 1 of Appendix 2 for a map of the location of these sites). The data from these other sites can be found in Tables 4 and 8 of Appendix 2.

Figure 6 of Appendix 2 suggests that reindeer and horse were behaving differently during the Late Glacial. Reindeer values from all of the sites overlap in distribution, while the horse values cluster by region. I assume, therefore, that the reindeer in both regions exploited similar niches and had similar subsistence strategies but that horse populations were more flexible and exploited different niches based on local availability of resources. This suggest that horse stable isotope values are likely better indicators of local environmental conditions than reindeer values at this time. This differentiation of horse values is particularly interesting because Kesslerloch is geographically closer to the Swabian Jura than to Champréveyres.

It is the $\delta^{15}N_{coll}$ stable isotope values of horse that reflect this distinction between the Swiss and Swabian Jura specimens the strongest. These $\delta^{15}N_{coll}$ stable isotope values do not overlap at all: the values from the Swabian Jura range from +2.1 to +4.5 ‰ while the values from Kesslerloch and Champréveyres range from +1.3 to +1.7 ‰. $\delta^{15}N_{coll}$ values from the Late Glacial are likely a reflection of soil activity (Drucker et al., 2012). During permafrost conditions, as are present in tundra environments and, in particular, areas close to glacial fronts, organisms in the soil are not very active. This means that the $\delta^{15}N_{coll}$ values of the soil are lower and animals that eat plants from areas with these conditions will also have lower $\delta^{15}N_{coll}$ values (Drucker et al., 2012). During the Late Glacial, Kesslerloch and Champréveyres were closer to the alpine glacier than the sites in the Swabian Jura (Becker et al., 2016), suggesting that the separation of horse $\delta^{15}N_{coll}$ values may reflect this proximity to the glacier.

5.3.3 Environmental diversity

The above discussion of the environmental and stable isotope results from Langmahdhalde indicates that the environment of the Lone Valley during the Late Glacial was more heterogeneous than modern polar environments. I argue that the valley was generally an open tundra but also included areas with denser vegetation that likely included trees, such as birch. More heterogeneous habitats generally have higher levels of species diversity (Ceballos et al., 1999; Cramer and Willig, 2002; Ganzhorn et al., 1997; MacArthur and MacArthur, 1961; Ricklefs and Relyea, 2014; Southwell et al., 1999; Williams et al., 2002). I would, therefore, expect that the landscape surrounding Langmahdhalde during the Late Glacial had a higher diversity of species than modern polar regions, which have a low diversity of mammals, amphibians, reptiles, most birds, and plants (Begon et al., 1990: 831; Payer et al., 2013). Lower species diversity in the modern polar regions is driven by extreme seasonality, a short growing season, the overall harshness of the climate, and widespread ice cover (Payer et al., 2013). The longer growing season (vegetative activity period) recorded in the Langmahdhalde remains supports the idea that the Lone Valley had a higher species diversity during the Late Glacial than do modern polar regions. The Reciprocal of Simpson's Diversity Index results that I report above do show higher levels of rodent and insectivore diversity in GH5 sub-layers 1 and 4, where the values are as high as those in the Holocene horizons (Appendix 2, Table 6). This heterogeneous environment was also probably more productive and provided a wider range of resources, which could have further promoted species diversity (Begon et al., 1990: 825).

5.4 Recolonization of the Swabian Jura During the Magdalenian

Taller et al. (2014) have shown that Magdalenian peoples recolonized the Swabian Jura during GS-2a (the "Pleniglacial") and have suggested that these people moved into this region as a result of population growth and their adaptation to specific environments, meaning steppe and tundra. The paleoenvironmental reconstructions I present here add more detail to this picture. In this dissertation, I have found evidence that the Late Glacial of the Lone Valley, and possibly the Swabian Jura as a whole, had environments that were more heterogeneous than modern polar regions, likely as a result of higher levels of precipitation, shorter winters, and longer periods of vegetative activity. This may have been one of the reasons that human resettlement of the region was successful.

It is even possible that the Lone Valley offered Magdalenian hunter-gatherers more resources than did areas to the west, where the colonizers originated. In the Swiss Jura, there are several Magdalenian sites that were occupied before the Swabian Jura, such as Kesslerloch and Champréveyres. As discussed above, these sites were closer to the front of the alpine glacier than the Swabian Jura was during the Late Glacial (Becker et al., 2016), as is reflected in the $\delta^{15}N_{coll}$ values of horse remains from both regions. Further, during the recolonization of the Swabian Jura (and most of Central Europe), paleoenvironmental studies of the Swiss Jura have indicated that it was a cold, open grassland with alpine and steppe vegetation. Leesch et al. (2012) summarize several pollen analyses and explain that from approximately 17,500 to 15,800 cal yr BP (local pollen assemblage zone CHb-1b), pollens are primarily "arctic alpine heliophilous flora" and the region was "grassland with alpine and steppe herbs." Additionally, in a study of environmental conditions during the Magdalenian and Azilian at Champréveyres, Coope and Elias (2000) emphasize the severity of climate conditions during the Magdalenian occupation of the site. They find that the landscape was open and patchy with few trees with mean temperatures of the warmest month between 8°C and 10°C and mean temperatures of the coldest month between -15^{o}C and -25^{o}C during the Magdalenian occupation. These temperature reconstructions are several degrees (as many as 12^{o}C) colder than those I reconstruct here using the microfauna at Langmahdhalde. This is not to suggest that environmental conditions, as opposed to population growth, were the motivation for Magdalenian expansion into Central Europe, only that the Swabian Jura, or at least the Lone Valley, had a different type of environmental situation during this period than the Swiss Jura.

I, therefore, suggest that Magdalenian peoples moving into the Swabian Jura from the west encountered a higher diversity of resources stemming from patches of denser vegetation. Further, these patches of denser vegetation likely included stands of trees and encouraged growth of associated vegetative communities, providing new niches for mammalian species that are not usually associated with tundra environments, such as red deer or European elk/moose. The diversity of game animals and vegetative resources on the landscape would have made the Lone Valley an attractive place to settle for Magdalenian hunter-gatherers expanding into new territories.

Chapter 6: Conclusions

In this dissertation, I present my results from a multi-method analysis of the faunal remains from Langmahdhalde, a newly discovered Magdalenian rock shelter in the Lone Valley of the Swabian Jura, southwestern Germany. These results come from a traditional zooarchaeological analysis of the macrofaunal remains, a taphonomic analysis of the microfaunal remains, and paleoenvironmental reconstructions based on microfauna and stable isotope analyses of horse and reindeer bone collagen. This work is one of the first studies of newly excavated remains from Magdalenian contexts in the Swabian Jura in decades. I find that human subsistence behavior at the rock shelter is consistent with current understandings of human subsistence behavior in Central Europe. The most common game animals during this time were horse and reindeer. Horse appear to have been adapted to local environmental conditions, whereas reindeer were adapted to more specific habitats that were moving northward. Importantly, I also provide some of the first paleoenvironmental reconstructions for the Late Glacial that are specific to the Swabian Jura. I argue that Magdalenian hunter-gatherers encountered a relatively diverse landscape in the Lone Valley, compared to modern tundra environments, that had a higher diversity of plant and animal resources. This level of resolution in paleoecological interpretations will, with the addition of more data, help to build a better understanding of landscape use by Magdalenian hunter-gatherers in the Swabian Jura, a particularly relevant research question for human behavior during times of large-scale climatic change.

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Appendix 1

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Human Subsistence and Environment during the Magdalenian at Langmahdhalde: Evidence from a new Rock Shelter in the Lone Valley, Southwest Germany

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Abstract: *The Magdalenian assemblages of southwestern Germany offer insights into human behavior, subsistence, art, and mobility. Work at Langmahdhalde, a newly excavated Magdalenian rock shelter, has demonstrated the potential of its assemblages to continue this tradition using new tools and methods. Here, we present a preliminary study of the Magdalenian faunal assemblages from the site and discuss how these assemblages will contribute to our current understanding of human subsistence and environmental change at the end of the Pleistocene. We find that a significant portion of the macromammal assemblage at the site is a result of human activity. We also find that the large microvertebrate assemblage at the site is ideal for paleoenvironmental reconstruction and reflects large-scale environmental change from the late Pleistocene to early Holocene. These assemblages have the potential to address questions of Magdalenian settlement patterns in the Swabian Jura and to reconstruct the local paleoenvironment.*

Keywords: *Swabian Jura, rock shelter, Late Pleistocene, Holocene, Magdalenian, fauna, paleoenvironment*

Menschliche Subsistenz und Umwelt im Magdalénien der Langmahdhalde: Zeugnisse aus einem neuen Felsschutzdach im Lonetal, Südwestdeutschland

Zusammenfassung: Die Magdalénieninventare aus Südwestdeutschland gewähren Einblicke in Verhaltensweisen, Subsistenz, Kunst und Mobilität von Menschen. Arbeiten an der Langmahdhalde, einem neu entdeckten Felsschutzdach im Lonetal mit Funden und Befunden aus dem Magdalénien, erweisen das Potential der Fundstelle, diesen Sachverhalt unter Nutzung neuer Auswertungswerkzeuge und Methoden zu untermauern. Der Beitrag präsentiert eine vorläufige Untersuchung der magdalénienzeitlichen Fauneninventare aus der Fundstelle und legt dar, in welcher Weise diese Inventare zu unserem gegenwärtigen Verständnis der menschlichen Subsistenz und des Umweltwandels am Ende des Pleistozäns beitragen können. Es zeigt sich, dass ein nennenswerter Anteil des Großsäugerinventars aus der Fundstelle auf menschliche Aktivitäten zurückgeht. Es zeigt sich ebenso, dass das Inventar der größeren Kleinsäuger aus der Fundstelle ideal für Rekonstruktionen der Paläoumwelt ist, und dass die Vergesellschaftung dieser Tiere den großmaßstäblichen Umweltwandel vom späten Pleistozän zum frühen

Holozän widerspiegelt. Diese Fauneninventare besitzen das Potential, Fragen zu Siedlungsmustern im Magdalénien der Schwäbischen Alb anzugehen und die Paläoumwelt der Region zu rekonstruieren.

Schlagwörter: Schwäbische Alb, Felsschutzdach, Spätpleistozän, Holozän, Magdalénien, Fauna, Paläoumwelt

Introduction

The German Magdalenian is a dynamic cultural period characterized by the reintroduction of human populations to previously uninhabited regions and a subsistence focus on large game. This cultural period occurs after the Last Glacial Maximum (LGM), when climates are unstable and characterized by both warming and cooling events, a rapid retreat of glaciers just after the LGM, and eventual climatic amelioration that included a slow return of forests and the development of rich grasslands (Frenzel 1983; Weniger 1989; von Koenigswald 2003; Otte 2009; Maier 2015). Overall, these changes led to an increase in biodiversity across southern Germany that is reflected in the paleontological, paleobotanical, and archaeological records (von Koenigswald 2003; Maier 2015). Central European human subsistence strategies during this time are generally focused on reindeer (*Rangifer tarandus*) and horse (*Equus ferus*; Jochim et al. 1999; Maier 2015), but continue to broaden, with an increased intake of small game, plant, and fresh water resources (Weniger 1989; Stiner and Munro 2002; von Koenigswald 2003; Conard et al. 2013).

The Magdalenian of southwestern Germany has several well-studied sites, including those from Petersfels, Brillenhöhle, Schmiechenfels, Schussenquelle, and Hohle Fels. These assemblages are characterized by blade industries, bone tools, reindeer antler, art objects made of bone, antler, stone, and shell, and few ivory artifacts compared to earlier Upper Paleolithic assemblages (Schmidt 1912; Eriksen 1991; Maier 2015). Magdalenian archaeofaunal assemblages from this region demonstrate human subsistence strategies that fall in line with trends seen throughout Central Europe: reindeer- or horse-dominated diets with evidence of broadening (Schmidt 1912; Eriksen 1991; Napierala et al. 2014; Maier 2015). For example, Petersfels and Brillenhöhle have some of the largest Magdalenian faunal assemblages in southwestern Germany. Both large game assemblages are dominated by horse and reindeer specimens, and both assemblages have an abundance of hare (*Lepus* sp.) and ptarmigan (*Lagopus lagopus*) remains (Peters 1930; Boessneck and von den Driesch 1973, tables 1 and 2; Albrecht 1979; Albrecht and Hahn 1991).

The Paleolithic caves and rock shelters of the Swabian Jura of southwest Germany are some of the best studied archaeological sites in Europe and have been explored archaeologically since the 1860s (Schmidt 1912; Weniger 1989; Conard and Bolus 2006; Taller et al. 2014). Fraas' excavation of the late Magdalenian site Schussenquelle in 1866 (Fraas 1867; Schuler 1994) is largely considered the first systematic scientific Paleolithic excavation in Central Europe. Other Magdalenian sites in the region include Vogelherd, Hohlenstein, and Bockstein in the Lone Valley, Brillenhöhle, Geißenklösterle, Hohle Fels, and Helga Abri in the Ach Valley, and Schmiechenfels in the Schmiech (Fig. 1) Valley. Like most of Central Europe, after the LGM, humans did not repopulate the Swabian Jura until the later stage of the Magdalenian. The Magdalenian occupation of this region began before the late glacial interstadial, during cold and dry conditions (finds from

Hohle Fels have yielded a date of 16,300 cal BP; Taller et al. 2014) and continued until approximately 12,700 cal BP (Hahn 1995; Housley et al. 1997; Gaudzinski and Street 2003; Kind 2003). The sites in the Swabian Jura can therefore contribute to our understanding of why the number of Central European archaeological sites increases dramatically starting in the early late Magdalenian.

Several paleoenvironmental reconstructions have been conducted on Paleolithic time periods in the Swabian Jura using palynological (e.g., Firbas 1949; Bertsch 1961), archaeobotanical (e.g., Riehl et al. 2014), faunal (Krönneck 2008, 2012), and geoarchaeological (e.g., Miller 2015) methodologies. These studies, though, focus primarily on periods pre-dating the Magdalenian. Further, although the power of microfaunal assemblages in paleontological and archaeological contexts to interpret past environments has long been acknowledged in Germany (e.g., Schmidt 1912; Ziegler and Dean 1998; Böhme 2007; Soergel-Rieth 2011[1924]), Magdalenian-aged microvertebrate assemblages in the Swabian Jura have not been the primary focus of research from this time period. New archaeofaunal datasets are therefore essential for reconstructing the environmental context of Magdalenian hunter-gatherers.

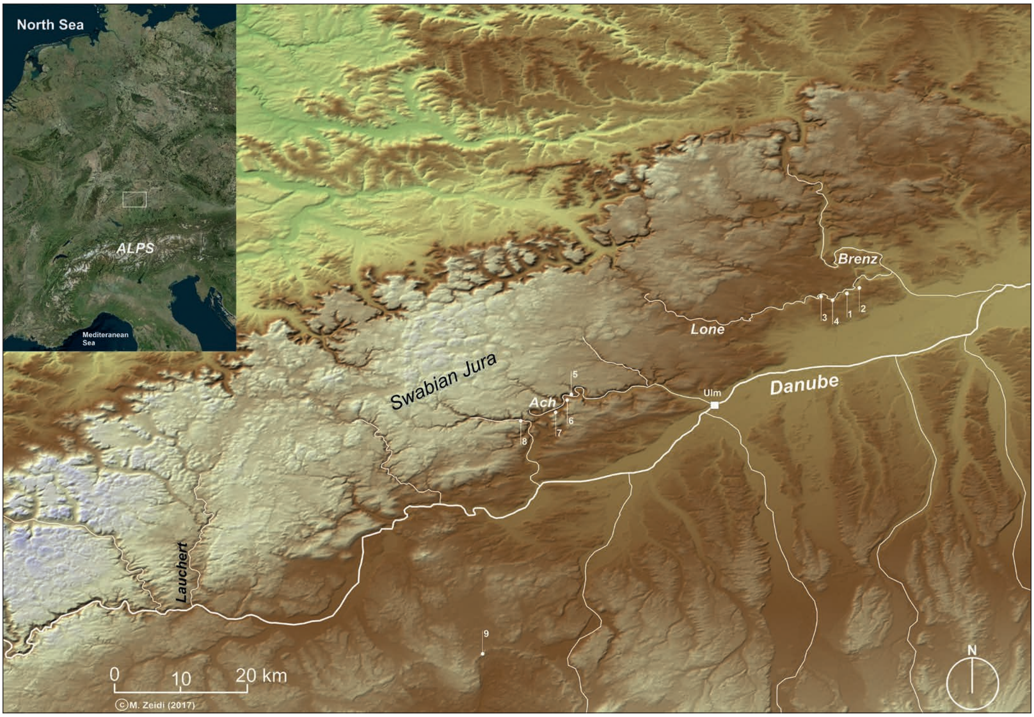

Fig. 1: *Location of Langmahdhalde and other sites mentioned in the text. 1 = Vogelherd; 2 = Langmahdhalde; 3 = Bockstein; 4 = Hohlenstein; 5 = Brillenhöhle; 6 = Geißenklösterle; 7 = Hohle Fels and Helga Abri; 8 = Schmiechenfels; 9 = Schussenquelle. Map prepared by M. Zeidi.*

Langmahdhalde is a newly excavated rockshelter in the Lone Valley with intact Magdalenian horizons. It is the first archaeological site from this time period to be identified in the Lone Valley for several decades, making it an ideal location to apply new techniques of excavation and analysis to a Magdalenian assemblage from the Swabian Jura. The site, which appears to be well-stratified, is still under excavation and has revealed an extensive Magdalenian horizon that consists of three combustion features, a significant stone tool assemblage, and several bone and antler artifacts. The archaeofaunal assemblage consists of macrovertebrate remains and a large microvertebrate assemblage. The site also has potential for the preservation of further Magdalenian remains and older Paleolithic deposits.

Fig. 2: *Langmahdhalde. Overview of the excavation, May 2017. Photo: M. Zeidi.*

In this paper, we present a preliminary analysis of the faunal remains from the Magdalenian occupation of Langmahdhalde, centered on both the micro- and macrovertebrates. Our goal is to determine whether the archaeofaunal assemblage from Langmahdhalde has the potential to address some of the gaps in our understanding of Magdalenian peoples of the Swabian Jura. We discuss whether the macrovertebrate remains from Langmahdhalde were deposited as a result of human activity and how taxonomic abundances compare to other Magdalenian assemblages from the Swabian Jura and general trends in Central European Magdalenian faunal data. We also evaluate the potential of the microvertebrate assemblage to reconstruct regional paleoenvironmental conditions during the entire human occupation of the site, which includes specimens from the, primarily Holocene, horizons above the Magdalenian remains. We consider the sample size, taxonomic representation, and spatial distribution of the microvertebrate assemblage as factors indicative of this potential.

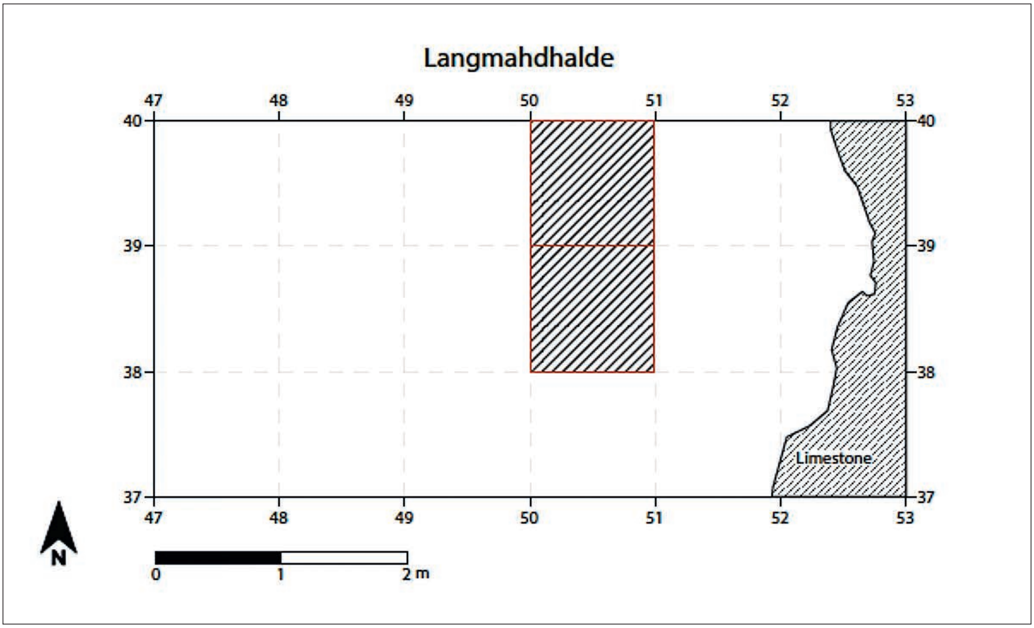

Fig. 3: *Langmahdhalde. Excavation area one by one meter quadrant system. The rock face is indicated by the shaded portion on the right. The quadrants used for the microvertebrate analysis are highlighted (50/38 and 50/39). Illustration prepared by M. Zeidi and A. Janas.*

Langmahdhalde

Langmahdhalde is a rock shelter in the Swabian Jura in southwest Germany. It is located in the Lone Valley, approximately 2 km northeast from the well-known archaeological site Vogelherd (Fig. 1). Test excavations began at the site in the late spring of 2016 and were conducted by the Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters at the University of Tübingen under the direction of N. Conard. These excavations opened two trenches under the rock shelter. Only one of these excavation areas demonstrated clear potential for additional archaeological deposits and was thus expanded. In late spring of 2017, excavations continued and the excavation area was expanded and deepened (Fig. 2); it currently consists of 18 1 meter x 1 meter quadrants (Fig. 3). Excavation will continue in 2018.

The site has six geological (GH) and archaeological (AH) horizons: GH 1/AHI; GH2/AHII; GH2a/AHIIa; GH 3/AH III; GH 4/AH IV; GH 5/AH V (see Conard et al. 2017 for more details). GH1/AHI is a modern humus layer. GH2/AHII yielded a radiocarbon age of 2,465-2,361 cal BP and includes several Iron Age ceramic fragments (Conard et al.

2017). GH2a/AHIIa is a thin horizon compared to the others and has few faunal remains, but a lithic assemblage that likely belongs to the Mesolithic. GH3/AHIII has few anthropogenic remains but a date from the bottom of this layer places it in the late Paleolithic (14,379-14,088 cal BP; Conard et al. 2017). GH4/AHIV revealed a surface of several combustion features, antler, bone, and numerous lithic and microvertebrate remains, that was partially uncovered in 2016 and further explored in 2017. It has been dated to the Magdalenian (15,291-15,159 cal BP; Conard et al. 2017). Based on stratigraphy and artifact assemblages, these Magdalenian features and artifacts appear to continue into GH5/AHV (Fig. 4), which was first excavated in 2017 and has yet to be directly dated.

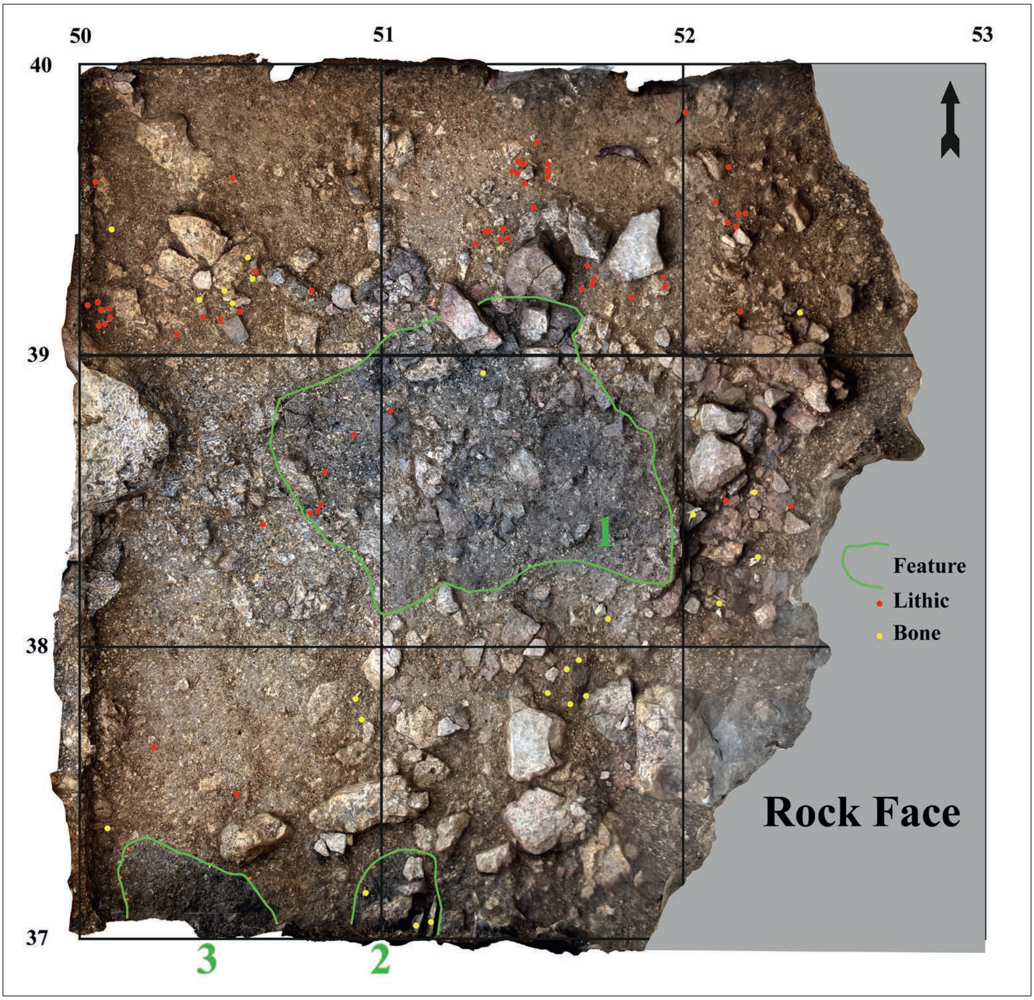

Fig. 4: *Langmahdhalde. Overview of GH5 during excavation. The three combustion features are visible as well as lithic and bone artifacts and the numerous burned limestone pieces that characterize this horizon and GH4. Illustration prepared by A. Janas. Full color version available online: mgfuopenaccess.org.*

In this paper, we focus on the Magdalenian deposits at the site. We include all macrofaunal remains from GH4/AHIV from the 2016 excavation and all macrofaunal remains from GH4/AHIV and GH5/AHV from 2017 that were observed during excavation and measured individually. Remains from the 2017 excavations that were recovered as collected finds or recovered during water screening and sorting were not yet available for study at the time of this analysis. The microvertebrate assemblage at this site is quite large (n > 200,000 specimens); as a result, we include only the microvertebrate remains from quadrants 50/38 and 50/39 from the 2016 excavations in this analysis. These quadrants have some of the largest microvertebrate assemblages at the site and they are highlighted in Fig. 3. In order to fully evaluate Late Pleistocene environments at the site, we conducted microvertebrate analyses on all geological and archaeological horizons except GH1/AHI, as it is modern. The Holocene horizons (GH2/AHII and GH2a/AHIIa) provide much needed context for the implications of the Pleistocene remains (GH3/AHIII and GH4/AHIV).

Methods

In this study, we define macrovertebrates as those species likely reflecting human consumption, such as reindeer, horse, medium-sized birds, and hare. Moreover, we define microvertebrates as specimens belonging to taxonomic groups that have strong potential to reconstruct regional Pleistocene environments and climates. For this study, these taxonomic groups are Rodentia (rodents) and Insectivora (i.e., shrews and moles). Rodents and insectivores have relatively short lifespans, reproduce quickly, and have large litter sizes, allowing them to respond quickly to climatic and environmental changes. This life history makes members of these taxonomic groups particularly appropriate for environmental and climatic reconstructions (Grayson 1981, 1984; Terry 2010; Broughton and Miller 2016, 95) and gives rise to larger sample sizes in the fossil record. Amphibian and reptile remains are also very useful in this respect as they are often adapted to specific habitats (Blain et al. 2009), but these taxa are represented by less than 10 specimens in this assemblage and are therefore not included. Fish remains are similarly useful and are represented at the site but these are primarily from the 2017 excavation and are not yet available for analysis. We do not include specimens belonging to the genus *Microtus* that could not be identified to the species-level because they cannot provide specific environmental information.

These definitions of micro- and macrovertebrates can, of course, have some overlap. Birds and hares, for example, often fall into both categories of classification. Medium-sized birds such as ptarmigan and grouse are common prey for humans and often also have specific environmental requirements. It is therefore important that we understand the taphonomic history and depositional context of these taxa and integrate micro- and macrovertebrate remains when we interpret past human behavior.

It should be noted that microvertebrate assemblages are rarely deposited by humans and are much more likely to be the result of mammalian carnivore or predatory bird activity (Andrews 1990; Fernández-Jalvo et al. 2016). Thus this portion of the assemblage is indicative, not of human consumption, but of non-human predator prey choice and, in turn, the habitats of those predators and their prey (Andrews 1990; Fernández-Jalvo et al. 2016).

We recorded all faunal remains using Stiner's (2005) coding system, modified for the specific taxa found in the German Late Pleistocene and early Holocene. We identified faunal remains to the lowest possible taxonomic level using modern zooarchaeological methods and references (Pales and Lambert 1971; Schmid 1972; Grayson 1984; Gilbert 1990; Lyman 1994, 2008; Hillson 2005; Gilbert et al. 2006; Reitz and Wing 2008) and the University of Tübingen's comparative vertebrate collection housed in the Institut für Naturwissenschaftliche Archäologie. We recorded evidence of taphonomic processes, such as burning (Stiner et al. 1995), weathering (Behrensmeyer 1978), mineral staining, breakage, and human-made cutmarks for all specimens (Lyman 1994; Fernández-Jalvo and Andrews 2016). We calculated the Number of Identified Specimens (NISP) and %NISP for each taxonomic category of macrovertebrates (Grayson 1984; Lyman 2008) using Stiner's (2005) landmark system. We calculated NISP and Minimum Number of Individuals (MNI; Grayson 1984; Lyman 2008) using Stiner's (2005) landmark system for each microvertebrate taxonomic category. Our calculations of MNI use the most commonly occurring element and, when applicable, take side into account. We have not yet refit the assemblage, but Stiner's (2005) system largely bypasses this, at least in a statistical sense, for calculating MNI.

Several unidentified horse tooth fragments are present in the sample. We did not include these specimens in NISP calculations as they would have greatly overestimated horse remains at the site compared to other taxa. Mammoth is represented by one piece of ivory that measures approximately 7 cm in length. We assigned specimens that could not be identified to a specific taxon to body-size groups.

A discussion of the calculation of MNI for micromammals merits further discussion as certain taxa are much more identifiable than others. Only cranial elements, mandibles, and teeth (primarily molars) were used to make genus- or species-level identifications on the rodent and insectivore remains, as these are the most widely accepted and reliable elements to make such identifications (Niethammer and Krapp 1978, 1982, 1990; Hillson 2005). This level of identification is necessary for environmental reconstruction (Niethammer and Krapp 1978, 1982, 1990).

Different taxonomic groups of micromammals are identifiable based on different teeth, and whether a species or genus is identifiable based on the mandible or cranial elements varies by taxon. For example, most members of the subfamily Arvicolinae (lemmings and voles) can be identified to the species-level based on the lower first molar (Niethammer and Krapp 1982), except in the case of the water voles (genus *Arvicola*), collared lemmings (*Dicrostonyx*), and brown and true lemmings (genus *Lemmus*), all of which can be identified using any molar (Agadjanian and von Koenigswald 1977; Reichstein 1982a, b, c; Tast 1982). Other species, such as the insectivores, are identifiable to at least the genus-level based on features of their mandible and several teeth (Repenning 1967; Niethammer and Krapp 1990). Due to these discrepancies in identifiability between elements for each taxon, NISP values can greatly overestimate certain taxa. For this reason, we did not use tooth fragments that could not be identified to a specific tooth to calculate MNIs for the micromammal assemblage and we consider NISP and MNI together.

Results

We analyzed a total of 1457 specimens for this study: 1081 rodents and insectivores, 303 macromammals, and 73 birds. Like most sites in the Ach and Lone valleys, the Magdalenian macrovertebrate assemblage at Langmahdhalde is relatively small compared to pre-LGM Upper Paleolithic faunal assemblages in the region. Table 1 summarizes the macromammal remains. Hare, reindeer, and horse dominate the assemblage; these taxa are typical of Magdalenian faunal assemblages. The large sample of medium mammals is primarily driven by the relatively large number of unidentifiable long bone shaft fragments in the assemblage (n=76).

Taxon	GH 4&5 / AH IV&V		Cutmarks	Spiral Fractures	Carnivore Damage
	NISP	%NISP			
Mammoth (*Mammuthus primigenius*)	1	1.3			
Wild Horse (*Equus ferus*)	15	19.2	5	3	1
Red deer (*Cervus elaphus*)	9	11.5			
Reindeer (*Rangifer tarandus*)	19	24.4	1	3	
Roe deer (*Capreolus capreolus*)	2	2.6			
Bos or *Bison* sp.	1	1.3			
Ibex (*Capra ibex*)	1	1.3			
Hare (*Lepus* sp.)	23	29.5		1	1
Cave lion (*Pantera spelaea*)	1	1.3			
Fox (*Vulpes* sp.)	4	5.1	1		
Arctic fox (*Vulpes lagopus*)	1	1.3			
Weasels/ferrets/etc. (*Mustela* sp.)	1	1.3			
Total	**78**	**100%**			
Small carnivore	3		1		
Large cervid	5				
Cervidae	2				
Medium ungulate	5		1	1	
Large ungulate	12		5	3	1
Medium/large ungulate	3		1		
Ungulate	2				
Small mammal	34				
Medium mammal	108		9	5	1
Large mammal	4			1	
Medium/small mammal	20		1	3	
Medium/large mammal	16		1	3	
Mammal	9				
Small mammal or bird	2				
Total	**225**		**26**	**23**	**4**

Table 1: *Macromammal summary table showing NISP and %NISP of each taxon in GH4/AHIV and GH5/AHV. %NISP was not calculated for those specimens that could only be identified to size class. The number of specimens that have cutmarks, spiral fractures, or carnivore alterations are also noted for each taxon/group.*

In general, there is significant damage from root etching and chemical weathering on most macromammal remains from the Magdalenian horizons. Most specimens also show pitting and fine cracks, and some peeling is also present. In some cases this weathering has impeded identifiability. Despite the degree of weathering, there are still some fairly complete bones. For example, a nearly complete horse pelvis was found in the top portion of GH4/AHIV, just above the combustion features (Fig. 5). It has a large anthropogenic hack mark on the right pubis. Four antler fragments were also recovered from the site, three of which have been identified to reindeer. One of these specimens measures over 35 cm in length (Fig. 6).

Table 2 summarizes the bird remains. Ptarmigen dominates the assemblage. Approximately half of the bird remains were only identifiable to size class; of these, the majority are medium-sized birds.

Taxon	**GH 4&5 / AH IV&V**	
	NISP	**%NISP**
Grouse/pheasant/partridge (Phasianidae)[M]	1	2.6
Ptarmigan (*Lagopus* sp.)[M]	17	48.6
Hazel grouse (*Tetrastes bonasia*)[M]	2	5.7
Black grouse (*Tetrao tetrix*)[M]	1	2.6
Doves and pigeons (Columbidae)[M]	1	2.6
Grey geese (*Anser* sp.)[M]	1[W]	2.6
Dabbling ducks (*Anas* sp.)[M]	1	2.6
Common teal (*Anas crecca*)[M]	2	5.7
Shore birds (Charadriiformes)[M]	3	8.6
Eurasian golden plover (*Pluvialis apricaria*)[M]	1	2.6
Grebes (Podicipedidae)[M]	1[SP]	2.6
White stork (*Ciconia ciconia*)[L]	1	2.6
Perching/song birds (Passeriformes)[S]	3[SP]	8.6
Total	**35**	**100%**
Small birds (Passeriformes/Piciformes/etc.)	6	
Medium birds (Galliformes /Columbiformes/Anseriformes/etc.)	29[CM,SP,CA]	
Large birds (raptors/owls/ vultures/geese/swans/etc.)	4[CA]	
Total Size Class NISP	**39**	

Table 2: *Bird summary table showing NISP and %NISP of each taxon in GH4/AHIV and GH5/AHV. %NISP was not calculated for those specimens that could only be identified to size class. S = small bird; M = medium bird; L = large bird; SP = one specimen has a spiral fracture; CM = one specimen has cutmarks; CA = one specimen has carnivore modifications; W = worked bone.*

We present a summary of the results of the micromammal analysis in Table 3, which shows the NISP and MNI for each taxonomic group by geological and archaeological horizon. There is a clear taxonomic trend in the data that separates the Holocene horizons (GH2/AHII and GH2a/AHIIa) from the Pleistocene horizons (GH3/AHIII and GH4/AHIV). The common and/or field vole (*Microtus arvalis/agrestis*) and red-backed voles (genus *Myodes*, represented by *Myodes glareolus* during the Holocene in Germany; Hutterer et al. 2016) dominate the Holocene assemblage. The common and/or field vole, narrow-headed vole (*M. gregalis*), and collared lemmings (genus *Dicrostonyx*) are the most common taxa in the Pleistocene assemblage. Common and field voles are regularly represented in German microvertebrate assemblages and their dominance is expected from the Late Pleistocene through the Holocene in this region (Kurtén 1968, 217; Storch 1973, 1987; von Koenigswald 1985; Ziegler 1995; Kowalski 2001, 243-247).

Fig. 5: *Langmahdhalde. Horse pelvis in situ in the Magdalenian horizon GH4/AHIV. The arrow points north and the scale is 25 cm long. Photo: A. Janas.*

Fig. 6: *Langmahdhalde. Reindeer antler in situ in the Magdalenian deposits. Photo: A. Janas.*

It is important to note that the apparent dominance of collared lemming specimens in GH4/AHIV, as reflected in the NISP, is likely a result of the high identifiability of this taxon, not of actual abundance. As stated above, unlike the genus *Microtus*, collared lemmings can be identified using every molar. This is clear when the NISP and MNI values are compared; common and/or field voles (both genus *Microtus*) has the largest MNI value for this horizon, followed by collared lemmings and narrow-headed voles.

Evidence of human activity on the faunal remains

It seems clear that humans deposited at least a significant proportion of the macrofaunal assemblage at Langmahdhalde. Table 1 indicates the number of specimens for each taxon or group that have evidence of cutmarks, spiral fractures, or carnivore modification. Several macromammal remains have evidence of human modification in the form of cutmarks, particularly horse, large ungulates, and medium mammals. There is one cutmark on a fox mandible that is likely the result of skinning (Binford 1981, 47). Further, several of the macromammal specimens also have spiral fractures, indicating that these elements were broken while still fresh. Although several processes can create spiral fractures (Shipman et al. 1981), humans often break bones for access to marrow and grease while they are fresh and this may be the cause of these breaks here. As of yet, we have observed no human modifications on the antler remains at Langmahdhalde. Carnivore modifications are rare in the macromammal assemblage (Table 1).

Taxon	**GH2 / AHII**		**GH2a / AHIIa**		**GH3 / AHIII**		**GH4 / AHIV**	
	NISP	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Common mole (*Talpa europaea*)	1	1	0	0	0	0	0	0
Shrews (Soricidae)	1	1	0	0	0	0	0	0
Long-tailed shrews/old world water shrews (*Sorex/Neomys*)	10	3	0	0	0	0	0	0
Eurasian water shrew (*Neomys fodiens*)	0	0	0	0	0	0	3	1
Long-tailed shrews (*Sorex* sp.)	5	1	0	0	0	0	3	1
Dormice and hazel mice (Gliridae)	1	1	0	0	0	0	0	0
Dormouse (*Glis glis*)	6	1	0	0	0	0	0	0
Yellow-necked/wood mouse (*Apodemus flavicollis/sylvaticus*)	15	2	1	1	0	0	1	1
Common/field vole (*Microtus arvalis/agrestis*)	17	10	2	2	2	1	188	91
Microtus arvalis/agrestis OR *gregalis*	0	0	0	0	0	0	2	1
Narrow-headed vole (*Microtus gregalis*)	0	0	0	0	0	0	100	50
Tundra vole (*Microtus oeconomus*)	0	0	0	0	1	1	4	2
Eurasian snow vole (*Chionomys nivalis*)	6	2	0	0	0	0	7	3
Collared lemming (*Dicrostonyx* sp.)	0	0	0	0	4	1	358	52
Red-backed voles (*Myodes* sp.)	78	11	4	1	1	1	1	1
Water voles (*Arvicola* sp.)	5	3	0	0	0	0	1	1
Pine voles (*Pitymys* sp.)	3	2	0	0	0	0	0	0
TOTAL	**148**	**38**	**7**	**4**	**8**	**4**	**668**	**204**

Table 3: *Micromammal summary table showing NISP and MNI of each taxon by geological and archaeological horizon.*

The base of the large antler specimen is preserved and demonstrates that the antler was collected after it was shed, indicating that this specimen was likely not deposited as a result of hunting. Similarly, the presence of a piece of mammoth ivory at the rock shelter does not necessarily imply that humans were hunting mammoth or that mammoth were present in the Lone Valley while humans used this rock shelter, as ivory is easily collected.

Like micromammals, small birds, such as those species belonging to the order Passeriformes, are very rarely hunted or collected by humans and are thus likely the remains of mammalian carnivore or predatory bird activity at the site. Of the larger species of bird, several are common in Magdalenian assemblages and have been documented as human food sources, the most prominent of which are those species belonging to the family Phasianidae (e.g., the genus *Lagopus*). For example, we mentioned above that Ptarmigans (*Lagopus* sp.) are common in the Magdalenian horizons of Brillenhöhle (Boessneck and von den Driesch 1973, tables 1 and 2) and Petersfels (Peters 1930; Albrecht 1979; Albrecht and Hahn 1991). There is one cut bird specimen in our sample. Unfortunately, we could not identify it above size class. It is a medium-sized bird sternum fragment with four cutmarks running diagonally across the bone that are approximately 3 mm in length. The assemblage also includes the distal humerus of a goose (*Anser* sp.) that is likely a needle blank (Conard et al. in prep). It is therefore likely that the Magdalenian bird assemblage at Langmahdhalde is the result of both human and non-human predator activity. This is also supported by the fact that two bird specimens (one large and one medium bird) show evidence of carnivore modifications.

Paleoenvironment

We identified seven different habitat preferences in the microvertebrate assemblage: rocky, open, woodland, humid/wet, dry, steppe, and tundra. The MNI values of each taxon were combined based on their habitat preferences and these values are presented in Fig. 7 as relative proportions for both the Holocene and Pleistocene horizons. The Eurasian snow vole (*Chionomys nivalis*) prefers rocky habitats (Amori 1999). Although this genus is not currently present in the Swabian Jura, the presence of rocky-adapted species in this region during the Holocene is not surprising considering the Swabian Jura is a karstic system. Pine voles (genus *Pitymys*; Kurtén 1968, 219) and narrow-headed voles (*Microtus gregalis*; Kurtén 1968, 219-220; Batsaikhan et al. 2016) prefer open habitats. Red-backed voles (genus *Myodes*; van Kolfschoten 1985; Hutterer et al. 2016) and dormice (*Glis glis*; Amori et al. 2016a) prefer woodland environments. In the category "humid/wet" we have included tundra voles (*Microtus oeconomus*; von Koenigswald 1985; Linzey et al. 2016) and pine voles (genus *Pitymys*; Kurtén 1968, 219), which prefer humid or moist conditions, as well as the water voles (genus *Arvicola*), who are tied to water sources. Species that are tied to water are expected in this assemblage as the site is less than 100 m from the Lone River. Red-backed voles, Eurasian snow voles, narrow-headed voles, and collared lemmings (genus *Dicrostonyx*; von Koenigswald 1985; Kurtén 1968, 219-220; Tsytsulina et al. 2016) prefer dry environments. Narrow-headed voles (Batsaikhan et al. 2016) prefer steppe and tundra environments and collared lemmings prefer tundra environments (Kurtén 1968, 219-220; Tsytsulina et al. 2016).

We did not use yellow-necked mice, wood mice, shrews, or common moles (*Apodemus sylvaticus*, *A. flavicollis*, genus *Sorex*, and *Talpa europaea*) for environmental reconstructions in this study. Yellow-necked and wood mice are only distinguishable based on measurements taken on molars (Niethammer 1978). This work is in progress and our future reconstructions will incorporate the specific habitat requirements of yellow-necked mice (Amori et al. 2016b). Similarly, species-specific identifications on shrews are underway and will be included in future work. The common mole does not have specific habitat

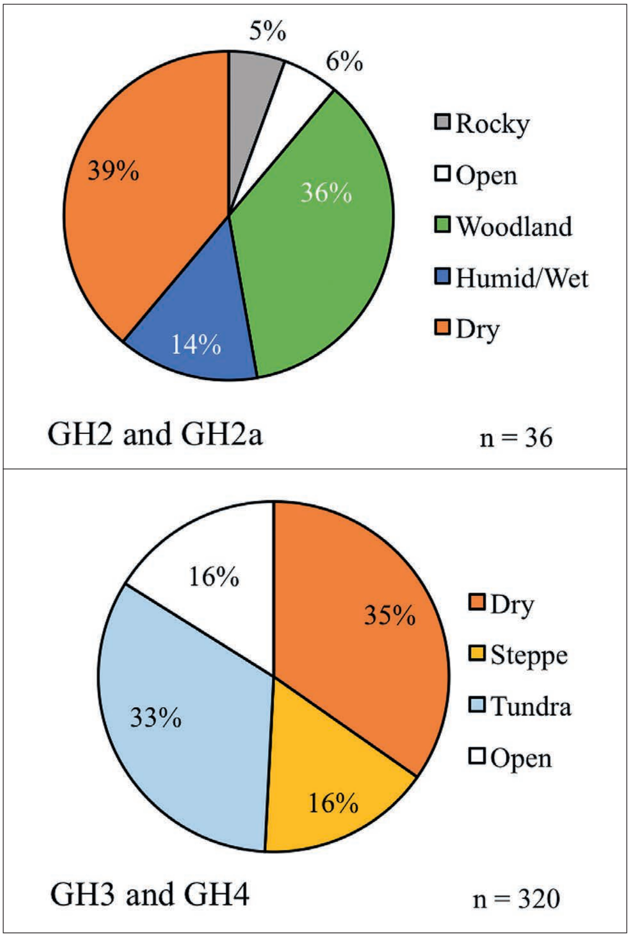

Fig. 7: *Langmahdhalde. Habitat preferences for the microvertebrate specimens of GH2 and GH2a (top) and GH3 and GH4 (bottom). Percentages are based on MNI counts presented in Table 1. Percentages that are 1% or less are not shown. Full color version available online: mgfuopenaccess.org.*

preferences and is present in most environments that have soils deep enough for tunneling (Mitchell-Jones et al. 1999). Common and field voles are also not included in our environmental reconstructions as they do not share specific habitat preferences and are indistinguishable in fossil contexts (Niethammer and Krapp 1982; Mitchell-Jones et al. 1999).

Fig. 7 depicts differences in Pleistocene and Holocene environments, as reconstructed from the Langmahdhalde micromammal assemblage. Extensive past research has demonstrated that the Holocene of Central Europe was more temperate and wooded whereas the Pleistocene was more open, had steppe/tundra conditions, and colder temperatures (see von Koenigswald 2003 and Otte 2009 for summaries; see Krönneck 2008 and 2012, Riehl et al. 2014, and Miller 2015 for local conditions). The Holocene assemblages at Langmahdhalde reflect micromammals with a preference for dry and woodland environments.

The Pleistocene assemblages demonstrate species with a preference for open, dry, steppe, and tundra environments, conforming to our current understanding of environments during the post-LGM Pleistocene. Interestingly, ptarmigan are also common in GH4 and this taxon prefers cold and open tundra habitats (Peterson et al. 2002). Further work with these assemblages will target understanding the specifics of climate fluctuations during these periods.

Discussion and Conclusions

In this paper, we have summarized the Magdalenian archaeofaunal assemblage from the newly excavated rock shelter, Langmahdhalde. This analysis has demonstrated that both the macro- and microvertebrate assemblages at the site have the potential to address current questions in Magdalenian research. Based on the archaeological context of the site and the taphonomy of the remains, we argue that a significant portion of the macrofaunal assemblage was deposited as a result of human activity. Additionally, the direct association of the anthropogenic remains (lithics, combustion features, and macrovertebrate remains) with an extensive microvertebrate assemblage makes this site even more compelling. Although the implications of the micromammal results presented here are very broad in scale, our ongoing work with this assemblage will focus on applying new methods of analysis, such as the Mutual Ecogeographic Range method (Agustí et al. 2009; Blain et al. 2009; Lyman 2016; Rey-Rodríquez et al. 2016) or bioclimatic analysis (Hernández Fernández 2001), that will allow us to make local- and regional-scale environmental and climatic reconstructions. These will compliment data from macrovertebrate assemblages from the Swabian Jura (Langmahdhalde included) and be applied to questions of Magdalenian socio-economic and settlement dynamics.

Taphonomic and geological studies of Langmahdhalde will also contribute to this question. The three combustion features in the Magdalenian horizons, as well as the density of lithic artifacts in association with them, suggests that this site was used intensely by Magdalenian humans, even if for a short period of time. The preservation of the faunal remains and overall taphonomy of the site indicate that this Magdalenian horizon was likely exposed for a period of time before deposition occurred. We are working on the dynamics of this depositional history and rates of sedimentation at the site, as these could have implications for human use of the site and likely explain why the macrovertebrate assemblage is small. Both emphasize the need for continued excavation and study of the site. Specifically, geoarchaeological studies and continued, detailed taphonomic analyses of the assemblage are necessary to fully evaluate these interpretations.

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Appendix 2

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Latest Pleistocene paleoenvironmental reconstructions from the Swabian Jura, southwestern Germany: Evidence from stable isotope analysis and micromammal remains

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ABSTRACT

Paleoenvironmental and climatic reconstructions are reported for latest Pleistocene (Paleolithic) contexts from the Swabian Jura of southwestern Germany. In particular, we focus on the late glacial interval, ~18,000 to 11,600 cal yr BP, using faunal remains from Langmahdhalde, a recently excavated Late Magdalenian site in the Lone Valley. We use two different proxies for reconstruction: (1) stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of bone collagen from reindeer (*Rangifer tarandus*) and horse (*Equus ferus*) and (2) the application of a bioclimatic model to the micromammal assemblage from the site. We use these results to discuss the environmental context of Magdalenian hunter-gatherers in the Lone Valley and argue that, although they generally lived in tundra environments, their landscape was heterogeneous and likely had pockets of trees and/or denser vegetation. Our study documents warmer winter temperatures, increased precipitation, and longer vegetative activity periods than those of modern tundra environments.

1. Introduction

Germany has a long research history of Pleistocene paleoenvironmental reconstructions using various disciplines and proxy data sources (e.g. Schmidt, 1912; Firbas, 1949; Bertsch, 1961; Storch, 1974; von Koenigswald, 1985; Böhme, 2007; Duprat-Oualid et al., 2017). These interpretations of past vegetation, animal distributions, environments, and climatic conditions have uncovered regional and large-scale trends that provide the context within which Paleolithic hunter-gatherers lived. These studies generally characterize the Late Glacial (~18,000 to 11,600 cal yr BP) in Central Europe as relatively unstable as glaciers quickly retreated after the Last Glacial Maximum, temperatures warmed, and forested regions and grasslands began to develop (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989). This period was, in general, a drier and colder time than today that included steppe and tundra environments and a slow return of forests to Central Europe. At the beginning of this period, environments were accompanied by animals, such as reindeer (*Rangifer tarandus*), ptarmigan (*Lagopus lagopus*), and collared lemming (*Dicrostonyx torquatus*), that are well-adapted to these conditions (Bell and Walker, 2005; Koenigswald, 2003; Koubek and Zima, 1999; Peterson et al., 2012; Tsytsulina et al., 2016; Weniger, 1989). Over time, trees and more vascular plants moved into Central Europe, allowing animals associated with more temperate environments to recolonize the region (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989).

During the Late Glacial, however, there is clear evidence that there existed regional differences in vegetation. For example, Maier (2015: 65–71) combines over 40 years of palynological research from 28 different sites and demonstrates that, during the Late Glacial, the vegetation of Central Europe was diverse and varied regionally. In general, he shows that three regions with different patterns of vegetation emerged: southwestern, northwestern, and eastern Central Europe. He shows that from approximately 16,900 to 14,700 cal yr BP, pollen records from the southwestern region primarily contain pollen from herbs and grasses, while in the northwestern region, Poaceae pollens are the most common. Finally, in the eastern region during this time, he shows that arboreal pollens dominate the records.

In southwestern Germany, where a rich Paleolithic record exists, primarily in the form of rock shelter and cave sites, several regional-scale studies have explored the ecological context of Paleolithic hunter-

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gatherers using zooarchaeology, archaeobotany, palynology, geoarchaeology, and geochemistry (e.g. Bocherens et al., 2011; Drucker et al., 2016, 2011; Immel et al., 2015; Krönneck, 2012, 2008; Miller, 2015; Rhodes et al., 2019, 2018; Riehl et al., 2014; Schmidt, 1912; Soergel-Rieth, 2011; Weniger, 1982). In this region, though, except for a few stable isotope studies (Drucker et al., 2011; Immel et al., 2015), we lack paleoenvironmental reconstructions for the Late Glacial that use recent quantitative methodological approaches. The complexity of ecological systems and inherent challenges of reconstructing past systems using proxy data makes having information from various sources a necessity in paleoenvironmental research.

To date, the majority of the paleoenvironmental data for southwestern Germany are regional in scale, addressing the "Swabian Jura" or "southwestern Germany" as a whole. The fundamental characteristics of the fossil record make more local-scale reconstructions challenging and often unattainable. But local-scale reconstructions are potentially more relevant to hunter-gatherers, who likely travelled only a few hundred kilometers annually (Weniger, 1991) and probably used local landscapes differently based on their unique attributes. The various river valleys of the Swabian Jura in southwestern Germany, for example, although within around 100 km of each other, have distinctive topographic and vegetative features, which might imply that hunter-gatherers would not have hunted, camped, or moved through these valleys in the same way.

One type of material from the fossil record that has the potential to address more local-scale research questions is microvertebrate remains, which result from avian predator and mammalian carnivore hunting and feeding (Andrews, 1990; Fernández-Jalvo et al., 2016) and are often deposited in association with archaeological materials. In the Swabian Jura, several rock shelter and cave sites have large microvertebrate assemblages in direct association with Paleolithic artifacts and features, making these assemblages excellent sources of information for addressing research questions in human paleoecology from this period. For example, Rhodes et al. (2018, 2019) have used the micromammal assemblages from Geißenklösterle and Hohle Fels to discuss the paleoenvironmental context of the Neanderthal and Aurignacian occupations of the region. Further, more recently developed quantitative models reconstruct past climate variables, such as temperature and precipitation, using microvertebrates, allowing researchers to compare these variables to modern data and begin to quantify how past environments differ from those that exist today (e.g. Agustí et al., 2009; Blain et al., 2009; Hernández Fernández, 2001a; Hernández Fernández and Peláez-Campomanes, 2005, 2003). This is very useful for understanding late Pleistocene climates as we know there can be no direct comparative for some of these; one of the more well-known examples being the "mammoth steppe" (Guthrie, 2001, 1982).

Scholars have conducted research on the Paleolithic of the Swabian Jura since the mid-1800s (Conard and Bolus, 2006; Schmidt, 1912; Taller et al., 2014; Weniger, 1989) when Oscar Fraas excavated the Magdalenian site Schussenquelle (Fraas, 1867; Schuler, 1994), which is generally considered one of the first systematic Paleolithic excavations in Central Europe. Today, several valleys are well-known for their contribution to Paleolithic research, in particular the Ach and Lone valleys, which house sites such as Hohle Fels, Geißenklösterle, Brillenhöhle, Hohlenstein, Vogelherd, and Bockstein.

The Magdalenian, of the late Upper Paleolithic, occurred during the Late Glacial, as people returned to Central Europe after the Last Glacial Maximum. Evidence of the Magdalenian occupation of the Swabian Jura comes from sites such as Brillenhöhle, Schmiechenfels, Schussenquelle, and Hohle Fels and began around 16,300 cal yr BP (Taller et al., 2014). Like most Late Magdalenian sites in Germany, the tools in Magdalenian lithic assemblages from the Swabian Jura are dominated by backed blades and bladelets, burins, and end-scrapers (Bolus, 2012; Hahn, 1991; Taller, 2014). The assemblages from these sites are also characterized by the presence of bone tools, reindeer antler, few ivory pieces compared to the early Upper Paleolithic, and art objects made on bone, antler, and stone (Eriksen, 1991; Maier, 2015; Schmidt, 1912; Taller, 2014). Magdalenian peoples of the Swabian Jura likely moved across the landscape seasonally, probably inhabiting small field hunting camps for short periods of time in small groups during the spring and summer and larger sites in large groups for longer periods of time during the fall and winter where communal hunting, fur and hide working, and meat storage occurred (Weniger, 1989, 1987).

Reindeer and horse (*Equus ferus*) seem to have been the most commonly hunted animals as they are the dominant taxa in archaeofaunal assemblages from this period in the Swabian Jura (and indeed most of Central Europe). Ptarmigan, hare (*Lepus* sp.), and smaller ungulates, such as ibex (*Capra ibex*), are also commonly found at these sites (for a summary of Magdalenian Central European faunal assemblages, including the Swabian Jura, see Eriksen, 1996, Gaudzinski and Street, 2003, and Maier, 2015). However, the faunal assemblages dating to the Magdalenian in Central Europe are by no means uniform in terms of taxonomic representation. Maier (2015: 72–79) finds that there is a regional pattern of taxonomic representation in faunal assemblages from this period, including that of horse and reindeer.

In this study, we aim to contribute to the current understanding of human paleoecology during the Magdalenian in the Swabian Jura by providing new paleoenvironmental reconstructions from Langmahdhalde, a recently excavated Magdalenian rock shelter in the Lone Valley of the Swabian Jura. We use the micromammal assemblage and stable isotope data from reindeer and horse bone collagen to discuss the environmental and climatic context of hunter-gatherers during the Late Glacial of this region.

2. Materials

Langmahdhalde (48.5669°N, 10.2133°W) is located approximately 2 km northeast of Vogelherd, the well-known archaeological site (Fig. 1). Excavations at Langmahdhalde have taken place annually since 2016 and uncovered ten geological horizons. In Table 1 we present radiocarbon dates taken on charcoal and bone collagen from the site and Fig. 2 shows the stratigraphy of the site from excavation seasons 2016 to 2019. Faunal remains in this study are from excavation years 2016 to 2018. During these field seasons, Geological Horizon (GH) 1 and Archaeological Horizon (AH) I to GH6/AHVI were exposed. This study therefore only discusses these horizons. GH1/AHI corresponds to the modern hummus layer with mixed archaeological materials, GH2/AHII has been dated to the Holocene (2680–2354 cal yr BP; Conard et al., 2017) and includes ceramics and lithics from the Neolithic, metal ages, and early middle ages. Based on the lithic assemblage, GH2a/AHIIa appears to be a Mesolithic horizon but dates on bone collagen and charcoal from are mixed and do not correspond to a specific cultural period, although they do all fall within the Holocene (Conard et al., 2019, 2018, 2017). The transition between GH2a/AHIIa and GH3/AHIII represents a clear shift from the Holocene to the Pleistocene, as demonstrated by the micromammal remains (Wong et al., 2017). GH2a/AHIIa and the layers above it contain taxa endemic to southwestern Germany in the Holocene, such as the bank vole (*Clethrionomys glareolus*), while GH3/AHIII and the layers below it contain taxa that have not been present in southwestern Germany since the Pleistocene, such as the collared lemming (*Dicrostonyx torquatus*; Wong et al., 2017). GH3/AHII has very few archaeological remains but a date from the bottom of this layer places it in the Late Glacial (14,653 to 14,034 cal yr BP; Conard et al., 2017).

GH4/AHIV, GH5/AHV, and GH6/AHVI are characterized by large numbers of lithic artifacts and bone and antler remains, compared to the layers above. All three horizons have overlapping dates that place them in the Late Magdalenian (dates range from 15,447 to 13,934 cal yr BP; Conard et al., 2017, 2018, 2019) and, therefore, fall within the end of the GS-2a event (Pleniglacial) and the GI-1e event in the NGRIP record (Meiendorf Interstadial; Litt et al., 2001; Lowe et al., 2008), which is traditionally associated with Magdalenian stages IV and

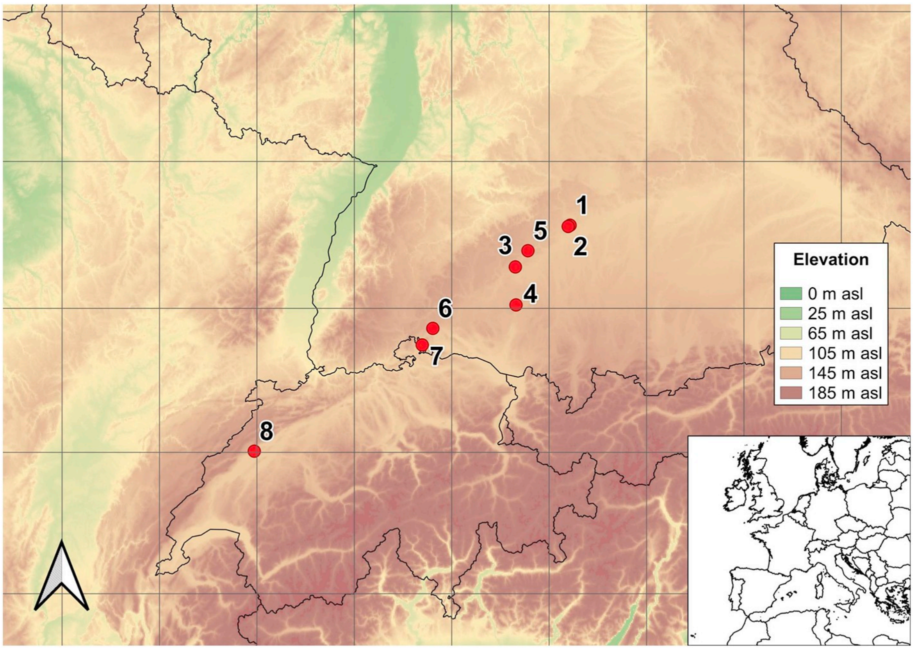

Fig. 1. Location of Langmahdhalde in the Swabian Jura of southwestern Germany and other sites mentioned in this study. 1 = Langmahdhalde (Magdalenian), 2 = Vogelherd (Middle Paleolithic to Neolithic), 3 = Felsställe (Upper Paleolithic, Mesolithic, and later Holocene), 4 = Schussenquelle (Magdalenian), 5 = Geißenklösterle (Middle Paleolithic to Mesolithic), 6 = Petersfels (Magdalenian), 7 = Kesslerloch (Upper Paleolithic, including Magdalenian), 8 = Champréveyres (Paleolithic to Middle Ages). Figure made in QGIS version 3.4 using raw elevation data from the European Environment Agency, raw data from ©EuroGeographics for the administrative boundaries, and latitude and longitude lines from Natural Earth.

V (Jochim et al., 1999). There is a change in lithic raw material from GH4/AHIV to GH5/AHV and there are six combustion features with associated burned limestones in GH5/AHV.

The interpretations of this study will focus on the Late Glacial period (GH4–6/AHIV-VI) but we will also present micromammal results from GHs 2, 2a, and 3 to provide context. The excavation covers approximately 30 m^2 and is based on a 1 × 1 m quadrant system (Fig. 3), which we dug by 1/4 m^2 in "Abträge" of 1 to 3 cm deep that follow the geological stratigraphy of the site. Here we refer to the Abträge as "sub-layers." Only for GHs 5 and 6 were sub-layers recorded for the measured finds and sediment. Sub-layer 1 represents the first, or highest sub-layer of the horizon and subsequent numbers indicate deeper sub-layers. The micromammal results are presented by GH and, to provide higher resolution, we present the results from GHs 5 and 6 by both GH and sub-layer.

The archaeofaunal assemblage at the site is relatively small (Number of Identified Specimens, or NISP, ≈350 for AHIIa; ≈50 for AHIII; ≈1200 for AHIV-VI; Wong et al., 2017). The Magdalenian archaeofaunal assemblage is, however, comparable in size to other Magdalenian faunal assemblages in southwestern Germany, such as Vogelherd (Niven, 2006: 223–232), Hohenstein Stadel (Geiling et al., 2015; Kitagawa, 2014), Hohle Fels (Napierala et al., 2014), and Bockstein (Krönneck, 2012, 2008). The Magdalenian faunal assemblage (AHIV, AHV, and AHVI) is mainly composed of horse and reindeer remains, including a nearly complete horse pelvis and mandible and several reindeer antler pieces (Conard et al., 2019, 2018, 2017; Wong et al., 2017). Ptarmigan (*Lagopus lagopus*), hare (*Lepus* sp.), and red deer (*Cervus elaphus*) remains are also found in the assemblage (Wong et al., 2017).

Like several rock shelter and cave sites in the Swabian Jura, Langmahdhalde has a large microvertebrate assemblage which is ideal for paleoenvironmental reconstructions. It is dominated by rodent, shrew, and mole remains and we estimate the total sample size to be over 400,000 specimens. As a result of this large size, this study is based on a sample of the microvertebrate assemblage; the results we present here are remains from quadrants 49/37, 50/38, and 50/39 (see Fig. 3). These quadrants were chosen based on sample size, proximity to anthropogenic activity areas, geological context, and their location in

Table 1
Radiocarbon dates from Langmahdhalde. Dates were calibrated using OxCal v4.3.2 (Bronk Ramsey, 2017, 2009) and IntCal13 atmospheric curve (Reimer et al., 2013). GH = Geological Horizon; AH = Archaeological Horizon. The sources for the previously published dates are as follows: 1 = Conard et al., 2017; 2 = Conard et al., 2018; 3 = Conard et al., 2019.

Lab number	Quadrant	Find number	GH	AH	Sub-layer	Feature	Material	Modifications	Date ^{14}C (yr uncal BP)	Date ^{14}C (yr cal BP)	Source
ETH-74893	51/38	43	2	II	–		Pig distal tibia		2418 ± 24	2680–2354	1
ETH-94572	49/36	31	2a	IIa	–		Pig distal humerus		4569 ± 23	5437–5071	3
ETH-94574	50/36	65	2a	IIa	–		Roe deer radius fragment		5636 ± 24	6483–6322	3
ETH-74894	51/39	170	3	III	–		Charcoal	–	12,295 ± 63	14,653–14,034	1
ETH-749895	50/38	201	4	IV	–	1	Charcoal	–	12,784 ± 37	15,381–15,090	1
ETH-94573	49/36	146	5	V	2		Deer femur fragment		12,159 ± 31	14,164–13,934	This work
ETH-83806	50/37	170	5	V	1	2	Charcoal	–	12,221 ± 58	14,376–13,928	This work
ETH-84042	48/38	170	5	V	1		Horse humerus fragment	Cutmarks	12,636 ± 47	15,210–14,765	2
ETH-84040	51/38	409	5	V	3	1	Large mammal long bone shaft fragment		12,714 ± 48	15,313–14,936	2
ETH-84039	51/37	166	5	V	1	2	Large ungulate long bone shaft fragment	Cutmarks	12,732 ± 48	15,335–14,979	2
ETH-84041	50/37	218	5	V	3	3	Medium mammal long bone shaft fragment		12,794 ± 48	15,447–15,084	2
ETH-94575	52/37	90	6	VI	2		Horse proximal third metatarsal	Cutmarks & cone fracture	12,476 ± 32	14,981–14,305	This work

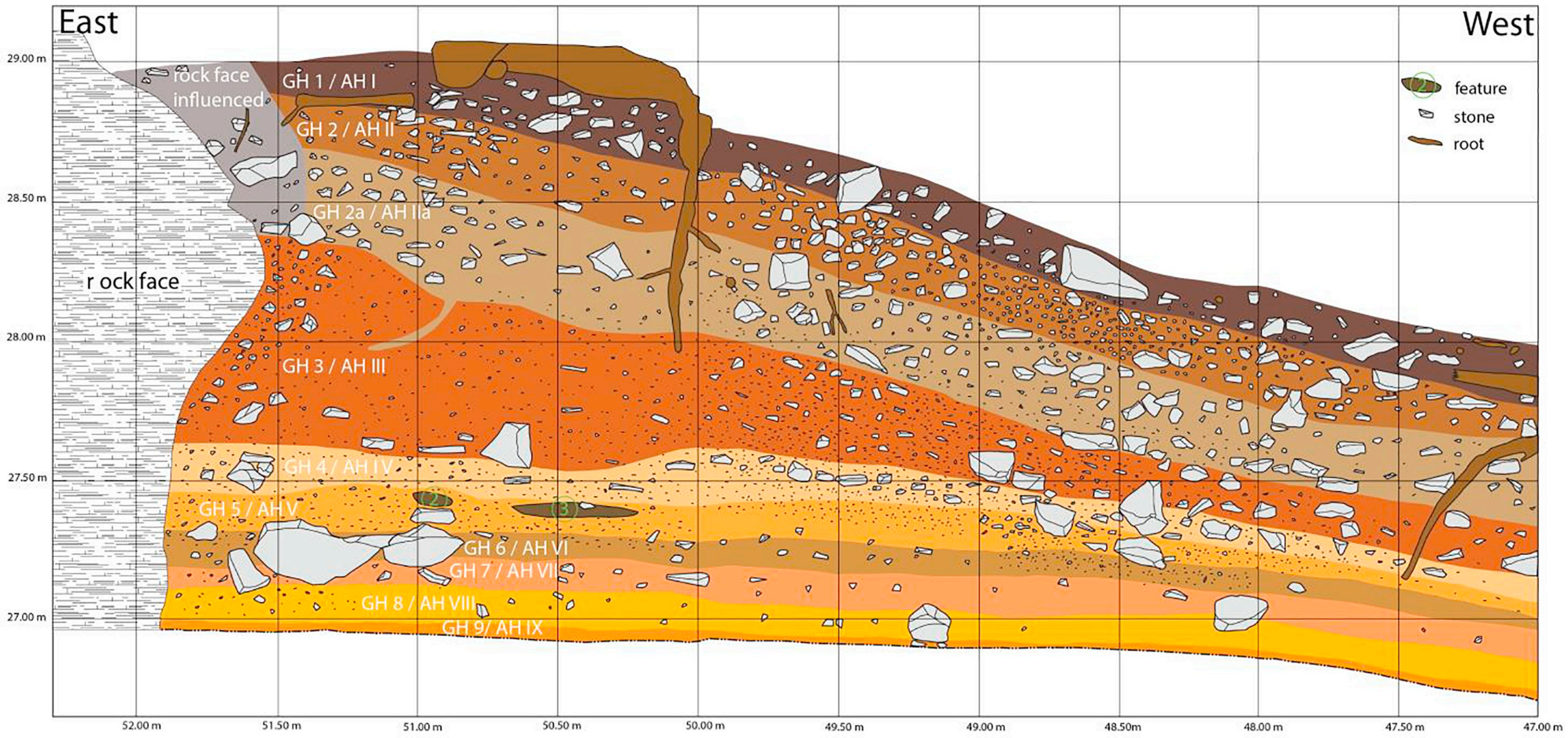

Fig. 2. The stratigraphy of Langmahdhalde during excavation years 2016 to 2019. This paper discusses only horizons from excavation years 2016 to 2018, meaning that the deepest horizon discussed here is GH6/AHVI. This stratigraphic profile is the southern wall of the site at the y-coordinate 37 (which runs east to west). GH1/AHI is a modern hummus layer. GH2/AHII has been dated to 2680–2354 cal yr BP. GH2a/AHIIa has artifacts from the Mesolithic but dates range throughout the Holocene. GH3/AHIII dates to the Late Glacial (14,653–14,034 cal yr BP). GH4/AHIV to GH6/AHVI are Late Magdalenian and have overlapping dates that range from 15,447 to 13,934 cal yr BP. Newly published dates and sources for previously published dates can be found in Table 1. Combustion features, stones, and roots can be identified based on the key in the upper right corner. Figure by A. Janas.

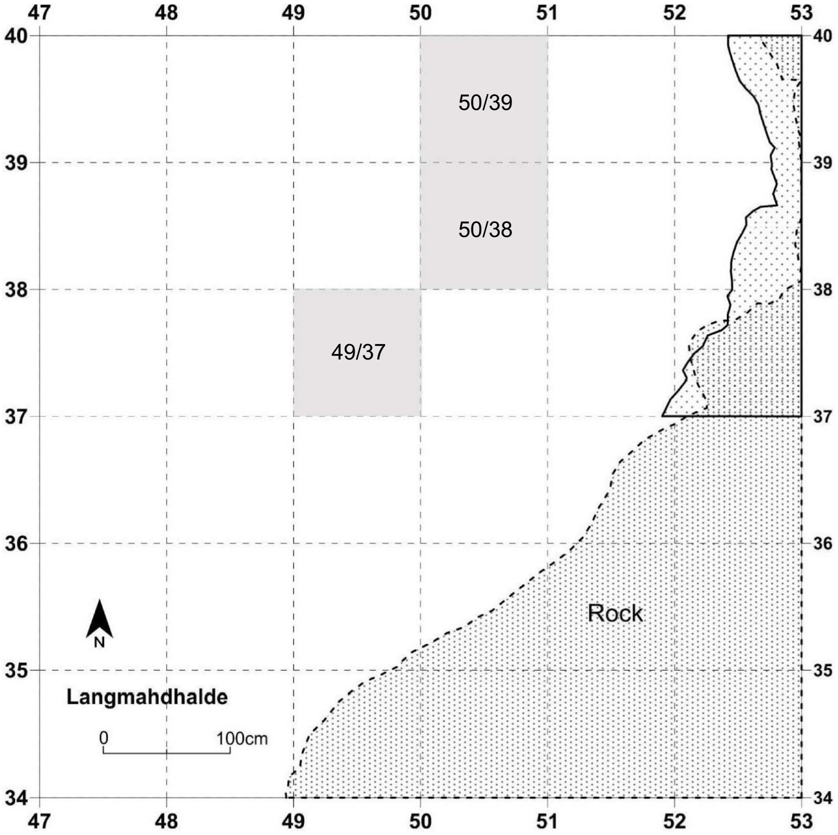

Fig. 3. Plan view of the excavation units at Langmahdhalde for the 2016 to 2018 excavations. The rockface is indicated by the stippled area on the right. Excavation units measure 1 × 1 m. The quadrants used for the micromammal analysis (49/37, 50/38, and 50/39) are shaded in grey. Figure by M. Zeidi.

relation to the rock face of the shelter (in reference to avian predator use of the shelter).

The microvertebrate remains from the site are recovered after excavated sediment is water screened through 1 × 1 mm mesh. For GHs 2, 2a, 4, 5, and 6 all sediment was kept for water screening, but due to the mostly archaeologically sterile nature of GH3, only one 50 × 50 cm sub-square of sediment from each 1 × 1 m quadrant in the excavation was kept for water screening from this GH. Further, in 2016 no sediment was kept for water screening from GH3 in quadrant 50/38. Therefore, there is a sampling bias towards fewer microvertebrate remains in GH3.

3. Methods

3.1. Microvertebrates

We define “microvertebrates” as specimens of small animals belonging to taxonomic groups that have a strong potential to reconstruct local environments and climates. In the case of this study, these are two mammalian orders: Rodentia and Eulipotyphla (when discussing Eulipotyphla further, we use the term “insectivores”). The species in these orders have relatively short lifespans, reproduce quickly, and have large litter sizes, causing them to respond quickly to climatic and environmental changes. This life history makes members of these orders particularly appropriate for environmental and climatic reconstructions (Grayson, 1981, 1984; Terry, 2010; Broughton and Miller, 2016: 95) and gives rise to larger sample sizes in the fossil record. Amphibian, reptile, and fish remains are also very useful in this respect, as they are often adapted to specific habitats (Blain et al., 2009; Broughton and Miller, 2016:18), but sample sizes for these taxa are small in the 2016–2018 Langmahdhalde assemblage, especially compared to rodent and insectivore remains, so these taxa are not included in this study.

In our analysis, we do not include specimens belonging to the genus *Microtus* that could not be identified to the species-level because they do not provide specific environmental or climatic information. There are two exceptions to this: those specimens identified to common or field vole (*M. arvalis* or *agrestis*) and to the Terricola group of the genus *Microtus* (see Niethammer and Krapp, 1982 and Wilson and Reeder, 2005 for discussions of this group). There is a long research history in Germany of not differentiating between the common and field vole but these species can be differentiated based on morphology (Borodin and Markova, 2015; Chaline, 1974; Dienske, 1969; Luzi, 2018; Luzi et al., 2017; Nadachowski, 1982) and metric analysis (Luzi, 2018; Nadachowski, 1984). Current research indicates that the differentiation between these two species does have implications for paleoenvironmental reconstructions (Luzi, 2018; Luzi et al., 2019, 2017; Luzi and López-García, 2017), although this concept has yet to be applied to the fossil record of the region studied here. We do not distinguish between the common and field vole in our work but did analyze a subset of these specimens from each horizon and each sub-layer of GHs 5 and 6 and determined, based on measurements and morphology, that both species are present in all horizons and every sub-layer of GHs 5 and 6. Our taxonomic identifications are based on several identification guides for insectivores and rodents (e.g. Repenning, 1967; von Koenigswald et al., 1974; Agadjanian et al., 1977; Niethammer and Krapp, 1978, 1982, 1990; Nadachowski, 1982) and the vertebrate comparative collection housed at the University of Tübingen's Institute for Archaeological Sciences. Our taxonomic classifications follow Wilson and Reeder (2005), except for our use of the order Eulipotyphla which is the recent version of the order including shrews, moles, and hedgehogs (Douady et al., 2002; Waddell et al., 1999).

Teeth were the most common element identifiable to a lower taxonomic category (i.e. genus or species), although we used mandibular and forelimb morphology where appropriate for insectivore identifications (Niethammer and Krapp, 1990; Repenning, 1967). We measured specimens belonging to the genera *Talpa*, *Sorex*, and *Apodemus* in order to assign them to the species-level. In the case of specimens identified to the genus *Sorex*, we used data taken from Ziegler (1995) and Maul (2001) to identify specimens to the species-level. In the case of *Apodemus* specimens, we used data on lower and upper first molar lengths reported in (Niethammer and Krapp, 1978: 326, 338, 361) to assign these specimens to the species-level. We measured humeri assigned to the genus *Talpa* and classified them to the species-level using measurements reported in von Koenigswald (1985) and Maul (2001). We took measurements using a Keyence Digital Microscope VHX-500F at the Institute for Archaeological Sciences at the University of Tübingen.

To prevent the overrepresentation of micromammal taxa that can be identified based on several elements, we use Minimum Number of Individuals (MNI; Grayson, 1984; Lyman, 2008) in our paleoclimatic and environmental reconstructions based on micromammals. We calculate the NISP (Grayson, 1984; Lyman, 2008) and MNI for each taxon by GH and sub-layer, where available.

3.2. Paleoenvironmental and climatic reconstruction using micromammals

To evaluate ecological diversity, we apply the reciprocal of Simpson's Diversity Index (Simpson, 1949) to the micromammal assemblage at Langmahdhalde. Simpson's Diversity Index measures the distribution of specimens across taxonomic categories and predicts the probability of picking two taxa at random that are different species. In this way, it measures “evenness.” An “even” assemblage is an assemblage in which all taxa are similarly abundant. An “uneven” assemblage is characterized by one or a few dominant taxa. Simpson's Diversity Index measures evenness by calculating the probability that two specimens in an assemblage will belong to the same taxon. The result of the calculation is the value “D,” which decreases as evenness increases. As this can make D confusing to interpret, we present values as 1/D, referred to as the reciprocal of Simpson's Index, as is common (Lyman, 2008), so that larger values are associated with greater evenness. We use the following version of the index, as it provides an unbiased estimate for finite samples, like zooarchaeological and paleontological samples (Pielou, 1969):

$$D' = \sum \left(\frac{n_i (n_i - 1)}{N (N - 1)} \right) \tag{1}$$

where n_i is the MNI of taxon i and N is the total MNI of the sample. Specimens not identified to the genus-level or below were not included in calculations of the Reciprocal of Simpson's Index. If, in a horizon, specimens existed that were identified to the genus *Talpa* and the species *Talpa europaea* or the genus *Sorex* and the species *Sorex araneus*, these specimens were grouped together for calculations. In GH6 sub-layers 1 and 2, we decided to include specimens identified to “Soricidae” and “Soricinae” in the calculations in order to represent the presence of insectivores in those sub-layers. The MNI values of these specimens were grouped together to represent one taxon in the calculations.

We also apply the Bioclimatic Analysis (BA; Hernández Fernández, 2001a, 2001b, Hernández Fernández and Peláez-Campomanes, 2003, 2005) to the micromammal assemblage from Langmahdhalde in order to reconstruct past environments and climates. The BA includes a qualitative model and several quantitative models, and uses Walter's (1970) climate zone nomenclature (Table 2). The qualitative model predicts the most probable climate zone that existed at a locality and the quantitative models predict specific climate variables for that locality. For each locality (or in this case, horizon) used in the BA, the researcher makes a species-to-climate zone matrix based on the modern occurrence of each species in Walter's (1970) climate zones. If the species does not exist in a climate zone, a value of 0 is given. The value given for each climate zone the species does exist in is equal to 1/n, n being the total number of climate zones the species exists in. (For details on how to determine whether a species inhabits a specific climate zone, see Hernández Fernández, 2001a.) The values assigned to a species for each climate zone are, together, referred to as the Climate Restriction Index, or CRI.

Table 2
Climate and Vegetation zones as defined by Walter (1970) and used in the Bioclimatic Analysis (Hernández Fernández, 2001b, 2001a; Hernández Fernández et al., 2007; Hernández Fernández and Peláez-Campomanes, 2005, 2003).

Zone	Climate	Vegetation type
I	Equatorial	Evergreen tropical rain forest
II	Tropical with summer rains	Tropical deciduous woodland
II/III	Transition tropical semi-arid	Savanna
III	Subtropical arid	Sub-tropical desert
IV	Subtropical with winter rains and summer drought	Sclerophyllous woodland-shrubland
V	Warm-temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	Steppe to cold desert
VIII	Cold-temperate (boreal)	Boreal coniferous forest (taiga)
IX	Polar	Tundra

We took CRI values for each species from Hernández Fernández (2001b). The CRI values for the modern narrow-headed vole (*Microtus gregalis*) are not included in Hernández Fernández (2001b), we therefore used modern narrow-headed vole distribution data from the International Union for Conservation of Nature's Red List (Batsaikhan et al., 2016) and criteria described in Hernández Fernández (2001a) to assign this species to climate zones VII, VIII, and IX. We used CRI values for *Lemmussibiricus* (Hernández Fernández, 2001b) for the specimen assigned to the genus *Lemmus* in this study.

Based on the species-to-climate matrix and the resulting CRI values, the researcher calculates the Bioclimatic Component (BC) for each climate zone in that horizon. The formula is as follows:

$$BC_i = (\Sigma CRI_i)100/S \tag{2}$$

where i is the climate zone, CRI is defined above, and S is the number of species present in the horizon. The BC value of each climate zone represents the percentage of the faunal assemblage that is characteristic of that climate zone. Together, the BC values of one horizon are referred to as the bioclimatic spectra. These BC values are then run through a discriminant function analysis constructed by Hernández Fernández and Peláez-Campomanes (2003) using 50 modern climate localities to predict the most probable climate zone (qualitative; Hernández Fernández and Peláez-Campomanes, 2003). We ran the linear discriminant function analysis in R Studio version 1.2.1335. To predict the climate variables of the quantitative models, the researcher applies the bioclimatic spectra to multiple linear regression models (Hernández Fernández and Peláez-Campomanes, 2005; see Supplementary Materials 1 for the multiple linear regression used for the quantitative models). We use the quantitative models to predict mean annual temperature, mean temperature of the warmest month, mean temperature of the coldest month, the thermicity index, winter length, vegetative activity period, free vegetative activity period, annual total precipitation, and drought length. Table 3 provides the details for each of these climate variables, including the determination coefficient and the standard error of the model for each variable.

These models were developed using different faunal groupings (e.g. “whole fauna” or all the mammals in the assemblage, rodent fauna, or micromammal fauna). In this study, we use the models developed specifically for rodents and, therefore, the results are based on the taxonomic composition of the rodent assemblage at Langmahdhalde.

Table 3

Climate variables reported in this study using the Bioclimatic Analysis for rodents. Information from Hernández Fernández and Peláez-Campomanes (2005). r^2 is the determination coefficient and SE is the standard error.

Abbreviation	Climate variable	Description	Units	r^2	SE
MAT	Mean annual temperature	Average of the mean monthly temperature	°C	0.930	3.6
MTW	Mean temperature of the warmest month		°C	0.746	4.8
MTC	Mean temperature of the coldest month		°C	0.932	5.1
It	Thermicity index	Measures the intensity of winter (It = 10(MAT + 2MTC))	0.1 °C	0.938	130.6
W	Winter length	Number of months in which the mean monthly temperature is < 0 °C	Months	0.920	1.0
VAP	Vegetative activity period	Number of months in which mean monthly temp is > 7 °C; estimates the length of plan winter dormancy and spring-summer growing periods	Months	0.955	0.9
FVAP	Free vegetative activity period	Gives the number of months in which both temperature and humidity allow the normal growing of vegetation (FVAP = VAP-D)	Months	0.918	1.3
P	Annual total precipitation		mm	0.746	471
D	Drought length	Estimates the length of the dry period or period in which $P < 2\text{MAT}$	Months	0.926	1.3

For the qualitative model, Hernández Fernández (2001a) found that when testing the accuracy of the BA values in predicting the climate zone in modern localities, rodents provide some of the best results and Hernández Fernández and Peláez-Campomanes (2003) report that 94% of localities classified to climate zone using rodent faunas were classified correctly. For the quantitative models, they show that using rodent faunas was, on average, better at reconstructing the climate variables than other faunal groups, especially in terms of predicting precipitation, which is one of the less reliable predictions in these regressions (Hernández Fernández and Peláez-Campomanes, 2005). They propose that these regressions do not predict precipitation as accurately as other climate variables because precipitation does not directly influence mammal populations and varies seasonally. They point out that it is vegetation, a secondary effect of precipitation, that more strongly affects mammal populations.

3.3. Stable isotope analysis

We extracted collagen from five horse and six reindeer specimens from GH4/AHIV and GH5/AHV (Table 4). We chose these specimens based on their age (adult specimens were preferred), the presence of cortical bone, their preservation, and element. Six of these samples have green fractures and two of the horse specimens have cutmarks, indicating that at least the remains with cutmarks were associated with human activities. One of the horse specimens has been dated to 15,210–14,765 cal yr BP (Table 4).

We extracted collagen in the laboratory of the Biogeology Working Group within the Department of Geosciences at the University of Tübingen and followed protocol based on Longin (1971) and modified by Bocherens et al. (1997). Briefly, the extraction procedure includes a step of demineralization in HCl 1 M, a step of soaking in 0.125 M NaOH, and a final step of solubilization in acidified water (pH = 2) before freeze-drying. Elemental analysis (C_{coll} and N_{coll}) was conducted at the Department of Geosciences at the University of Tübingen. The Laboratory of Chronology, Finnish Museum of Natural History, University of Helsinki, conducted the isotopic analysis ($\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$) using an NC 2500 elemental analyzer coupled to a DeltaPlusAdvantage or a DeltaVPlus isotope ratio mass spectrometer. Measurement data for $\delta^{13}C$ and $\delta^{15}N$ were calibrated using the known values of international reference materials USGS-40 ($\delta^{13}C = -26.39‰$, $\delta^{15}N = -4.5‰$), USGS-41 ($\delta^{13}C = +37.63‰$, $\delta^{15}N = +47.6‰$). Multiple measurements of matrix matched in-house reference materials (modern camel and elk bone) indicate an external reproducibility (1σ) of ± 0.19‰ for $\delta^{13}C$, ± 0.24‰ for $\delta^{15}N$ values. The error in the reproducibility for the amounts of C and N was better than 4%. Measuring the chemical composition of collagen can establish the reliability of the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values, with $C{:}N_{coll}$ atomic ratio ranging from 2.9 to 3.6 (DeNiro, 1985) and percentage of C_{coll} and N_{coll} above 8% and 3%, respectively (Ambrose, 1990).

4. Results

4.1. Micromammal results

Table 5 shows the NISP and MNI of each taxon represented in the Langmahdhalde micromammal assemblage by GH and sub-layer for GHs 5 and 6. Fig. 4 shows a selection of specimens from the micromammal assemblage representing the most common taxa. For more details on the morphology and taxonomic identifications of the assemblage, see Supplementary Materials 2. In total, we included 5144 specimens in this study (Table 5). Common/field voles, collared lemmings, red-backed voles, and narrow-headed voles are the most commonly represented species. Collared lemmings are primarily present in GH4 to GH6. There is one collared lemming specimen in GH2 but we assume this specimen is intrusive. In terms of the horizons associated with the Magdalenian, cold-adapted species are more common, such as lemmings, who prefer alpine, tundra, and tundra forest environments and polar and subpolar climates (Hansson, 1999; Tsytsulina et al., 2016). The narrow-headed vole, similarly, inhabits tundra environments but also steppic and grassy open areas (Batsaikhan et al., 2016) and is present in relatively high numbers in GHs 4 through 6. GH3 has very few specimens compared to the other horizons and it is unclear whether this reflects a true trend in deposition or the field sampling bias of this horizon.

4.1.1. Diversity index

The results of the reciprocal of Simpson's Diversity Index calculations are presented in Table 6. GH3 has the highest evenness values at Langmahdhalde, meaning all taxa are represented fairly equally, although this is potentially a factor of the sampling bias of this horizon, not of the actual evenness of this assemblage. Excluding GH3, the Holocene horizons (GH2 and GH2a) have higher evenness values than the Pleistocene horizons.

4.1.2. Bioclimatic analysis

The results of the quantitative models are presented in Table 6 and Fig. 5, while the results of the qualitative model are presented in Table 7. In Supplementary Materials 3, we report the Bioclimatic Spectra for each horizon at Langmahdhalde, including by sub-layer for GH5 and GH6. In Supplementary Materials 4, we present the R code used to perform the discriminant function analysis for the qualitative model.

When performing the discriminant function analysis for the qualitative model, we were unable to replicate the coefficients Hernández

Table 4
Information for the specimens we conducted stable isotope analysis on from Langmahdhalde as well as those specimens we use to discuss broader trends. Dates were calibrated using OxCal v4.3.2 (Bronk Ramsey, 2017) and IntCal13 atmospheric curve (Reimer et al., 2013) and ranges reported represent the 95% confidence interval. The original uncalibrated dates come from these sources: 1 = Stevens and Hedges, 2004; 2 = Bodu et al., 2009; 3 = Napierala, 2008.

Region	Site	Lab number	Species	Element	Excavation number	Horizon	Cultural association	Ref ^{14}C	Date ^{14}C	Date ^{14}C	Source ^{14}C dates
									yr uncal BP	yr cal BP	
Swabian Jura	Langmahdhalde	LGN-6	Reindeer (*Rangifer tarandus*)	Tibia R	LH 47/37_156	GH5/AHV sub-layer 2	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-9	Reindeer (*Rangifer tarandus*)	Metatarsal	LH 48/39_129	GH4/AHIV	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-10	Reindeer (*Rangifer tarandus*)	Mandible R	LH 50/38_297	GH5/AHV sub-layer 3	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-12	Reindeer (*Rangifer tarandus*)	Mandible R	LH 51/37_201	GH5/AHV sub-layer 2	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-13	Reindeer (*Rangifer tarandus*)	Metatarsal	LH 52/38_100	GH5/AHV sub-layer 1	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-14	Reindeer (*Rangifer tarandus*)	Metatarsal	LH 50/39_133	GH4/AHIV	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 363	Reindeer (*Rangifer tarandus*)	Metapodial L distal		P1 AH2	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 364	Reindeer (*Rangifer tarandus*)	Metapodial R distal		P1 AH2	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 365	Reindeer (*Rangifer tarandus*)	Calcaneus R		P1 AH2	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 366	Reindeer (*Rangifer tarandus*)	Talus R		P1 AH2	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 367	Reindeer (*Rangifer tarandus*)	Tibia R distal		P1 AH2	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 368	Reindeer (*Rangifer tarandus*)	Calcaneus L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 369	Reindeer (*Rangifer tarandus*)	Talus L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 370	Reindeer (*Rangifer tarandus*)	Tibia L distal		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 371	Reindeer (*Rangifer tarandus*)	Calcaneus L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 373	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 374	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 375	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 376	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 377	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 379	Reindeer (*Rangifer tarandus*)	Tibia L		P1 AH3	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 380	Reindeer (*Rangifer tarandus*)	Metapodial R distal		P1 AH4	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 381	Reindeer (*Rangifer tarandus*)	Metapodial R		P1 AH4	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 382	Reindeer (*Rangifer tarandus*)	Metapodial R distal		P1 AH4	Magdalenian				
Swabian Jura	Petersfels	RA-PTF 383	Reindeer (*Rangifer tarandus*)	Tibia R		P1 AH4	Magdalenian				

(*continued on next page*)

Table 4 (*continued*)

Region	Site	Lab number	Species	Element	Excavation number	Horizon	Cultural association	Ref ^{14}C	Date ^{14}C	Date ^{14}C	Source ^{14}C dates
									yr uncal BP	yr cal BP	
Swabian Jura	Schussenquelle	SCH-1	Reindeer (*Rangifer tarandus*)	Femur R			Magdalenian				
Swabian Jura	Schussenquelle	SCH-2	Reindeer (*Rangifer tarandus*)	Femur R			Magdalenian				
Swabian Jura	Schussenquelle	SCH-3	Reindeer (*Rangifer tarandus*)	Femur R			Magdalenian				
Swabian Jura	Schussenquelle	SCH-4	Reindeer (*Rangifer tarandus*)	Femur R			Magdalenian				
Swabian Jura	Schussenquelle	SCH-5	Reindeer (*Rangifer tarandus*)	Femur R			Magdalenian				
Swabian Jura	Felsställe	FLS-7	Reindeer (*Rangifer tarandus*)	Mandible	Q8 Nr1515	AH3	Late Magdalenian				
Swabian Jura	Felsställe	FLS-8	Reindeer (*Rangifer tarandus*)	Mandible	Q304 Nr59 Nr54 + 43	AH3a	Late Magdalenian				
Swabian Jura	Felsställe	FLS-9	Reindeer (*Rangifer tarandus*)	Mandible	Q300 Nr352 + 365	AH3b	Late Magdalenian				
Swiss Jura	Kesslerloch	RA-KSL-620	Reindeer (*Rangifer tarandus*)	Metacarpal							
Swiss Jura	Kesslerloch	RA-KSL-628	Reindeer (*Rangifer tarandus*)	Tibia R		KSLH Is					
Swiss Jura	Kesslerloch	RA-KSL-632	Reindeer (*Rangifer tarandus*)	Humerus R		KSLH IIs					
Swiss Jura	Kesslerloch	RA-KSL-633	Reindeer (*Rangifer tarandus*)	Humerus R		KSLH IIs					
Swiss Jura	Kesslerloch	RA-KSL-635	Reindeer (*Rangifer tarandus*)	Humerus L		KSLH IIIn					
Swabian Jura	Langmahdhalde	LGN-4	Horse (*Equus ferus*)	Humerus R	LH 48/38_170	GH5/AHV sub-layer 1	Magdalenian	ETH-84042	12,636 ± 47	15,210–14,765	This work
Swabian Jura	Langmahdhalde	LGN-5	Horse (*Equus ferus*)	Metatarsal R	LH 47/37_124	GH4/AHIV	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-7	Horse (*Equus ferus*)	Metatarsal R	LH 47/38_129	GH4/AHIV	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-8	Horse (*Equus ferus*)	Metacarpal	LH 47/38_142	GH5/AHV sub-layer 1	Magdalenian				
Swabian Jura	Langmahdhalde	LGN-11	Horse (*Equus ferus*)	Radius	LH 50/39_171	GH5/AHV sub-layer 1	Magdalenian				
Swabian Jura	Geißenklösterle	OxA-5158	Horse (*Equus ferus*)					OxA-5158	12,450 ± 120	14,850–14,282	1
Swabian Jura	Schussenquelle	SCH-10	Horse (*Equus ferus*)	Metatarsal distal L	Nr.4816.14		Magdalenian	GrA-45305	12,250 ± 50	14,248–14,051	This work
Swiss Jura	Kesslerloch	KSL-1	Horse (*Equus ferus*)	1st phalanx anterior	NESH:232	KESLN	Magdalenian	KIA-11825	12,774 ± 54	15,316–15,113	3
Swiss Jura	Kesslerloch	KSL-2	Horse (*Equus ferus*)	Metacarpal L	MEQ1:253	KESLM	Magdalenian	KIA-11826	12,502 ± 52	15,031–14,482	3
Swiss Jura	Kesslerloch	KSL-5	Horse (*Equus ferus*)	Metacarpal L	HE33:24	KESLH IIIn	Magdalenian	KIA-11829	12,897 ± 53	15,569–15,251	3
Switzerland	Champréveyres	CHM-2	Horse (*Equus ferus*)	Astragalus R	HrCh85 O21 #12	Sector 1	Magdalenian	OxA-20700	12,815 ± 65	15,387–15,142	2
Switzerland	Champréveyres	CHM-4	Horse (*Equus ferus*)	Astragalus R	HrCh85 L22 #178	Sector 1	Magdalenian	OxA-20701	12,805 ± 75	15,361–15,131	2

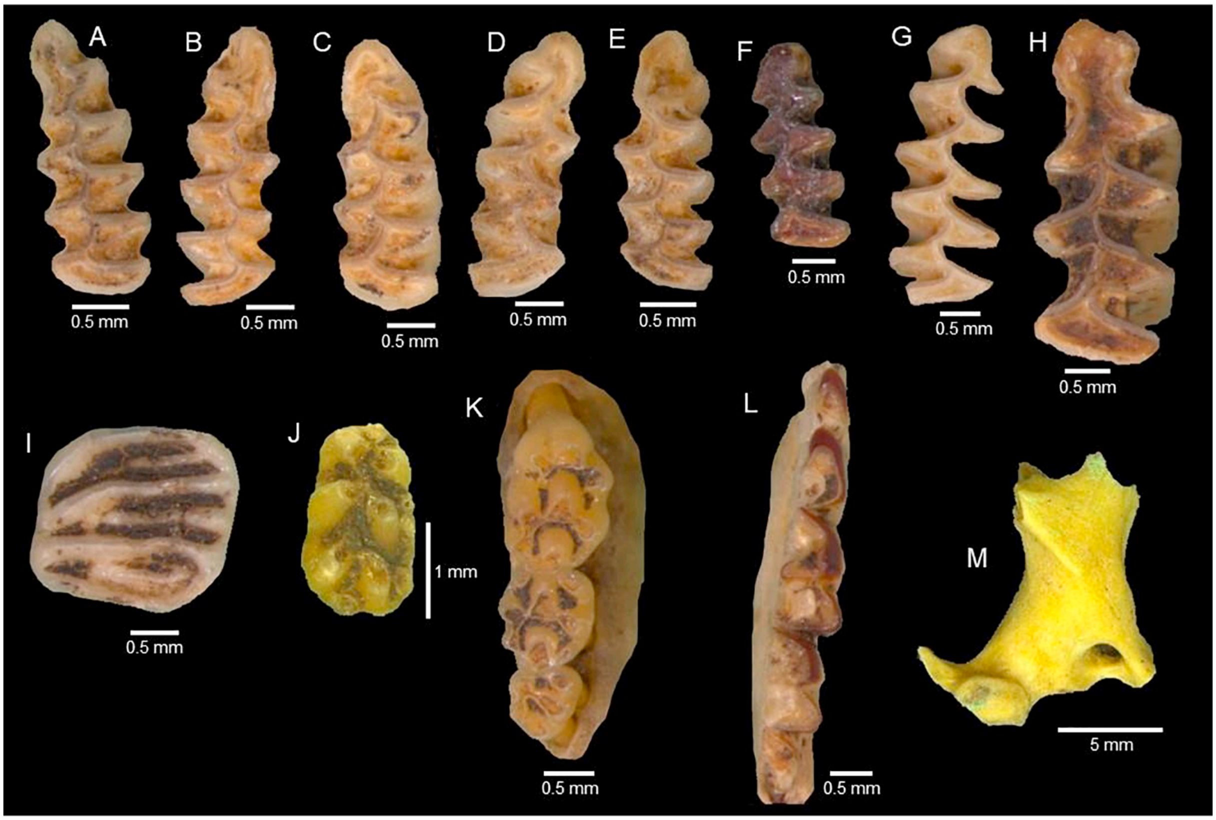

Fig. 4. Specimens from the Langmahdhalde micromammal assemblage. Occlusal view of teeth shown. A = left lower M1 of *Microtus arvalis/agrestis* (LH50/38_375); B = right lower M1 of *Microtus arvalis/agrestis* (LH49/37_164); C = left lower M1 of *Chionomys nivalis* (LH49/37_159); D = right lower M1 of *Microtus oeconomus* (LH49/37_159); E = left lower M1 of *Lasiopodomys gregalis* (LH49/37_153); F = right lower M1 of *Myodes glareolus* (LH50/38_61); G = right lower M1 of *Dicrostonyx* sp. (LH49/37_153); H = left lower M1 of *Arvicola amphibius* (LH50/38_44); I = left upper M2 of *Glis glis* (LH50/39_62); J = right lower M1 of *Apodemus flavicollis* (LH49/37_31); K = right upper M1, M2, and M3 of *Apodemus flavicollis* (LH51/38_92); L = right lower P3, P4, M1, M2, and M3 of *Sorex araneus* (LH50/38_44); M = humerus of *Talpa europaea* (LH49/37_139). All specimens are stored at the Institute for Archaeological Sciences at the University of Tübingen.

Fernández and Peláez-Campomanes (2003) report for their rodent qualitative model (see their Appendix 2.2). We were, however, able to confirm that the linear discriminant function analysis we created in R, using the original 50 localities from the qualitative model, works (Supplementary Materials 4). It is likely that this discrepancy between our work in R and the work of the original authors lies in the algorithms in SPSS, which are not publicly available, or that we normalized the data or set the discriminant function analysis slightly differently than the original authors but this should not adversely affect the results of our model.

The results of the qualitative model suggest that throughout the occupation of Langmahdhalde, zones VI (typical temperate climate with nemoral broadleaf-deciduous forest vegetation) and IX (polar climate with tundra vegetation) were the most common climate zones. The quantitative models for the Late Glacial horizons (GH4 through GH6) predict that mean annual temperatures ranged between −3.2 °C and 0.3 °C, with summers as warm as 12 °C and winters as cold as −12 °C or −13 °C (Table 6). The difference between the Holocene and Pleistocene results of the quantitative models are very pronounced in Fig. 5. There is a clear difference in the intensity and duration of winter between the Holocene horizons (GH2 and 2a) and the Pleistocene horizons (GH3 through 6): the Pleistocene appears to have had longer and more intense winters that lasted between three and five months, a third or more of the year, whereas Holocene winters are reconstructed as only one or two months. Both measures of vegetative activity period (VAP and FVAP) indicate that vegetative growth was occurring for less than five months out of the year and as little as three months and a few weeks during the Late Glacial. Finally, precipitation and drought values suggest there was never a full month of drought and annual precipitation ranged between approximately 800 and 1000 mm per year during the Late Glacial. In the Holocene horizons, temperatures are warmer, the length of winter is shorter, vegetative activity periods are longer by two to four months, and annual precipitation is one and a half times more than in the Pleistocene.

Across the Late Glacial horizons and sub-layers, we see similar climate variables reconstructed by the quantitative models, with some exceptions. GH4 shows the warmest temperatures and the shortest and least intense winter, however, these values are not greatly different from the values of the other horizons and sub-layers. The vegetative activity periods (VAP and FVAP) are both higher in this horizon than the other values from the Late Glacial. GH6 sub-layer 1 also stands out in terms of precipitation and drought; this sub-layer has the lowest value for precipitation and the only non-negative value for drought.

4.2. Stable isotope results

Table 8 shows the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ results from the Langmahdhalde horse and reindeer specimens as well as stable isotope values of bone collagen from reindeer and horse from other archaeological sites in the Swabian Jura and Switzerland (see Fig. 1 for the location of all sites mentioned in this paper). Fig. 6 shows these values graphically: 6A has only the results from Langmahdhalde, 6B displays the reindeer $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ results from both Switzerland and the Swabian Jura (including Langmahdhalde), and 6C shows the same for horse. The $\delta^{13}C_{coll}$ values for the horse specimens from Langmahdhalde range from −21.0‰ to −20.7‰ and from −20.1‰ to −19.4‰ for reindeer. The Langmahdhalde $\delta^{15}N_{coll}$ values for horse range from +2.1‰ to +3.1‰ and from +1.6‰ to +2.5‰ for reindeer.

Table 5
Langmahdhalde micromammal summary table showing the NISP and MNI of each taxon by geological horizon. GH5 and GH6 are presented by sub-layer. Totals appear on the far right and the bottom of the table. Data are based on specimens from quadrants 49/37, 50/38, and 50/39 from excavation years 2016–2018.

Common name	Taxon	GH2		GH2a		GH3		GH4		GH 5 sub-layer 1		GH5 sub-layer 2	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Moles	*Talpa* sp.	5	2	5	2			1	1				
Common mole	*Talpa europaea*	1	1					1	1				
Shrews	Soricidae indet.	4	1										
Red-toothed shrews	Soricinae indet.	5	2	1	1			2	1				
Long-tailed shrews	*Sorex* sp.	1	1					1	1				
Common shrew	*Sorex araneus*	1	1					2	1				
Eurasian water shrew	*Neomys fodiens*							1	1				
White-toothed shrews	*Crocidura* sp.			1	1								
Dormice and hazel mice	Gliridae indet.	1	1										
Edible dormouse	*Glis glis*	11	1							1	1		
Yellow-necked/wood mouse	*Apodemus flavicollis/ sylvaticus*	6	1									1	1
Yellow-necked mouse	*Apodemus flavicollis*	15	5	4	2			1	1				
Common/field vole	*Microtus arvalis/ agrestis*	36	18	30	15	3	2	400	201	52	28	73	40
Common/field vole OR narrow-headed vole	*Microtus arvalis/ agrestis* OR *Lasiopodomys gregalis*			1	1			15	8			1	1
Narrow-headed vole	*Lasiopodomys gregalis*					1	1	259	142	27	18	21	14
Tundra vole	*Microtus oeconomus*			1	1	1	1	10	5	2	2	3	3
Terricola group	Genus *Microtus*	6	3	3	2								
Eurasian snow vole	*Chionomys nivalis*	4	3	1	1			10	5				
Collared lemming	*Dicrostonyx* sp.	1	1			5	2	649	112	116	21	245	45
Brown lemmings and true lemmings	*Lemmus* sp.									1	1		
Water vole	*Arvicola amphibius*	18	6	15	4			1	1			1	1
Red-backed vole	*Myodes glareolus*	161	24	144	23	3	1	4	1	2	1	1	1
	Total	276	71	206	53	13	7	1357	482	201	72	346	106

Common name	GH5 sub-layer 3		GH5 sub-layer 4		GH5 sub-layer 5		GH5 sub-layer 6		GH6 sub-layer 1		GH6 sub-layer 2		GH6 sub-layer 3		Total NISP	Total MNI
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI		
Moles															11	5
Common mole															2	2
Shrews			1	1					1	1					6	3
Red-toothed shrews									4	1	1	1			13	6
Long-tailed shrews			1	1											3	3
Common shrew			1	1											4	3
Eurasian water shrew															1	1
White-toothed shrews															1	1
Dormice and hazel mice															1	1
Edible dormouse															12	2
Yellow-necked/wood mouse							1	1	8	1					16	4
Yellow-necked mouse															20	8
Common/field vole	112	65	70	38	35	22	36	19	40	22	81	42	53	30	1021	542
Common/field vole OR narrow-headed vole	4	3	9	5	4	2			3	3	2	2	4	3	43	28
Narrow-headed vole	54	30	44	24	22	13	27	17	37	19	38	22	42	22	572	322

(*continued on next page*)

Table 5 (*continued*)

Common name	GH5 sub-layer 3		GH5 sub-layer 4		GH5 sub-layer 5		GH5 sub-layer 6		GH6 sub-layer 1		GH6 sub-layer 2		GH6 sub-layer 3		Total NISP	Total MNI
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI		
Tundra vole	4	2	1	1	1	1	1	1							24	17
Terricola group															9	5
Eurasian snow vole			1	1					1	1					17	11
Collared lemming	500	82	300	45	185	26	223	37	315	44	321	59	148	35	3008	509
Brown lemmings and true lemmings															1	1
Water vole	6	2	1	1					1	1					43	16
Red-backed vole			1	1											316	52
	680	184	430	119	247	64	288	75	410	93	443	126	247	90	5144	1542

We also report $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values for a previously unpublished horse specimen from Schussenquelle. The $\delta^{13}C_{coll}$ value for this specimen is −21.2‰ and the $\delta^{15}N_{coll}$ value is +4.5‰, making it the highest ^{15}N and lowest ^{13}C relative amounts discussed in this paper. This specimen has been directly dated to 14,248 to 14,051 cal BP (GrA-45305; see Table 4).

5. Late Magdalenian paleoecology in the Swabian Jura

One of the more powerful aspects of the BA is that it allows researchers to compare predicted paleoclimate variables with modern ones. In Fig. 5 we display the results of the quantitative models from Langmahdhalde and modern temperature and precipitation data. These modern data represent the last ten years (from 2009 to 2018) as recorded at the weather station in Hermaringen, approximately 6 km northeast from Langmahdhalde (station "Hermaringen-Allewind," ID# 7331; data downloaded on 8 November 2019 from the Deutscher Wetterdienst, Climate Data Center version 2.0.v1907). The temperature graph of Fig. 5 shows that the MTW and MAT values from Langmahdhalde are all lower than today, while the Holocene values of MTC from Langmahdhalde are usually colder except in GH2, where they are warmer. Further, modern precipitation values are much lower than those that we have reconstructed based on the micromammals from Langmahdhalde.

We can also compare the climate variables from those GHs and sub-layers assigned to polar climates with tundra vegetation (zone IX) to those same climate variables from today's polar regions. The temperature values we report for the sub-layers assigned to polar climates (GH3, GH5 sub-layers 5 and 6, and GH6 sub-layers 2 and 3) generally fall within the range of modern polar climates with the exception of winter temperatures, which today can average approximately −34 °C ("The Tundra Biome", 2004). Vegetative activity periods and growing seasons in modern tundra environments are very short, only two to two and a half months (Woodward, 2012a), less than what we find in the Magdalenian horizons at Langmahdhalde with the BA. Modern polar regions are generally treeless, in part because of the short growing season (Grace et al., 2002; Payer et al., 2013). The longer vegetative activity periods we find may have therefore promoted tree growth, indicating that, although the environment was generally open, trees could have been present.

The precipitation values that our quantitative model predicts are quite different than those of modern polar climates. We predict between 965 and 982 mm of annual precipitation, while modern tundra environments usually have very low precipitation, < 127 mm per year (Woodward, 2012a). As mentioned above, and as highlighted by the authors of the model (Hernández Fernández and Peláez-Campomanes, 2005), the r^2 and standard error values (Table 3) of the quantitative models indicate that precipitation predictions are not as reliable as other variables, such as temperature. But we argue that taking all of our data into account, it is likely that our higher precipitation values are a reflection of a less uniform environment and pockets of more vascular vegetation, including stands of trees, and their associated faunal communities in the region. The standard error for precipitation values in the quantitative models is 471 mm (Table 3), indicating that Late Glacial precipitation in the area of Langmahdhalde could have actually been about half what we predict. Even taking this into account, the micromammal assemblage at Langmahdhalde still predicts more precipitation than the average modern tundra environment receives. Coupled with our data on longer vegetative activity periods, the data support the presence of more densely vegetated areas.

Above, we mention the similarity of the values from the quantitative models across GHs 4, 5, and 6. At first glance, this and the relative uniformity of the results of the reciprocal of the Simpson's Diversity Index for these horizons do not seem to indicate that the environment was mosaic in nature. Further, the reindeer $\delta^{13}C_{coll}$ values from both Langmahdhalde and other Swabian Jura sites indicate a generally open

Table 6

Results of the reciprocal of Simpson's Diversity Index on the micromammal assemblage and the quantitative models from the BA on the rodents from Langmahdhalde for each GH. GH5 and GH6 are presented by sub-layer. Data are based on specimens from quadrants 49/37, 50/38, and 50/39 from excavation years 2016–2018.

Calculated variable	GH 2	GH 2a	GH 3	GH 4	GH 5 sub-layer 1	GH5 sub-layer 2	GH 5 sub-layer 3	GH 5 sub-layer 4	GH 5 sub-layer 5	GH 5 sub-layer 6	GH 6 sub-layer 1	GH 6 sub-layer 2	GH 6 sub-layer 3
Reciprocal of Simpson's	4.19	3.35	10.50	3.07	3.44	2.88	2.79	3.16	2.98	2.85	2.97	2.72	2.97
MAT (°C)	6.7	4.2	−1.7	1.2	−0.4	−0.6	−0.7	−3.2	−2.0	−2.0	0.3	−1.5	−1.5
MTW (°C)	15.4	14.6	10.3	12.3	11.4	11.7	11.2	12.0	9.4	9.4	12.1	9.6	9.6
MTC (°C)	−1.1	−5.4	−12.9	−9.1	−11.5	−12.3	−11.8	−12.0	−12.5	−12.5	−10.7	−11.5	−11.5
It (0.1 °C)	44.3	−65.4	−274.6	−170.6	−234.5	−251.3	−242.8	−242.1	−269.0	−269.0	−211.3	−244.7	−244.7
W (months)	0.6	1.9	4.5	3.4	4.1	4.3	4.4	4.2	4.6	4.6	4.1	4.4	4.4
VAP (months)	5.6	5.0	3.0	4.0	3.5	3.5	3.4	3.7	2.8	2.8	3.9	2.9	2.9
FVAP (months)	7.1	6.2	4.1	4.7	4.3	4.1	3.8	4.0	3.7	3.7	3.8	3.8	3.8
P (mm)	1515	1282	982	1047	987	913	887	869	965	965	840	996	996
D (months)	−1.7	−1.3	−1.3	−0.8	−1.0	−0.7	−0.5	−0.4	−1.1	−1.1	0.0	−1.0	−1.0

environment, as they are all higher than −21‰ (Table 8; Bocherens, 2003; Drucker et al., 2008). But when we take scale into account, a more complex picture emerges. Stable isotope results obtained from bone collagen are time averaged over the lifetime of the individual sampled. The interpretations based on these results therefore operate at a larger spatial scale compared to the scale data obtained from micromammal assemblages. Within the smaller-scale micromammal results, the quantitative models predict climate variables at the annual scale which can make interpretations of precipitation, and other more seasonal variables, difficult. The stable isotopes, quantitative models, and diversity index all reconstruct an open environment with a low faunal diversity and polar climate, as several studies have done in the past. But, our study takes all of these data from one site and considers them together, with the addition of the qualitative model. Together, these different scales of environmental data provide a more detailed interpretation and support the idea that Late Glacial landscapes in the Swabian Jura were more heterogeneous than today's polar regions.

We expected the qualitative model applied to the Langmahdhalde rodent assemblage to classify GHs 3 to 6 as zone VII, VIII, or IX, as Late Glacial environments of Central Europe have generally been characterized as steppe or tundra (Frenzel, 1983; Koenigswald, 2003; Otte, 2009; Weniger, 1989). This is the case for GH3, two sub-layers of GH5, and two sub-layers of GH6, but the remaining horizons and sub-layers were assigned to zone VI, nemoral broadleaf-deciduous forest. The qualitative model does not, therefore, predict one continuous climate during the Late Glacial in the region of Langmahdhalde and even suggests that more temperate forests, requiring more precipitation, were present. Our results could be interpreted as change over time or, perhaps more likely, a mosaic of environments across the landscape, with temperate mammalian taxa coming into and out of the region as the climate ameliorated.

At first glance, the results of the qualitative and quantitative models during the Late Glacial at Langmahdhalde seem to disagree with one another. While the qualitative model for several horizons and sublayers reconstructs a nemoral forest, the values for the climate variable reconstructed by the quantitative model fit more within vegetative zones with lower temperatures and shorter growing periods than exist in modern nemoral forests (Woodward, 2012b). Hernández Fernández (2006) also finds discrepancies between the quantitative and qualitative models that he applied to the rodent remains from Gigny, in eastern France. He suggests two possible explanations for these discrepancies: (1) the presence of birch (*Betula* sp.) trees in the past environment and (2) potential differences in the relationship between vegetation and climate due to different concentrations of atmospheric CO_2 in the past and today. He explains that, when abundant, birch, a broadleaved-deciduous tree, can provoke vegetative growth that is similar to that in nemoral forests. The presence of birch in the Swabian Jura during the Late Glacial does have explanatory potential as modern tundra environments do often have birch trees (Woodward, 2012a). In fact, pollen records in southwest Germany do demonstrate the presence (Maier, 2015: 69), and even increase (Duprat-Oualid et al., 2017), of birch during the time of occupation at Langmahdhalde.

Regarding differences in atmospheric CO_2, Hernández Fernández (2006) describes how broadleaf-deciduous forests could develop even when temperatures are colder than commonly found in modern areas with this type of vegetation. If the atmospheric levels of CO_2 were lower, the optimal temperature for photosynthesis in C3 plants would also be lower (Cowling and Sykes, 1999), allowing deciduous forests to persist in regions with cooler temperatures. It is possible that atmospheric CO_2 levels were lower during the time span of Langmahdhalde as Figge and White (1995) find a decrease in atmospheric CO_2 levels at approximately 12,200 yr uncal BP (approximately 14,183 to 14,003 yr cal BP; Bronk Ramsey, 2017, 2009; Reimer et al., 2013), which overlaps with some of the dates from the Late Glacial horizons at Langmahdhalde (see Table 1).

As discussed by Drucker et al. (2012), the $\delta^{13}C_{coll}$ values of Late Glacial reindeer appear to track a transition in the diets of these populations in southern Central Europe. Specifically, there is a decrease of lichens in their diets as more vascular plants expand into the environment. Both the reindeer values from Langmahdhalde and the results of the qualitative model reflect this change and provide further evidence for the slow loss of preferred habitat for these animals, leading to the addition of more browsing in their diet. This is further supported by the longer vegetative activity periods and higher precipitation values we find with the quantitative models.

The horse and reindeer stable isotope data reported here also provide a compelling history of large ungulate ecology in different regions during the Late Glacial. Table 8 includes $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values from not only Langmahdhalde but also other contemporary archaeological sites in the Swabian Jura and Switzerland. Our results suggest that reindeer and horse were behaving differently from one another during this period. The reindeer values in both the $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ are similar in southern German and in Swiss specimens and it can therefore be assumed that these populations exploited similar niches and had similar subsistence strategies. The horse values, conversely, display a more regional signal: those from southern Germany and those from Switzerland cluster separately, suggesting that horse populations were more flexible and exploited different niches based on their local

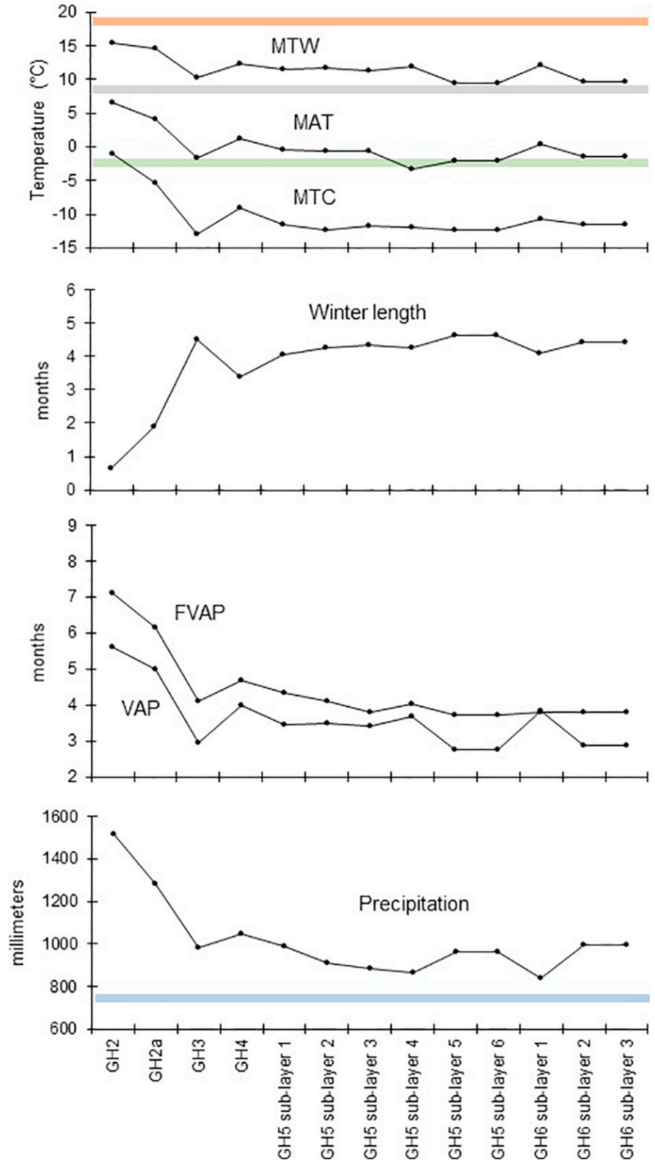

Fig. 5. Temperature, winter length, vegetative activity period, and precipitation results of the qualitative models from the BA using the rodent assemblage at Langmahdhalde. The orange band on the temperature graph represents the modern MTW near Langmahdhlade, which is approximately 18.5 °C; the gray band represents the modern MAT, approximately 8.0 °C; the green band represents the modern MTC, approximately -2.2 °C. The light blue band on the precipitation graph represents the modern average annual precipitation, which is approximately 671 mm. Results are presented by GH (where GH2 is the most recent and GH6 is the oldest). GHs 5 and 6 are presented by sub-layer. The rodent material is from quadrants 49/37, 50/38, and 50/39. MTW = mean temperature of the warmest month; MAT = mean annual temperature; MTC = mean temperature of the coldest month; FVAP = free vegetative activity period; VAP = vegetative activity period. These climate variables are defined in Table 3. Modern data from the Deutscher Wetterdienst Climate Data Center from weather station Hermaringen-Allewind (ID# 7331) for 1 January 2009 to 31 December 2018.

Table 7
Results of the qualitative model from the BA on the rodents from Langmahdhalde for each GH.GH5 and GH6 are presented by sub-layer. Data are based on specimens from quadrants 49/37, 50/38, and 50/39 from excavation years 2016–2018. P1: probability of the highest probability climate zone; P2: probability of the second highest probability climate zone.

GH	Highest probability climate zone	P1	2nd highest probability climate zone	P2
2	VI	1.00	VIII	0.00
2a	VI	1.00	VIII	0.00
3	IX	0.59	VI	0.41
4	VI	1.00	VIII	0.00
5 sub-layer 1	VI	1.00	IX	0.00
5 sub-layer 2	VI	1.00	VIII	0.00
5 sub-layer 3	VI	0.83	IX	0.17
5 sub-layer 4	VI	0.99	IX	0.01
5 sub-layer 5	IX	1.00	VI	0.00
5 sub-layer 6	IX	1.00	VI	0.00
6 sub-layer 1	VI	0.99	IX	0.01
6 sub-layer 2	IX	1.00	VI	0.00
6 sub-layer 3	IX	1.00	VI	0.00

environment. The horse stable isotope values are thus likely a better indicator of local environmental conditions than the reindeer values during this time period. This is particularly interesting because the specimens from Kesslerloch are geographically closer to the Swabian Jura horse specimens than to the other Swiss specimens from Champréveyres.

This separation of horse stable isotope results is more evident in their $\delta^{15}N_{coll}$ values. The specimens from Kesslerloch and Champréveyres (Switzerland) range in $\delta^{15}N_{coll}$ values from +1.3 to +1.7‰ while the specimens from Langmahdhalde, Geißenklösterle, and Schussenquelle (Swabian Jura) range from +2.1 to +4.5‰ (Table 8). The regional values do not overlap and the Swabian Jura values are at least 0.4‰ higher than the Swiss values. As proposed by Drucker et al. (2012), $\delta^{15}N_{coll}$ values from the Late Glacial are likely a reflection of soil activity. Permafrost is present in tundra environments and, in particular, close to glacial fronts. When soil is frozen, as under permafrost conditions, organisms in the soil are not very active, meaning the soil has lower $\delta^{15}N_{coll}$ values and animals that eat plants from areas closer to glacial fronts will thus likely have lower $\delta^{15}N_{coll}$ values (Drucker et al., 2012). During the Late Glacial, the extent of the alpine glacier was closer to both Kesslerloch and Champréveyres than to any of the Swabian Jura sites we discuss here (Becker et al., 2016). This separation of horse values, at least in terms of nitrogen stable isotopes, therefore likely reflects the proximity of the horses' territory at both Kesslerloch and Champréveyres to a glacial front.

It is important to note, though, that the specimens discussed here from both Switzerland and the Swabian Jura date to the end of GS-2a and to GI-1e, a time of abrupt warming (Litt et al., 2001; Lowe et al., 2008). The dates on Kesslerloch and Champréveyres specimens we use in this paper are more centered on GS-2a than GI-1e so it is possible that the differences in $\delta^{15}N_{coll}$ values of horse between the samples from these sites and those from the Swabian Jura are the result of different environmental conditions. However, the horse specimen from Langmahdhalde that has been dated falls within GS-2a and has the second highest $\delta^{15}N_{coll}$ values discussed in our study. Our hypothesis that the difference in $\delta^{15}N_{coll}$ values between these two regions is a result of proximity to glacial fronts therefore remains supported.

To summarize, we find that Magdalenian hunter-gatherers in the Swabian Jura lived in environments that were generally open tundra in nature but also included areas with denser vegetation, likely including stands of trees. This reflects the slow loss of the reindeer's preferred habitat in the region surrounding Langmahdhalde and the occasional presence of more temperate adapted plants and animals. Our stable isotope results suggest that the horses of Central Europe, in contrast to reindeer, are more flexible and adapt to their regional environment,

Table 8
Measured $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values for each specimen discussed in this work. Further information on these specimens and their context can be found in Table 4. Sources for the stable isotope values not reported here for the first time are: 1 = Drucker et al., 2011; 2 = Bocherens et al., 2011; 3 = Stevens and Hedges, 2004.

Lab number	Coll yield (mg/g)	C_{coll} (%)	N_{coll} (%)	C/N_{coll}	$\delta^{13}C_{coll}$ (‰)	$\delta^{15}N_{coll}$ (‰)	Source $^{13}C^{15}N$
LGN-6	77.8	42.5	14.9	3.3	−19.4	1.6	This work
LGN-9	33.4	37.3	13.1	3.3	−19.9	2.0	This work
LGN-10	46.8	38.2	13.5	3.3	−19.9	1.8	This work
LGN-12	89.1	40.6	14.4	3.3	−19.8	2.0	This work
LGN-13	45.5	36.5	12.9	3.3	−19.8	2.0	This work
LGN-14	125.8	42.1	14.8	3.3	−20.1	2.5	This work
RA-PTF 363	54.9	45.2	15.3	3.4	−19.8	2.4	1
RA-PTF 364	104.8	45.6	15.6	3.4	−19.6	2.1	1
RA-PTF 365	25.6	42.5	14.4	3.4	−19.9	2.3	1
RA-PTF 366	55.0	34.6	12.5	3.2	−20.0	1.2	1
RA-PTF 367	17.8	31.8	11.6	3.2	−19.9	1.2	1
RA-PTF 368	41.7	43.5	15.3	3.3	−19.4	2.4	1
RA-PTF 369	55.3	39.4	13.8	3.3	−20.2	2.6	1
RA-PTF 370	31.2	40.6	13.9	3.4	−19.1	2.3	1
RA-PTF 371	147.0	45.9	15.5	3.5	−19.7	2.1	1
RA-PTF 373	41.6	43.7	14.9	3.4	−19.7	2.5	1
RA-PTF 374	30.5	41.5	14.2	3.4	−19.7	1.4	1
RA-PTF 375	30.4	42.1	14.4	3.4	−20.0	3.3	1
RA-PTF 376	48.0	44.1	15.1	3.4	−19.7	2.4	1
RA-PTF 377	51.4	42.8	14.8	3.4	−19.9	2.0	1
RA-PTF 379	44.4	41.8	14.1	3.5	−19.5	2.6	1
RA-PTF 380	141.1	44.6	14.3	3.6	−19.6	2.4	1
RA-PTF 381	134.3	44.4	14.5	3.6	−19.3	2.3	1
RA-PTF 382	63.8	43.6	15.0	3.4	−19.1	1.9	1
RA-PTF 383	103.7	44.3	14.5	3.6	−19.4	2.9	1
SCH-1	100.8	44.7	15.5	3.4	−19.8	2.5	1
SCH-2	124.5	44.5	15.9	3.3	−19.7	2.8	1
SCH-3	135.2	45.1	15.5	3.4	−20.1	1.8	1
SCH-4	129.9	44.0	15.7	3.3	−19.4	1.9	1
SCH-5	136.6	45.8	15.4	3.5	−19.5	2.2	1
FLS-7	14.9	35.4	12.4	3.3	−19.8	2.1	1
FLS-8	14.2	34.5	12.3	3.3	−19.3	2.2	1
FLS-9	16.7	33.4	11.7	3.3	−20.2	2.1	1
RA-KSL-620	28.7	34.4	12.1	3.3	−19.1	2.4	1
RA-KSL-628	48.7	43.7	15.0	3.4	−19.9	2.6	1
RA-KSL-632	43.7	39.0	13.4	3.4	−19.8	2.7	1
RA-KSL-633	19.1	36.8	13.1	3.3	−20.3	2.9	1
RA-KSL-635	23.3	34.5	12.2	3.3	−19.9	2.8	1
LGN-4	17.1	39.0	13.8	3.3	−20.9	3.1	This work
LGN-5	16.9	38.0	13.5	3.3	−20.7	2.3	This work
LGN-7	45.2	35.6	12.5	3.3	−20.9	2.1	This work
LGN-8	5.7	31.8	11.5	3.2	−20.8	2.4	This work
LGN-11	65.2	36.8	13.1	3.3	−21.0	2.7	This work
OxA-5158				3.2	−20.9	2.2	3
SCH-10	206.6	40.1	15.4	3.0	−21.2	4.5	This work
KSL-1	37.4	45.3	15.5	3.4	−20.6	1.3	2
KSL-2	34.8	45.3	15.5	3.4	−20.4	1.6	2
KSL-5	28.3	43.0	14.9	3.4	−20.0	1.7	2
CHM-2	14.2	35.7	13.9	3.0	−19.8	1.6	2
CHM-4	8.8	33.9	13.4	3.0	−20.1	1.5	2

indicating that a more heterogeneous environment may not negatively affect horse populations as it likely did reindeer populations.

In general, when habitats are more heterogeneous species diversity is higher (Ceballos et al., 1999; Cramer and Willig, 2002; Ganzhorn et al., 1997; MacArthur and MacArthur, 1961; Ricklefs and Relyea, 2014: 426; Southwell et al., 1999; Williams et al., 2002). We therefore expect the Late Glacial environments surrounding Langmahdhalde to have had a higher diversity of species than modern polar regions, which generally have low diversity for mammals, most birds, amphibians, reptiles, and plants (Begon et al., 1990: 831; Payer et al., 2013). This low species diversity in modern polar climates compared to lower latitudes is driven by extreme seasonality, the short growing season, the overall harshness of the climate, and widespread ice cover (Payer et al., 2013). As the growing season we have predicted with the quantitative models is longer than that of modern polar climates, we suggest that there was a higher diversity of species in the Swabian Jura during the Late Glacial than in modern polar regions. We did find a higher species diversity in GH5 sub-layers 1 and 4, where the reciprocal of Simpson's values are as high or almost as high as those of the Holocene horizons (GH 2 and 2a; Table 6). This heterogeneous environment was also likely more productive, providing a wider range of resources, further promoting species diversity (Begon et al., 1990: 825). It may have been, in part, the productivity and species diversity of this region that made recolonization of the Swabian Jura attractive for Magdalenian hunter-gatherers.

6. Conclusions

We have presented Late Glacial paleoenvironmental and climatic evidence from two proxy sources from the recently discovered archaeological site Langmahdhalde: stable isotopes of horse and reindeer remains and the micromammal assemblage. This represents the first study in the Swabian Jura that considers both data types together to reconstruct human paleoecology in this region.

The stable isotope results indicate that although deer populations at this time appear to have occupied similar niches across several regions, horses follow a different pattern and group based on their local ecology and environmental conditions. This suggests that stable isotopes from horse collagen are better proxies for local environmental conditions than those of reindeer.

Our new micromammal and stable isotope data from the Late Glacial can be used to discuss the relationships between human hunting and settlement behavior and the regional landscape and environmental conditions. We find that during the Late Magdalenian occupation of Langmahdhalde, a polar climate with tundra vegetation prevailed in the Swabian Jura of southwestern Germany, but it is likely that pockets of different plant and animal communities associated with temperate or cold-temperate forests existed on the landscape as a result of the relatively unstable nature of Late Glacial climates. As such, winter temperatures, precipitation, and the length of the growing season were greater than in modern polar climates. Our stable isotope results provide further support for the decrease of lichens in the region, as already noted by previous studies (e.g. Drucker et al., 2012). The Magdalenian occupants of Langmahdhalde lived, therefore, in a generally cold, open environment which was less uniform and more mosaic in nature than the modern tundra, perhaps similar to modern transitional zones between vegetative communities.

Magdalenian hunter-gatherers returning to the Swabian Jura after the Last Glacial Maximum thus encountered landscapes that were home to not only tundra plant and animal species, but also to more temperate species, including trees, that were able to exist in the region thanks to higher annual rainfall and longer vegetative activity periods than are common in the modern tundra. We argue that this heterogeneous environment was likely more productive, in terms of the range of resources available, and therefore had a higher diversity of species than modern tundra environments. This may have been one of the reasons that the settlement of Magdalenian peoples in this region was successful and may at least in part explain the regional nature of Central European settlement strategies during this time.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2019.109527.

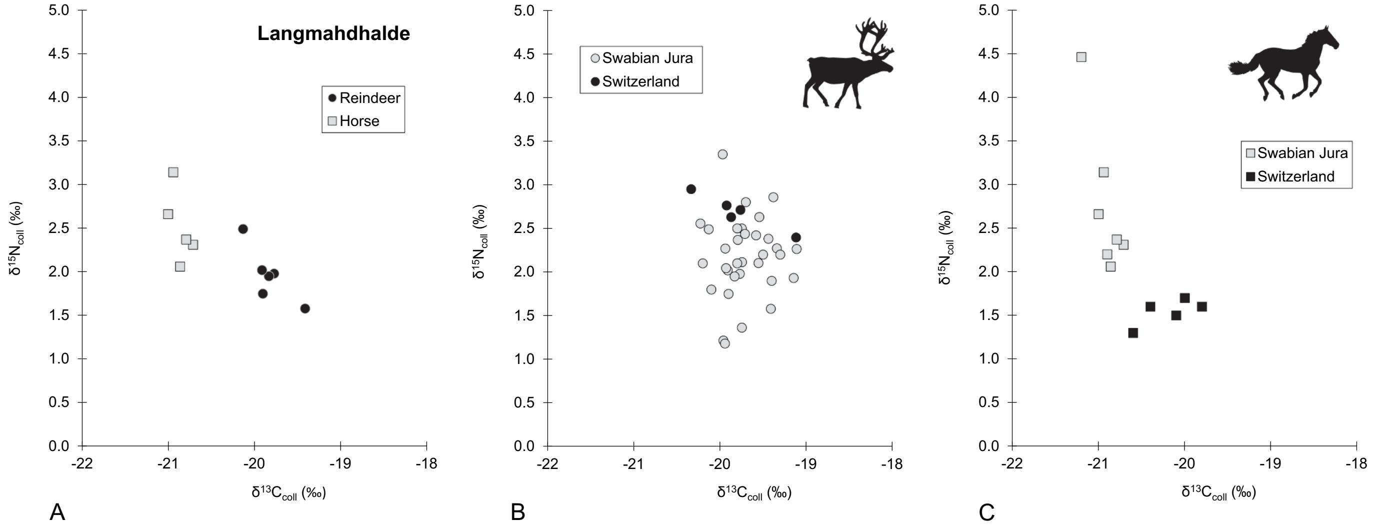

Fig. 6. $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ stable isotope results from (A) Langmahdhalde, as reported in this work, (B) reindeer from the Swabian Jura (Langmahdhalde, Petersfels, Schussenquelle, and Felsställe) and Switzerland (Kesslerloch), and (C) horse from the Swabian Jura (Langmahdhalde, Geißenklösterle, and Schussenquelle) and Switzerland (Kesslerloch and Champréveyres). Sources and information regarding these values can be found in Tables 4 and 8.

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Appendix 3

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New perspectives on human subsistence during the Magdalenian in the Swabian Jura, Germany

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Abstract

The Swabian Jura of southwestern Germany is famous for its Paleolithic sites which have been studied since the mid-1800s. While there is a rich tradition of research on the Magdalenian, many of the best-known sites were excavated early, and recently few discoveries of new sites have been made. Thus, much of the information on this period comes from sites lacking data collected using modern standards. This has left open questions regarding the recolonization of the Swabian Jura and hunter-gatherer subsistence and settlement during the Magdalenian in the region. Langmahdhalde is a recently discovered rock shelter in the Lone Valley of the Swabian Jura that has intact, well-stratified horizons dating to the Magdalenian with associated lithic artifacts, faunal remains, and combustion features. In this paper, we present a study of the faunal materials from this new site. We use the macrofaunal remains to discuss human subsistence and a taphonomic analysis of the microfaunal remains to determine the spatial scale of our previously published paleoenvironmental interpretations. Our results on human subsistence support previous interpretations from other Magdalenian assemblages in Central Europe. Further, our taphonomic study of the microfauna suggests that our paleoenvironmental analyses are relatively local, within a maximum of 70 km^2 from the rock shelter. We place these results within the larger context of human paleoecology in the region and suggest that the successful resettlement of the Swabian Jura by Magdalenian peoples during the Late Glacial was probably facilitated by the presence of a higher diversity of resources on the landscape.

Keywords: zooarchaeology; taphonomy; paleoenvironment; Late Glacial; human subsistence; Magdalenian

1. Introduction

During the Last Glacial Maximum (LGM; 27, 200 to 23,500 cal yr BP; Sanchez Goñi and Harrison 2010), Central Europe was largely uninhabited by humans. Later, as the glaciers retreated and climates began to ameliorate during the Late Glacial (~18,000 to 11,600 cal yr BP), Magdalenian people recolonized Central Europe. By approximately 16,500 cal yr BP, it was largely resettled, except for areas further north that remained close to glacial fronts (Kretschmer 2015). The archaeological record suggests that the Swabian Jura of southwestern Germany was recolonized by populations from the west (Taller et al. 2014; Maier 2015, 2017) by 16,300 cal yr BP, before the Meiendorf-Interstadial (Taller et al. 2014) or GI-1e of the NGRIP record (Litt et al. 2001; Lowe et al. 2008). The timing of this recolonization indicates that Magdalenian peoples entered the region not at the onset of an interstadial, as originally thought, but during the cold and dry conditions of the late Pleniglacial or GS-2 on the NGRIP record (Litt et al. 2001; Lowe et al. 2008). Taller et al. (2014) argued that the resettlement of the Swabian Jura during the Magdalenian was, therefore, not driven by ameliorating climates, but by population growth and these populations' adaptations to specific environmental conditions.

There is a long history of archaeological research in the Swabian Jura of southwestern Germany. One of the first Magdalenian sites discovered in this region, indeed one of the first systematically excavated Paleolithic sites in the Swabian Jura, is Schussenquelle, an open air site that was excavated by Oscar Fraas in the mid-1800s (Fraas 1867; Schuler 1994). Local artifact assemblages dated to the Magdalenian are characterized by backed-bladelet industries, bone tools, reindeer antler, and fewer art objects compared to the earlier Upper Paleolithic (Schmidt 1912; Eriksen 1991; Taller 2014; Maier 2015). Studies of the faunal assemblages of these sites indicate that the most commonly hunted animals were reindeer (*Rangifer tarandus*) and horse (*Equus ferus*), large migratory game, but ibex (*Capra ibex*), hare (genus *Lepus*), fox (genus *Vulpes*), and ptarmigan (*Lagopus lagopus*) are also commonly found in these assemblages (Riek 1973a; Eriksen 1996; Gaudzinski and Street 2003; Napierala et al. 2014; Maier 2015). Studies of artifact assemblages and raw material sourcing find that the Magdalenian sites in Central Europe can be broken into distinct regional groups (Maier 2012, 2015; Kretschmer 2015). These studies group the sites of the Swabian Jura with other sites near the Federsee and in the Franconian Jura (Kretschmer 2015; Maier 2015). Further, Maier (2012) argues that the social networks of Magdalenian peoples in Central Europe were primarily within these groups.

Weniger (1987, 1989) conducted what is still the most in-depth study of settlement patterns in southwestern Germany during the Magdalenian. He described a pattern of seasonal mobility that includes the use of small, medium, and large sites. Small sites, he argues, are short-term field camps that were occupied by smaller bands of people during the spring and/or summer and used for short periods of time for hunting ibex and horse. Assemblages from these sites are thus characterized by few cores, stone tools, and organic artifacts, no portable art, and small faunal assemblages in which reindeer and horse are equally represented or horse is the dominant taxon. He calls his medium sites "residential camps of local groups" (Weniger 1987, 1989). These occur in both the lowlands and hills, are occupied during spring and summer, have hearths, and approximately equal amounts of horse and reindeer remains. Large sites represent areas occupied during the winter by larger aggregations of people. Here, hunting focused on reindeer and more intensive activities such as food storage and hide working. These sites therefore have portable art and many more cores and stone tools.

Despite the long research history in the region, the Magdalenian record in the Swabian Jura is relatively small compared to that of the earlier Paleolithic periods and is often poorly preserved, severely affected by taphonomic processes, or in contexts that are mixed with early Holocene materials. Few studies, therefore, focus on this period, with the exception of the cave sites of Schussenquelle (Fraas 1867; Schuler 1994) and Brillenhöhle (Riek 1973b), the rock shelter Felsställe (Kind 1987), and recent studies of Magdalenian remains from Hohle Fels (Napierala et al. 2014; Taller 2014). Until the past few years, no new archaeological sites with intact and well-stratified Magdalenian horizons have been discovered in the Swabian Jura since Kind's (1987) work at Felsställe. Newly excavated sites with Magdalenian deposits in this region are, therefore, necessary to address current research questions, such as whether there were local patterns in human subsistence and what factors drove the recolonization of the Swabian Jura.

Recent work in the Swabian Jura has led to the discovery of new Magdalenian sites (e.g. Conard et al. 2017, 2018, 2019; Kind and Beutelspacher 2018; Floss 2019). In 2016, the University of Tübingen began excavations at a rock shelter in the Lone Valley called Langmahdhalde, which revealed intact archaeological horizons dating to the Magdalenian, prompting annual excavations (Conard et al. 2017, 2018, 2019). Our recent study (Wong et al. 2017) of the faunal remains from this site provided the first look at what faunal data from a new site with intact horizons dating to this time period can contribute to our understanding of human subsistence behavior and past environmental conditions. This study, though, presented results from only a portion of the faunal assemblage and a more comprehensive exploration of the remains from the site is necessary.

Following our initial study, we produced the first high resolution paleoenvironmental reconstructions for the Late Glacial in the Swabian Jura based on microfaunal remains and stable isotope data from horse and reindeer bone collagen (Wong et al. 2020). With this work, we demonstrated that Late Glacial environments in the Swabian Jura were more heterogeneous than modern tundra environments and likely even included stands of trees. In general, more heterogeneous environments have a higher species diversity (MacArthur and MacArthur 1961; Ganzhorn et al. 1997; Ceballos et al. 1999; Southwell et al. 1999; Cramer and Willig 2002; Williams et al. 2002; Ricklefs and Relyea 2014: 426), indicating that Magdalenian hunter-gatherers in the Swabian Jura had access to a larger diversity of animal and plant resources than are available in modern tundra environments (Wong et al. 2020).

Taphonomic analyses of microfaunal remains further refine paleoenvironmental interpretations made based on the microfaunal data because they can indicate which non-human predator(s), such as predatory birds or small mammalian carnivores, probably deposited these remains at a site (Andrews 1990; Fernández-Jalvo et al. 2016). An understanding of that predator's behavior, such as hunting range and diet breadth, can have implications for the scale of paleoenvironmental interpretations that are based on the assemblage (Andrews 1990; Fernández-Jalvo and Andrews 1992; Fernández-Jalvo et al. 2011, 2016).

Here, we present our latest work with the Langmahdhalde faunal assemblage which includes (1) a complete analysis of the macrofaunal remains from the site dating to the Magdalenian and (2) a taphonomic analysis of the microfaunal remains. We use the results of these two analyses, coupled with previous paleoenvironmental results, to discuss how this new record of human subsistence from the Swabian Jura adds to our understanding of the Magdalenian and to suggest factors influencing the resettlement of the Swabian Jura during the Late Glacial.

2. Langmahdhalde

Langmahdhalde (48° 34' 0.84'' N, 10° 12' 47.88'' E) is located approximately 2 km from the well-known archaeological site Vogelherd (Figure 1). This study includes materials excavated during 2016, the first year of excavation, through 2018. During these seasons, excavators uncovered seven geological horizons (GH) and archaeological horizons (AH): GH1/AHI, GH2/AHII, and GH2a/AHIIa are Holocene, while GH3/AHIII, GH4/AHIV, GH5/AHV, and GH6/AHVI date to the Late Glacial (Conard et al. 2017, 2018, 2019; Wong et al. 2020). We summarize the cultural affiliations and dating for each of these horizons in Table 1 (see also Conard et al. 2017, 2018, 2019; Wong et al. 2020).

As this study focuses on the Magdalenian, we concentrate on GH3/AHIII to GH6/AHVI, the Late Glacial horizons. Excavators have found lithic refits between GH4/AHIV, GH5/AHV, and GH6/AHVI during excavations. These horizons are characterized by more lithic and faunal artifacts than the layers above, including sections of reindeer antler, several almost complete horse elements, some small pieces of mammoth (*Mammuthus primigenius*) ivory, and a needle blank made on a goose humerus (*Anser* sp.; Wong et al. 2017). GH5/AHV includes six combustion features and burnt limestone rocks in association with these features.

Following the University of Tübingen system, workers excavate the site in 1 x 1 m quadrants named by the coordinates of their southwestern corner (Figure 2). The team excavated GH5/AHV and GH6/AHVI in 2 to 3 cm deep sub-layers that follow the geology of the site. Following the methods of our paleoenvironmental reconstructions (Wong et al. 2020), we present the microfaunal results for GH5/AHV and GH6/AHVI by sub-layer. Because GH3/AHIII has very few archaeological remains, excavators did not water-screen all sediment from this horizon; they only water-screened the southwestern 50 x 50 cm sub-quadrant from each 1 x 1 m quadrant. All other horizons discussed in this study had all sediment water screened. This may result in the underrepresentation of small taxa and elements that are usually recovered during water-screening, as opposed to during excavation, in GH3/AHIII.

3. Methods

We define macrofaunal materials as those specimens that were likely deposited at the site as a result of human or large carnivore use of the rock shelter. In the Upper Paleolithic of the Swabian Jura, these could therefore include taxa ranging in size from hare or ptarmigan to large ungulates like bison (*Bison* sp.). We define microfauna as small animals that have strong potential to reconstruct local environments. For our study, this includes only taxa from the orders Rodentia and Eulipotyphla (shrews, moles, and hedgehogs; we refer to this order as “insectivores” throughout the paper). Microfaunal assemblages are almost always deposited by non-human predators, such as small mammalian carnivores or predatory birds (Fernández-Jalvo et al. 2016).

3.1. Macrofauna

Our taxonomic identifications of the macrofaunal remains from Langmahdhalde were based on the vertebrate comparative collection in the Institute for Archaeological Sciences at the University of Tübingen and several osteological atlases (e.g. Pales and Lambert 1971; Schmid 1972; Gilbert 1990; Hillson 2005; Gilbert et al. 2006). We identified all specimens to the lowest taxonomic level possible and recorded specimens using Stiner's (2005) landmark system with some modifications. If specimens were not identifiable to a specific taxon, we assigned them to a body size category, such as “medium mammal.” Species-level identifications of hare remains were based on tooth morphology (Donard 1982; Callou 1997; Niethammer and Krapp 2003) and post-cranial measurements (Donard 1982; Pelletier et al. 2015). Species-level identifications of fox remains were based on tooth measurements (Baumann 2016). We calculated the Number of Identified Specimens (NISP) for each taxonomic category and the Minimum Number of Individuals (MNI) for each specific taxon (Grayson 1984; Lyman 2008). Our MNI calculations used the most common element and took side into account when possible. If specimens articulate, we gave them a total NISP value of one. We included long bone shaft fragments in NISP counts but we did not include small unidentifiable ungulate tooth fragments. We documented taphonomic signatures on all faunal remains, such as burning (Stiner et al. 1995), weathering (Behrensmeyer 1978), mineral staining, breakage, tooth marks, and any human modifications (Lyman 1994; Fernández-Jalvo and Andrews 2016).

When possible, we also recorded indicators of age, such as epiphyseal fusion, tooth eruption, and tooth wear (Severinghaus 1949; Silver 1969; Payne 1973; Miller 1974; Levine 1979, 1982; Hufthammer 1995). When aging reindeer remains, we used tooth wear stages from Miller (1974) and Severinghaus (1949) and epiphyseal fusion information from Hufthammer (1995). We follow Miller's (1974) reindeer age categories and define juveniles as 0 to 25 months old, subadults as 27 to 39 months old, and adults as 41 months or older. When aging horse remains we used tooth eruption and long bone fusion information from Silver (1969) and tooth wear information from Levine (1979, 1982). We follow Turner's (2002) horse age categories and define juvenile horses as 0 to 2 years old, prime adults as 3 to 6 years old, and old horses as 7 years old or older.

To evaluate whether density mediated attrition affected the representation of skeletal elements in the macrofaunal assemblage at the site, we used two methods. First, we conducted a Spearman’s rank-order correlation between bone density and survivorship (percent minimum animal units or %MAU) for scan sites for which bone density values are available (following Lyman 1994). The MNI values we used to calculate survivorship for each horizon can be found in Supplementary Materials 1. We ran the correlation using the Stats package in RStudio version 1.2.1335. A significant positive correlation between survivorship and bone density would imply that density mediated attrition might have affected the preservation of the assemblage. We calculated %MAU following Binford (1978, 1984). Due to sample size, we conducted this analysis for only two taxonomic groups: hare (all specimens identified to mountain hare, *Lepus timidus*, European hare, *Lepus europaeus*, or the genus *Lepus*) and medium ungulate. We define medium ungulates as those ungulates weighing between approximately 40 and 250 kg which, at this site includes specimens assigned to ibex, red deer (*Cervus elaphus*), reindeer, “large deer” (e.g. the genera *Cervus* and *Rangifer*), and the broader taxonomic category “medium ungulate.” For our calculations with medium ungulates we used bone density data for reindeer from Lam et al. (1999; without corrections for marrow cavities, called “BMD_1”), as Lam et al. (1999) found that variations in relative bone density across different taxa are low enough to allow for accurate interpretations using density data from similar species. In our examination of hares, we used bone density values of snowshoe hare from Pavao and Stahl (1999; referred to as *Lepus canadensis* in the text).

The second method we used to examine whether density mediated attrition impacted the assemblage is a ratio of teeth to cranial bone (cranial elements and mandibles). In general, we assume that as carcasses were transported from kill sites the teeth remained inside the crania, thus cranial bone and teeth would arrive at the rock shelter together and have equal minimum number of elements (MNE; Lyman 1994) values. Tooth enamel, though, has a higher mineral content than bone so teeth are more likely to preserve in the archaeological record (Lyman 1994; Hillson 2005). If tooth MNE to cranial bone MNE ratio values are higher than one, density mediated attrition may be impacting the assemblage.

To evaluate potential decisions made by the hunter-gatherers at Langmahdhalde regarding carcass transport, we examine the representation of different skeletal elements at the site for the major taxonomic groups: hare, fox, horse, and medium ungulates. The hare and medium ungulate groups are defined above and the fox group includes specimens identified as arctic fox (*Vulpes lagopus*) and to the genus *Vulpes*. Based on Stiner (1991), we divide the skeleton into nine anatomical regions. We calculated the MAU for each region by dividing MNE by the number of times the elements of the region occur in the skeleton (Binford 1978, 1984).

3.2. Microfauna

The microfaunal assemblage at Langmahdhalde is large (n > 400,000) and, as such, we sampled the assemblage and analyzed only the remains from the southwestern corner of quadrant 50/38 (Figure 2). There is one exception to this: excavators did not save any sediment from GH3/AHIII for water-screening from quadrant 50/38, we therefore analyzed the taphonomy of the microfauna from the southwest corner of quadrant 49/37 (Figure 2) for GH3/AHIII. We included GH2/AHII and GH2a/AH2a in this analysis to provide context for GH3/AHIII to GH6/AHVI.

Our taphonomic analysis of the microfauna from Langmahdhalde follows the methodology established by Andrews (1990) and expanded on by other researchers (e.g. Fernández-Jalvo and Andrews 1992; Fernández-Jalvo et al. 2016 and references cited within). These and other studies have demonstrated that accumulations of micromammalian bones left by avian and mammalian predators show patterns in species representation, breakage, digestion, and skeletal element representation that are unique to certain categories of predator (Dodson and Wexlar 1979; Korth 1979; Andrews and Evans 1983; Andrews 1990; Stewart et al. 1999). Andrews (1990: 88-90) defines five predator categories, each associated with specific predators, based on the level of digestion on molars, incisors, and long bones, and the level of breakage observed in the assemblage. Category 1 predators leave little modification on their prey assemblages, meaning digestion is either absent or light and there is little breakage. Category 2 predators leave intermediate levels of modification. Category 3 predators leave moderate levels of modification. Category 4 predators greatly modify their prey assemblages. Finally, category 5 predators leave extreme levels of digestion on prey teeth and long bones and high levels of breakage in prey bone assemblages.

We recorded skeletal element representation, breakage, and digestion in the microfaunal remains from Langmahdhalde. We calculated the relative abundance of each skeletal element in the assemblage by horizon and sub-layer based on the MNI value of the entire horizon or sub-layer. We calculated MNI following Andrews (1990) and used all rodent and insectivore remains from the horizon. We calculated the percent relative abundance of each skeletal element by horizon by multiplying the actual number of the element represented in that horizon or sub-layer by 100 and dividing by the number of that element that we would expect in the horizon based on the MNI (Andrews 1990: 46-47). For example, if a horizon has an MNI of 10, we would expect there to be 20 femora in the horizon because each individual rodent or insectivore has two femora. In Andrews (1990), vertebrae are grouped together as one “skeletal element.” We did the same here and included only cervical, thoracic, lumbar, and sacral vertebrae in this category and set the expected number of vertebrae for one individual as 32, following (Andrews 1990). We did not calculate the relative abundance of *in situ* teeth (teeth in the alveolar socket of the maxilla or mandible) or include them in correlations with Andrews’ (1990) known predator assemblages. We compared the relative abundance of skeletal elements in the Langmahdhalde microfaunal assemblage to that of Andrews' (1990: 213) actualistic results with modern avian and mammalian predators, using Kendall's tau b, following Rhodes et al. (2018), using the Stats package in RStudio version 1.2.1335. The correlation coefficient (tau) of Kendall's tau b ranges from -1 to 1; when tau is 0 it indicates that there is no relationship, when it is 1 it indicates that there is complete positive agreement, and when it is -1 it indicates that there is complete negative agreement. We only ran correlations against predator species distributed in Central Europe during the Pleistocene and/or Holocene.

We recorded breakage in long bones, mandibles, and maxillae using Andrews' (1990: 51, 53, and 56) portion and breakage categories. We also calculated the relative proportion of isolated molars and incisors using the following equation:

$$\frac{100 * (number\ isolated\ teeth)}{(number\ teeth\ missing)}$$

where the number of teeth missing is equal to the number of *in situ* teeth present in the assemblage subtracted from the number of expected teeth. We use the relative proportion of isolated molars and incisors to discuss mandible and maxilla breakage, as we assume teeth are consumed by a predator while in the bone. A proportion of isolated teeth over 100% would indicate that there are more isolated teeth in the assemblage than can be explained by the number of intact alveolar sockets in the assemblage, thus suggesting that significant breakage of the mandibles and maxillae occurred. To further evaluate the level of breakage in cranial elements, we also calculated percent molar and incisor loss using the following equation:

$$\frac{100 * (tooth\ loss)}{(number\ of\ expected\ teeth)}$$

where the number of expected teeth is defined above and tooth loss is the number of empty alveolar sockets preserved in the mandibles and maxillae of the assemblage.

Finally, we recorded digestion on molars, incisors, proximal femora, proximal ulnae, and distal humeri. When categorizing levels of digestion on teeth and the ends of long bones, we used Andrews' (1990) categories: light, moderate, heavy, and extreme but also added the categories "light/moderate" and "moderate/heavy" (following Rhodes et al. 2018, 2019). For molar digestion, we present results only for Arvicolid molars, excluding lemmings (genera *Dicrostonyx* and *Lemmus*). Lemmings have no enamel on the buccal and lingual edges of the triangles of their molars which makes comparing levels of digestion on these specimens with digestion on the molars of other arvicolids difficult. We have excluded insectivore and Murid molars because the categories of light and moderate digestion on molars of these taxa are either not visible or difficult to identify (Fernández-Jalvo and Andrews 2016: 241; Fernández-Jalvo et al. 2016).

4. Results

4.1. Macrofauna

4.1.1. Taxonomic representation

We present the NISP and MNI values for the Langmahdhalde macrofaunal remains in Table 2. GH3/AHIII has the smallest amount of macrofaunal remains, followed by GH6/AHVI, whereas GH4/AHIV and GH5/AHV have the highest NISP values. Across all four archaeological horizons hare, reindeer, horse, ptarmigan, and small carnivores are the most common mammalian groups represented. Several hare teeth and one innominate are identifiable to the species-level in GH4/AHIV through GH6/AHVI, demonstrating that both European and mountain hare are present in the assemblage. The innominate is from GH4/AHIV and we assigned it to mountain hare based on measurements (diameter of transverse condyle = 12.6 mm; maximum diameter of anterior-posterior condyle = 13.1 mm; Donard 1982; Pelletier et al. 2015). Small carnivores are mostly represented by foxes and Mustelids which are present across all horizons except GH3/AHIII which has no Mustelid remains.

Ungulates, in particular deer, are quite common in the assemblages of all four AHs. Reindeer NISP and MNI values include several pieces of antler, one of which is attached to a fragment of the cranium (Figure 3) and another has an intact base, indicating that it was collected after it was shed. Both are from AH V. The macrofaunal assemblage also includes three pieces of mammoth ivory, one in GH5/AHV and two in GH6/AHVI. Large carnivore remains are rare in the assemblage except for nine cave lion (*Panthera spelea*) remains. The mammal categories based on body size have much higher NISP values than any other taxonomic category. These numbers are primarily driven by long bone shaft fragments which, in GH3/AHIII, GH4/AHIV, and GH5/AHV make up over 80% of the NISP values for the categories small, medium, and large mammal and in GH6/AHVI make up between 50% and 65% of the NISP values for these categories.

Very few bird remains are present in GH3/AHIII. In GH4/AHIV, GH5/AHV, and GH6/AHVI, most of the bird specimens identifiable to the species-level are ptarmigan and other medium birds, including ducks and other Phasianids (Table 2). There are also several small bird remains, such as Passeriforms, in the assemblages from AHIV and AHV (Table 2).

4.1.2. Density Mediated Attrition

In Table 3, we present the results of a Spearman’s rank-order correlation between bone density values and survivorship (%MAU) for the hare and medium ungulates at Langmahdhalde. A Spearman’s rank-order correlation found no significant *p*-values for any horizon or any strong correlations. We show the tooth and bone MNE values and ratios for horse, medium ungulate, and hare by horizon in Table 4. In GH3/AHIII the sample sizes are small but the tooth to bone ratio suggests that both are equally preserved, with ratio values of 1. The same is generally true in GH5/AHV, where the ratio of the total MNEs is 1.14. In GH6/AHVI there are very little data, only an MNE of three but the total tooth to bone ratio for the horizon is larger than one. In contrast to the other horizons, in GH4/AHIV teeth are present more often than cranial bones and every tooth to bone ratio is above one. The total tooth to bone ratio in this horizon is primarily driven by hare remains.

Overall, we find no evidence that density mediated attrition has affected the assemblage, except in GH4/AHIV.

4.1.3. Taphonomy

We summarize the taphonomic modifications on the macrofaunal remains from Langmahdhalde in Tables 5 and 6. Many of the macrofaunal specimens from GH4/AHIV to GH6/AHVI have either intensive root etching or chemical weathering on their surfaces, making identifications of some modifications, such as cut marks, difficult. Chemical weathering occurs on between 0.2 and 3.9% of specimens, while root etching occurs on 16.7 to 19.5% of specimens depending on the horizon (Table 5).

We recorded several specimens in the macrofaunal assemblage with spiral fractures, cone fractures, cut marks, and other signs of human modification. Four long bone shaft fragments display cone fractures and two specimens are bone negatives of cone fractures (Table 5). Between approximately 3 and 7% of the specimens have spiral fractures, depending on the horizon. In terms of evidence of butchering, we observed cutmarks on 0.6 to 1.8% of the specimens, depending on the horizon (Table 5). The majority of the specimens displaying cut marks are long bone shaft fragments of medium mammals but in GH4/AHIV horse, reindeer, and fox remains have cut marks, as does one medium bird specimen. In this horizon, there is one fox (*Vulpes* sp.) mandible with two parallel cut marks on the buccal side that suggest it was skinned, potentially for its fur (Binford 1981: 47; Wong et al. 2017). We observed cut marks on horse and reindeer specimens in GH5/AHV and on horse specimens in GH6/AHVI. Other observed human modifications on the faunal remains include a small (approximately 3.5 cm long) antler fragment that has been grooved from GH6/AHVI and the above mentioned reindeer antler from GH5/AHV that is connected to the braincase, which has been notched close to the base (Figure 3).

In general, there are very few diagnostic burned remains at the site; most burned faunal remains are small, unidentifiable fragments weighing less than 0.1g (9.5% of the specimens in AHIII are burned and 0 to 3.2% of specimens in GH4/AHIV through GH6/AHVI are burned; Table 5). Although there are six combustion features in AHV, there are very few burned faunal remains associated with these features and those that are associated are small fragments of teeth, long bone shafts, or unidentifiable elements, most of which are not diagnostic (Table 6). Further, these burned fragments are mostly from Feature 1, the largest combustion feature at the site, and Feature 6 (Table 6).

We observed carnivore modifications on all categories of taxa, excluding carnivores. Less than 1% of the specimens in each horizon of the assemblage have evidence of carnivore bite marks or gnawing. In GH6/AHVI there are three digested specimens.

4.1.4. Aging

Some specimens from the macrofaunal assemblage at Langmahdhalde provide information on the age at which the animal died and we provide a complete summary of this information in Supplementary Materials 2. In GH4/AHIV through GH6/AHVI there are six juvenile hare specimens, six juvenile fox specimens, and 12 medium bird specimens that are unfused. There is a fetal pelvis in GH3/AHIII, both the left and right sides, that is probably ungulate. Most specimens that provide aging information are reindeer or horse. Of these, there are nine that can be assigned to specific age categories, none of which are from GH3/AHIII or GH5/AHV. In GH4/AHIV, there are two juvenile and one adult reindeer and one old horse. In GH6/AHVI, we identified one reindeer specimen as juvenile.

4.1.5. Skeletal Element Representation

In Figure 4, we display the representation of each anatomical region of the body by AH for hare, fox, horse, reindeer, and medium ungulate at Langmahdhalde. The samples are small but some patterns are visible. For hare, most of the body is represented in GH4/AHIV and GH5/AHV and the feet, lower hind limb, and front limb are almost always represented. There are few fox remains in the assemblage, resulting in few clear trends in the skeletal element representation for this taxon except that feet are present in every horizon. For horse, both upper front limbs and lower hind limbs are almost always present and in GH5/AHV, head elements are overwhelmingly represented compared to other elements and other horizons. For reindeer, antler and crania are present and are the most common elements for every horizon except GH3/AHIII, which has neither. The lower hind limb of reindeer is present in every horizon. In the category “medium ungulates” (which includes reindeer), cranial elements are always present and, otherwise, the majority of the body is present in every horizon except GH3/AHIII, although axial elements are nonexistent.

4.2. Microfauna taphonomy

The taphonomic analysis of the microfaunal remains included 7,861 specimens. In Table 7, we report the total number of microfaunal specimens included in our taphonomic analysis by horizon and sub-layer. No microfaunal remains that are identifiable to element were observed in GH5/AHV sub-layer 1 of our sample, so we exclude this sub-layer from our taphonomic analysis. In Table 8, we report the number of specimens in the microfaunal assemblage that show evidence of burning or oxide staining. Only three of the microfaunal remains included in the taphonomic analysis are burned, all of which are upper molars. Between 13 and 40% of the microfaunal specimens exhibit oxide staining, depending on horizon. The greatest percentage of oxide stained specimens is in GH4/AHIV (40.4%).

4.2.1. Skeletal element abundances

Table 7 reports the relative abundance of each skeletal element in the microfaunal assemblage at Langmahdhalde for each horizon and sub-layer as well as the overall MNI value for each horizon and sub-layer. The Kendall’s tau b correlations between the relative abundance data and those from modern avian and mammalian carnivore assemblages (Andrews 1990: 213) show that each horizon or sub-layer is significantly correlated with several predators. We therefore summarize these results in Table 9 by reporting the predator with the highest tau value for each horizon or sub-layer; the tau and *p*-values for all other correlations can be found in Supplementary Materials 3. Owls are the most common predator and have the strongest correlations with several horizons and sub-layers in Langmahdhalde. These include little owls (*Athene noctua*), Eurasian eagle owls (*Bubo bubo*), short-eared owls (*Asio flammeus*), and great grey owls (*Strix nebulosa*). Three horizons, though, are strongly correlated with small carnivores – red fox (*Vulpes vulpes*; GH3/AHIII and GH5/AHV sub-layer 2) and pine marten (*Martes martes*; GH2a/AHIIa) – and the relative abundance of skeletal elements from GH2/AHII is most strongly correlated with that of prey assemblages from hen harrier (*Circus cyaneus*).

4.2.2. Breakage

We present the representation of long bone portions in the microfaunal assemblage from Langmahdhalde in Table 10. In general, few complete specimens are present in the assemblage; GH5/AHV sub-layer 2 has the highest percentage of complete long bones (humeri, 20%). There are no complete long bones in the Holocene horizons or GH3/AHIII. In GH2/AHII and GH2a/AHIIa, distal portions are the most common. In GH3/AHIII, the proximal portion is the most common and in GH4/AHIV to GH6/AHVI proximal and distal ends are similarly represented, making up about 28% to 46% of the long bone specimens.

In Table 11 we report information on maxilla and mandible breakage, including Andrews’ (1990) breakage categories, molar and incisor loss, and the relative proportion of isolated molars and incisors (% isolated molars and incisors). As with long bone breakage, we find very few complete mandibles in the Langmahdhalde microfaunal assemblage. Most of the mandibles are missing their ascending rami and have broken inferior borders. Across all horizons and sub-layers where maxillae are present, they are highly fragmented; most maxillae no longer retain their zygomatic arch and none are present in skulls. The percent molar and incisor loss values for all horizons and sub-layers at Langmahdhalde are quite low (almost all values fall below 50%), further indicating that mandibles and maxillae are quite fragmented in the assemblage.

We could not calculate the relative proportion of isolated teeth for GH2a/AHIIa because there are no mandibles or maxillae in this horizon. Only in GH4/AHIV is there a value less than 100% for the relative proportion of isolated molars, indicating that there was less tooth row breakage in this horizon; all other horizons have values over 140% for the relative proportion of isolated molars. GH2/AHII has the highest value with 309.3% isolated molars, indicating that this horizon likely had the highest amount of tooth row breakage. Finally, all horizons (except GH2a/AHIIa) have relative proportions of isolated incisors over 110%, indicating higher levels of breakage for anterior mandibles and maxillae. GH6/AHVI sub-layer 1 and 2 have the highest values (428.6% and 339.1%, respectively).

4.2.3. Digestion

In Table 12, we report all recorded evidence of digestion on long bones in the Langmahdhalde microfaunal assemblage. We provide all incisor digestion data in Table 13 and all molar digestion data in Table 14. The majority of the molars, incisors, and long bones in the assemblage are not digested, except for the long bones in GH2/AHII which most commonly show moderate levels of digestion. In GH2a/AHIIa and GH3/AHIII, there are very few long bones that we could include in the analysis, of these, only two are digested, both from GH2a/AHIIa. In all horizons and sub-layers from GH4/AHIV to GH6/AHVI, except GH5/AHV sub-layer 2, there are specimens that have light, medium, and heavy digestion. In GH4/AHIV, approximately 40% of long bones are digested, with light and medium digestion being the most common. All sub-layers of GH5/AHV and GH6/AHVI have remarkably similar proportions of digested long bones. The majority of the long bones in these horizons that are digested have similar proportions of digestion-level categories (light to extreme), across all sub-layers: light digestion is the most common, followed by medium. Most incisors and molars show no evidence of digestion and those that do usually have low levels. No *in situ* incisors are digested. We identified four isolated incisors (one from GH4/AHIV and three from GH5/AHV sub-layer 6) and three molars (from GH5/AHV sub-layers 4 and 6 and GH6/AHVI sub-layer 2) as extremely digested. Because very few molars were recovered in mandibles and maxillae, we can say little regarding digestion on *in situ* versus isolated molars.

5. Discussion

5.1. Accumulators of the microfauna

In the Langmahdhalde microfaunal assemblage, most teeth and long bones are not digested (the only exception being the long bones of GH2/AHII), implying that a category 1 predator, which modifies prey remains very little prior to their deposition, was responsible for depositing this assemblage. This interpretation, though, does not explain the high levels of breakage we observed in mandibles, maxillae, and long bones across the sample or the percentages of long bones and teeth that are digested in the assemblage. It is therefore probable that more than one type of predator accumulated the microfaunal assemblage at the site, as also suggested by the results of the correlation between skeletal element abundances at Langmahdhalde and known predator assemblages (see Table 9 and Supplementary Materials 3). However, we cannot eliminate the possibility that the high levels of breakage in the assemblage could also be the result of trampling or breakage during water-screening. Our discussion therefore focuses mostly on levels of digestion. Below, we examine each horizon and sub-layer individually, presenting the likely predator(s) responsible for the assemblage. For this discussion we rely on Andrews' (1990: 88-90) summary of predator modifications on micromammal assemblages, as well as Rhodes et al.'s (2019) table 12 that summarizes Andrews' predator categories according to digestive modification.

In GH2/AHII, the percentage of incisors that are digested and the prevalence of moderate levels of digestion on long bones falls in line with a category 2 predator, whereas the percentage of digested molars and long bones indicate a category 3 predator. Further, as mentioned above, a category 1 predator is suggested by the fact that most molars and incisors are not digested. Examining the predators associated with these levels of modification, we find that there is some overlap and that most types of owls for which there are data fit these criteria. The relative abundance of skeletal elements for this horizon, though, is correlated most strongly with hen harrier, which is a category 4 or 5 predator. We argue that the data overwhelmingly suggest that the microfauna from this horizon was deposited by an owl such as the Eurasian eagle owl, tawny owl, snowy owl, short-eared owl, or barn owl. Most of these owls prefer to feed on Arvicolids (Andrews 1990: 178-193), which are the most common species represented in the Langmahdhalde microfaunal assemblage (Wong et al. 2020). The tawny owl and Eurasian eagle owl are the exception, as they are both opportunistic feeders whose diets are a good reflection of the natural occurrence of their prey species on the landscape (Andrews 1990: 188-193). All of these owl species have small hunting ranges, with a maximum of 10 km from the nesting location (Andrews 1990: 188-193). In summary, Arvicolids are probably overrepresented in the assemblage compared to their natural occurrence, but the contributions of generalist predators as well, indicates that the presence or absence of microfauna taxa in the assemblage is likely a good indicator of their presence or absence on the natural landscape.

GH2a/AHIIa and GH5/AHV sub-layer 5 have similar digestion results. In both, the percentage of digested incisors and long bones suggests a category 2 predator, while the percentage of digested molars suggests a category 3 predator. When this is combined with the fact that the majority of molars, incisors, and long bones show no evidence of digestion, it seems most probable that these assemblages were deposited by owls such as the long-eared owl, great grey owl, Eurasian eagle owl, tawny owl, barn owl, short-eared owl, and snowy owl. This is similar to GH2/AHII, with the addition of the long-eared owl which is a selective hunter that prefers Arvicolids as prey and has a large hunting range of ten times that of the tawny owl (Andrews 1990: 182-184). We therefore find that, like in GH2/AHII, Arvicolids may be overrepresented in the assemblages of these two horizons compared to their relative abundance on the landscape but that presence/absence data for the taxa in the assemblage will probably reflect the present/absence of most taxa on the landscape as generalist feeders, such as the Eurasian eagle owl and tawny owl, likely also contributed to the assemblage.

GH3/AHIII and GH6AHVI sub-layer 2 have similar results in terms of the category of predator suggested by the levels of digestion on the microfaunal remains. Both show low percentages of digestion on incisors and long bones, indicating a category 1 predator and higher percentages of molar digestion (30 to 40%) that are more characteristic of a category 3 or 4 predator. These horizons, then, are similar to GH2/AHII and GH2a/AHIIa and were likely deposited by owls that include both generalist and specialized hunters. But we must also consider that in GH6/AHVI sub-layer 2 there is a molar that is extremely digested, suggesting that a category 5 predator, such as a mammalian carnivore or hen harrier, contributed to this assemblage. It is possible that in GH6/AHVI sub-layer 2 the contribution of a mammalian predator was responsible for driving the higher percentage of digested molars and that a category 1 predator was responsible for the rest of the assemblage. If this is the case, then a high modifying predator, such as a pine marten or red fox, and a low modifying predator, such as a barn owl, snowy old, long-eared owl, great grey owl, or short-eared owl probably deposited the assemblage. These owls prefer Arvicolid prey but the great grey owl also preys on enough other taxa that studies have shown that the presence/absence of taxa in its prey remains can reflect the natural composition of the environment (Andrews 1990: 178-185, 189-191). Small mammalian predators and hen harriers do not generally create assemblages that are a good reflection of prey available on the landscape. Red fox diets, for example, vary by location and depend on the easy capture of the prey and familiarity with the prey item (Andrews 1990: 206-207). For GH6/AHVI sub-layer 2, then, Arvicolid prey is probably overrepresented, while taxa that were present on the landscape may be missing from the assemblage.

GH4/AHIV and GH5/AHV sub-layer 4 have similar levels of digestion on the teeth and long bones in their samples and the relative abundance of skeletal elements for both are highly correlated with that of little owls. The most common digestion category and the percentage of digested incisors in both samples suggest a category 1 predator while the percentage of digested molars and long bones are indicative of a category 2 predator. These assemblages, then, like GH2/AHII and GH2a/AHIIa were probably deposited by owls that are both generalists and specialists. In both GH4/AHIV and GH5/AHV sub-layer 4 we also observed one tooth with an extreme level of digestion so it is likely that a mammalian predator or hen harrier which highly modified the remains was also involved.

GH5/AHV sub-layer 2 seems to have been deposited by a mix of category 1 and 2 predators, indicated by the most common level of digestion, and the percentage of digestion on teeth and long bones, respectively. This suggests that, like in GH6/AHVI sub-layer 2, owls such as long-eared owls, great grey owls, snowy owls, barn owls, and short-eared owls accumulated these rodent and insectivore remains. Again, as these birds prefer specific prey, the taxonomic representation in the assemblage will not likely reflect the natural landscape. Further, the relative abundance of skeletal elements in this sub-layer is most strongly correlated with that of small mammal assemblages deposited by red foxes (Table 9), whose prey assemblages rarely reflect natural abundances of prey taxa.

There are four sub-layers that have microfaunal samples with similar patterns of digestion: GH5/AHV sub-layers 3 and 6 and GH6/AHVI sub-layers 1 and 3. In these sub-layers, the percentage of digested incisors and the most common level of digestion suggest a predator which belongs to Andrews' (1990) category 1. The percentage of molar digestion, though, is more characteristic of a category 3 predator and the percentage of digested long bones is more characteristic of a category 2 predator. Like most of the other horizons, then, these remains seem to have been deposited by both specialist hunters, such as barn and short-eared owls, and opportunistic hunters, like tawny and Eurasian eagle owls. It should also be noted that in GH5/AHV sub-layer 6, there are three molars that have extreme levels of digestion, suggesting that a category 5 predator also contributed to this assemblage.

This taphonomic analysis also suggests that the small birds and young small mammals in the macrofaunal assemblage could have been deposited by the avian and mammalian predators responsible for the microfaunal remains at the site. The diets of long-eared, short-eared, and tawny owls include birds (Andrews 1990). Further, several owls, including the Eurasian eagle owl, hunt Lagomorphs (Andrews 1990). None of these specimens are burned or have evidence of human modification, although there are five hare specimens in the assemblage with bite or puncture marks which indicates that at least some of the hares were brought to the site by non-human carnivores.

Based on the taphonomic analysis of the microfaunal assemblage from Langmahdhalde, we hypothesize that in most of the horizons and sub-layers of the site, generalist hunters such as Eurasian eagle owls and tawny owls contributed to the assemblage, making the presence or absence of taxa a good reflection of their presence or absence on the landscape. But because birds which strongly prefer Arvicolids as prey were also probably responsible for the deposition of these materials, the relative abundances of these species in the assemblage are unlikely to be accurate reflections of the situation in the natural environment. Analytical methods that rely on the presence or absence of taxa in the Langmahdhalde microfaunal assemblage to reconstruct past environmental conditions are therefore more accurate than those that use taxonomic abundance data.

In GH5/AHV sub-layer 2 and GH6/AHVI sub-layer 2, though, we find that the predators accumulating the assemblage were probably specialized hunters which prefer Arvicolids. This suggests that rodents and insectivores present on the landscape are likely missing from the microfaunal assemblages of these sub-layers. Indeed, GH6/AHVI sub-layer 2 has the lowest degree of taxonomic diversity at the site, although taxonomic diversity in GH5/AHV sub-layer 2 is similar to that of GH4/AHIV and the other sub-layers of GH5/AHV and GH6AHVI (Wong et al. 2020). The paleoenvironmental reconstructions from GH5/AHV sub-layer 2 and GH6/AHVI sub-layer 2 are, therefore, probably not as accurate as those from the rest of the site. Overall, though, this does not change our interpretations of Late Glacial environments in the Swabian Jura.

Finally, our reconstructions of the primary accumulators of the microfaunal assemblage at Langmahdhalde have implications for the scale of the paleoenvironmental reconstructions. Long-eared owls, tawny owls, and short-eared owls have home ranges that are less than 10 km^2 (Andrews 1990: 182, 192), while hen harriers, Eurasian eagle owls, barn owls, and small mammals, like red foxes and pine martens, have ranges between 10 and 30 km^2 (Haller 1978; Picozzi 1978; Mikkola 1983; Andrews 1990: 206, 207; Arroyo et al. 2005; Martin et al. 2008). Finally, the predators with the largest home ranges are snowy owls and great grey owls, with ranges between 50 to 70 km^2 (Bull et al. 1988; Chang and Wiebe 2018). As all horizons and sub-layers in the assemblage seem to be associated with snowy and/or great grey owls, this suggests that paleoenvironmental reconstructions from Langmahdhalde apply to within 70 km^2 of the rock shelter. For context, we note that the Lone Valley is approximately 44 km long.

5.2. Human use of the rock shelter

Overall, the macrofaunal remains from Langmahdhalde support current understandings of human subsistence behavior in southwestern Germany during the Magdalenian. The main prey animals were horse and reindeer, large migratory game that travel in herds and were readily available on the landscape. The presence of collected and worked reindeer antler at the site suggests that reindeer were not only a source of food, but also of raw materials. The people using Langmahdhalde also took smaller game, like ptarmigan, hare, and fox. In the case of fox, Langmahdhalde provides evidence that these animals were also used as a source of fur. We find evidence that butchering, marrow extraction, needle-making, and antler working took place at the site. It is unclear whether the cave lion remains in the Langmahdhalde assemblage represent use of the rock shelter by cave lions or the use of cave lion by the humans who occupied the site.

The macrofaunal assemblage provides little evidence for which season(s) the rock shelter was occupied, although the likely ungulate fetal pelvis in GH3/AHIII suggests that the site may have been occupied during late winter and/or spring, as most ungulates give birth during spring or summer. Based on element representation of the major human prey taxa at the site (Figure 4), it is possible that for all horizons only certain portions of fox, reindeer, and horse were transported to the site. However, sample sizes for the MAU calculations are quite small and we are cautious of making interpretations based on skeletal element representation in GH4/AHIV because this horizon could be affected by density mediated attrition. In GH4/AHIV and GH5/AHV, though, the majority of the anatomical regions of the body are present for medium ungulates and hare. Based on the reindeer and horse results, it seems unlikely that medium ungulates were generally transported whole to the site, but again, sample sizes are small. Looking at the age of reindeer and horse specimens at the site, we see that most of the specimens for which age can be determined are juveniles but that adult and old individuals are represented. It is therefore clear that the hunter-gatherers using Langmahdhalde hunted more vulnerable juvenile individuals, at least during the occupations represented by GH4/AHIV and GH6/AHVI.

The small sample size in the macrofaunal remains from GH3/AHIII, representing the end of the Late Glacial sequence at Langmahdhalde, may be the result of a decline in use or abandonment of the rock shelter by humans. The absence of significant amounts of lithics and other artifacts in this horizon suggest this is a likely scenario, although a geoarchaeological examination of the site is necessary to rule out natural processes, such as erosion or increased sedimentation, that would decrease artifact abundances. It is possible that the low number of small birds and small carnivores in this horizon is a result of the sampling bias in water-screening, as most of the specimens belonging to these taxa are recovered from screened materials. As GH4/AHIV and GH5/AHV have the highest number of remains, and GH5/AHV has several combustion features, it is possible that these horizons represent a more intensive use of the rock shelter, although we cannot say whether this means use for longer periods of time, more repeated use of the rock shelter, or larger group sizes in residence.

The faunal assemblages and combustion features in GH3/AHIII to GH6/AHVI at Langmahdhalde suggest that the site falls within Weniger's (1987, 1989) medium site category, classifying it as a “residential camp of local groups.” Further, thus far excavators at Langmahdhalde have recorded over 100 stone tools and approximately 30 cores from these horizons, both classifying Langmahdhalde as more of a medium site in Weniger’s system. Overall, Weniger (1987, 1989) classifies most of the Magdalenian sites of southwestern Germany as small sites, including Vogelherd and Hohlenstein-Stadel, the only sites from the Lone Valley included in his study. He classifies Brillenhöhle and Hohle Fels as medium sites and Felsställe and Schussenquelle as large sites (Weniger 1987). Recent excavations at Hohle Fels and work with the assemblages from both Hohle Fels and its neighboring site Helga Abri, though, suggest that the Magdalenian occupation of Hohle Fels was larger than previously thought (Taller 2014; Hess 2019). Compared to archaeological sites to the west of the Swabian Jura, such as Petersfels, Kesslerloch, or Champréveyres in Switzerland, Langmahdhalde has greater relative proportions of horse remains and fewer examples of worked antler and bone (Albrecht 1979; Albrecht et al. 1983; Leesch 1997; Morel and Müller 1997; Napierala 2008). It also lacks the mobile art present at these sites. Within the context of the Swabian Jura, Langmahdhalde continues to offer evidence of larger or, perhaps, more repeated, use of the region by Magdalenian peoples, especially in the Lone Valley, where only smaller Magdalenian sites were known previously.

5.3. Paleoecology

Our reconstructions of the environment during the Late Glacial based on the stable isotope analysis of bone collagen of reindeer and horse from the site, the bioclimatic analysis (Wong et al. 2020), and the taphonomic analysis of the microfauna suggest that within 70 km^2 of Langmahdhalde, the environment was generally open tundra. This tundra, though, likely had warmer winter temperatures, more annual precipitation, and longer vegetative activity periods than modern tundra environments, allowing for a more mosaic environment to develop that included patches of trees (Wong et al. 2020). This may explain the presence of a European elk/moose (*Alces alces*) phalanx in the macrofaunal assemblage of GH4/AHIV. Modern European elk/moose prefer deciduous and mixed forests but, in the summer, can penetrate deep into the tundra (Nygrén 1986). The more heterogeneous environment may have allowed some individuals of this species to occupy the region, at least temporarily. There is also one roe deer (*Capreolus capreolus*) specimen in the macrofaunal assemblage (in GH3/AHIII). This species is usually associated with wooded areas that provide some cover (Walker 1968: 1404) and is rare in Central European assemblages dating to the Magdalenian. We suggest two possible explanations for the presence of this specimen in the assemblage. First, it is possible that, like the European elk/moose, a few roe deer were occasionally present in the Swabian Jura during this time. Another possibility is that the specimen is younger than the date from GH3/AHIII, as excavators recovered it from an area of the site where the stratigraphy is less clear.

The ecological complexity of the Late Glacial of the Swabian Jura is further highlighted by the situation among different deer taxa in the region. Stable isotope results from Langmahdhalde and other sites demonstrate that, during the Late Glacial, the preferred habitats of reindeer shifted northward (Drucker et al. 2012; Immel et al. 2015; Wong et al. 2020), but reindeer, known to subsist on a variety of vegetation (Walker 1968: 1402; Spiess 1979: 31), remained in the region. As a result, there is more and more evidence that their niches overlapped with the other deer species on the landscape. This is visible in the $\delta^{13}C$ and $\delta^{15}N$ values from bone collagen of horse and deer specimens. In Figure 5, we compare these stable isotope results from several sites in the Swabian Jura across the Upper Paleolithic and find that the Magdalenian results, including those from Langmahdhalde, overlap much more than those from the Aurignacian and Gravettian (see Supplementary Materials 4 for the stable isotope data and sources and Supplementary Materials 5 and 6 for the methods associated with these values). This probably meant that these species were in increasingly direct competition with each other for resources.

6. Conclusions

Previously known sites in the Lone Valley of the Swabian Jura have demonstrated the presence of only small field camps that were likely occupied for short periods of time during the Magdalenian (Weniger 1987, 1989). Langmahdhalde, though, provides evidence for repeated occupations or larger groups of Magdalenian people coming together at residential camps in this valley. Our work with the faunal remains from the site also demonstrates that these people were hunting large game whose niches were shifting and beginning to overlap. Paleoenvironmental reconstructions based on faunal remains from Langmahdhalde have shown that environments in the region were more heterogenous and diverse than previously thought. Additionally, our taphonomic analysis of the microfauna from the site suggests that this environmental reconstruction applies specifically to the Lone Valley and its surroundings (within 70 km^2 of the site); further studies are necessary to determine whether this trend is visible throughout the Swabian Jura.

The unique vegetative situation of the Swabian Jura may have made it an attractive place to settle for Magdalenian peoples moving into the area from the west. As current work indicates that the Swabian Jura was recolonized during the colder Pleniglacial (Taller et al. 2014), this region may have provided a greater diversity of vegetative and faunal resources for human populations compared to surrounding regions. This may have been especially true since humans living to the west of the Swabian Jura at sites such as Kesslerloch, Champréveyres, and Petersfels, were in closer proximity to glacial fronts (Becker et al. 2016; Wong et al. 2020). Environmental reconstructions from the Swiss Jura also suggest that temperatures were colder than those reconstructed for the Swabian Jura and environments were open grassland with alpine and steppe vegetation (Coope and Elias 2000; Leesch et al. 2012). Our work indicates, then, that expansion into the Swabian Jura was not driven exclusively by adaptations to specific environments (Taller et al. 2014), but also by the availability of diverse resources in this region, further emphasizing the need for regional- and local-scale paleoenvironmental data.

Conflicts of interest/Competing interests

The authors declare no conflicts of interest or competing interests.

Availability of data and materials

All newly published results and data are included in the manuscript. Archaeological data from Langmahdhalde, including zooarchaeological data, are managed by the Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters at the University of Tübingen and can be accessed on request.

Code availability

Not applicable

Figures

Fig. 1 Map of Langmahdhalde and other archaeological sites mentioned in the text. 1 = Langmahdhalde; 2 = Vogelherd; 3 = Schussenquelle; 4 = Felsställe; 5 = Hohle Fels; 6 = Brillenhöhle. Map made in QGIS version 3.4 with topographic data from SRTM NASA version 3, hydrology data from the Landesanstalt für Umwelt Baden-Württemberg, administrative boundaries from ©EuroGeographics, and ocean data from Natural Earth

Fig. 2 Overview of the excavation quadrants at Langmahdhalde. Each quadrant is 1 x 1 m in dimension and named based on the coordinates of its southwestern corner. The dotted areas on the right side of the figure indicate the rock shelter. The 50 x 50 cm southwestern sub-quadrants, highlighted in grey, are the sub-quadrants selected for the taphonomic analysis of the microfauna (49/37 for GH3 and 50/38 for all other horizons). Figure by M. Zeidi

Fig. 3 Reindeer antler from GH5/AHV of Langmahdhalde. It is attached to the cranium and has been notched at its base, likely in an attempt to remove it from the cranium. The scales in the magnified photos are 1 cm long in total. Figure by A. Blanco Lapaz

Fig. 4 Skeletal element representation of, from top to bottom, hare, fox, horse, reindeer, and medium ungulate remains at Langmahdhalde by horizon. The anatomical region is on the x-axis (after Stiner 1991) and MAU values are on the y-axis. For the anatomical regions, region 1 = horn/antler, 2 = head, 3 = neck, 4 = axial, 5 = upper front, 6 = lower front, 7 = upper hind, 8 = lower hind, and 9 = feet. Notice that not all y-axes are the same scale

Fig. 5 Stable isotope values on bone collagen from reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), giant deer *(Megaloceros giganteus),* and horse (*Equus ferus*) remains from the Upper

Paleolithic of the Swabian Jura. The symbol key for the graphs of all three periods is in the upper right. Values are from the following archaeological sites: Fellställe, Geißenklösterle, Hohle Fels, Hohlenstein Stadel, Langmahdhalde, Petersfels, and Schussenquelle. The stable isotope values and sources are listed in Supplementary Materials 4. For those values that are not previously published, see Supplementary Materials 5 for the methods associated with these values

Tables

Table 1. Stratigraphic information for Langmahdhalde including the dating and cultural affiliation of each horizon. GH = Geological Horizon; AH = Archaeological Horizon. 1 = Conard et al. 2017; 2 = Wong et al. 2020; 3 = Conard et al. 2018; 4 = Conard et al. 2019.

Table 2. NISP and MNI values for the mammal and bird macrofaunal remains from Langmahdhalde, organized by horizon.

Table 3. Spearman's rank-order correlation between bone density values and % survivorship by horizon for the taxonomic groups "Hare" and "Medium Ungulate." Hare bone density values from snowshoe hare values reported in Pavao and Stahl (1999). Medium ungulate density values from reindeer values reported in Lam et al. (1999) without corrections for marrow cavities.

Table 4. MNE values of teeth and crania and the ratio of tooth MNE to cranial MNE for the taxonomic categories horse, medium ungulate, hare, and fox organized by horizon. The final row for each horizon ("Total") presents these MNE values summed. The medium ungulate group includes specimens identified as ibex, red deer, reindeer, large deer, and medium ungulate. The hare group includes specimens identified as European hare and mountain hare, as well as specimens assigned to the genus *Lepus*. The fox group includes specimens identified as artic fox and assigned to the genus *Vulpes*.

Table 5. Summary of taphonomic modifications on macrofaunal specimens (mammal and bird) from Langmahdhalde organized by horizon. Total NISP for each horizon included in the column header.

Table 6. Number of Specimens (NSP) and NISP associated of the macrofaunal assemblage of Langmahdhalde that are associated with features and burned. All features are in GH5/AHV. Specimens included in NSP counts are both diagnostic and not diagnostic.

Table 7. The % relative abundance of each element and total NISP by horizon and sub-layer of the microfaunal assemblage at Langmahdhalde. MNI values for each horizon or sub-layer are based on all rodent and insectivore remains from the horizon or sub-layer and are reported in the table. We did not calculate the % relative abundance of *in situ* (in bone) teeth. Actual # = the actual number of that element represented in the assemblage of that horizon or sub-layer. Expected # = the number of that element we would expect in the horizon based on the MNI of the horizon. % relative abundance is calculated by multiplying "actual #" by 100 and dividing the result by the "expected #" (Andrews 1990: 46-47).

Table 8. Information on specimens in the microfaunal assemblage of Langmahdhalde that show evidence of burning or oxide staining. The burn stages follow Stiner et al. (1995). The burned specimen in GH5/AHV is from sub-layer 3.

Table 9. The results of the Kendall's tau b correlation between the horizons and sub-layers at Langmahdhalde and the modern predator assemblages reported in (Andrews 1990: 213). In this table, we show only the results from the predator with the highest tau value for each horizon. Correlation results for the remaining predators for each horizon and sub-layer can be found in Supplementary Materials 3. * = statistically significant (≤0.05).

Table 10. Representation of long bone portions of microfauna from Langmahdhalde by horizon and sub-layer, following (Andrews 1990: 50-52).

Table 11. Breakage of mandibles and maxillae in the microfauna assemblage at Langmahdhalde by horizon and sub-layer (following Andrews 1990). No maxillae were present in skulls in the sampled

Langmahdhalde microfaunal material. Molar and incisor loss is defined by the number of empty alveolar sockets. The % molar or incisor loss is calculated by multiplying tooth loss by 100 and dividing by the expected number of teeth. The expected number of teeth is the total number of teeth that should be present in the number of mandibles or maxillae present in the assemblage, we use three molars and one incisor for each quadrant on the mouth to calculate the expected number. The relative proportion of isolated teeth ("% isolated molars" and "% isolated incisors") is calculated by multiplying the number of isolated teeth by 100 and dividing by the number of teeth missing, where the number of teeth missing is calculated by subtracting the number of *in situ* teeth from the number of expected teeth.

Table 12. Long bone digestion in the rodent and insectivore remains at Langmahdhalde by horizon and sub-layer.

Table 13. Incisor digestion in the microfaunal assemblage of Langmahdhalde by horizon and sub-layer. The %NISP for each level of digestion is calculated using the total number of incisors in the horizon or sub-layer. The %NISP of isolated or *in situ* incisors is calculated using the total number of isolated or *in situ* incisors in the horizon or sub-layer. The %NISP for total isolated or *in situ* incisors in calculated using the total number of incisors in the horizon or sub-layer.

Table 14. Molar digestion on Arvicolids in in the microfaunal assemblage of Langmahdhalde by horizon and sub-layer, excluding lemmings (genera *Dicrostonyx* and *Lemmus*). The % NISP for each level of digestion is calculated using the total number of molars in the horizon or sub-layer. The % NISP of isolated or *in situ* molars is calculated using the total number of isolated or *in situ* molars. The % NISP for total isolated or *in situ* molars in calculated using the total number of molars.

Supplementary Materials

Supplementary Materials 1. MNI values for the aggregated taxonomic groups "Hare" and "Medium Ungulate" organized by horizon. We use these values to calculate %MAU. The hare group includes specimens identified as European hare and mountain hare, as well as specimens assigned to the genus Lepus. The medium ungulate group includes specimens identified as ibex, red deer, reindeer, large deer, and medium ungulate.

Supplementary Materials 2. Aging information for macrofaunal remains at Langmahdhalde, organized by horizon. I = incisor, C = canine, P = premolar, and M = molar. Age categories for reindeer are based on Miller (1974: 72) who defines juveniles as 0 to 25 months old, subadults as 27 to 39 months old, and adults as 41 months and older. Age categories for horse are based on those used by Turner (2002: 40) who defines juvenile horses as 0 to 2 years old, prime adults as 3 to 6 years old, and old horses as 7 years or older. Aging sources: 1 = Hufthammer 1995; 2 = Payne 1973; 3 = Habermehl 1985; 4 = Miller 1974; 5 = Severinghaus 1949; 6 = Silver 1969; 7 = Levine 1979, 1982.

Supplementary Materials 3. The results of the Kendall's tau b correlation between the horizons and sub-layers at Langmahdhalde and the modern predator assemblages reported in (Andrews 1990: 213). * = statistically significant (≤0.05). Cells highlighted in grey represent the correlations with the highest tau correlation coefficient for each horizon or sub-layer.

Supplementary Materials 4. The stable isotope data and sources used for Figure 5. a = initially identified as European elk/moose but lately shown to be deer based on genetic sequence (Immel, personal communication 2015); b = initially identified as horse, lately re-attributed to reindeer; c = taxonomic identification revised/confirmed based on ZooMS analysis. 1 = Drucker et al. 2011; 2 = Wong et al. 2020; 3 = Bocherens et al. 2011; 4 = Immel et al. 2015; 5 = Stevens and Hedges 2004; 6 = Higham et al. 2012; 7 = Drucker et al. 2015; 8 = Fellows Yates et al. 2017; 9 = Münzel et al. 2017; 10 = Conard and Bolus 2008; 11 = Richter et al. 2000. The methods associated with specimens first reported in this work can be found in Supplementary Materials 5.

Supplementary Materials 5. The methods used for stable isotope analysis of specimens presented in this paper for the first time.

Supplementary Materials 6. Summary of the locations where collagen extraction and stable isotope analyses of unpublished data were performed.

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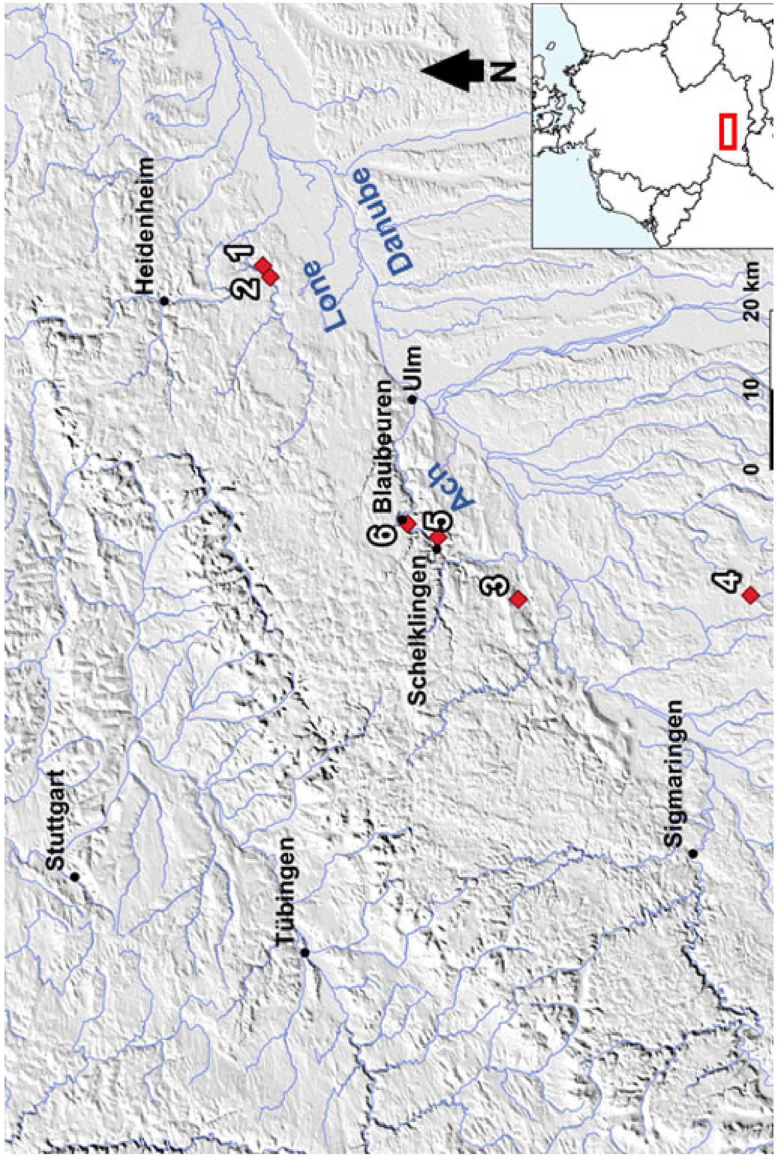
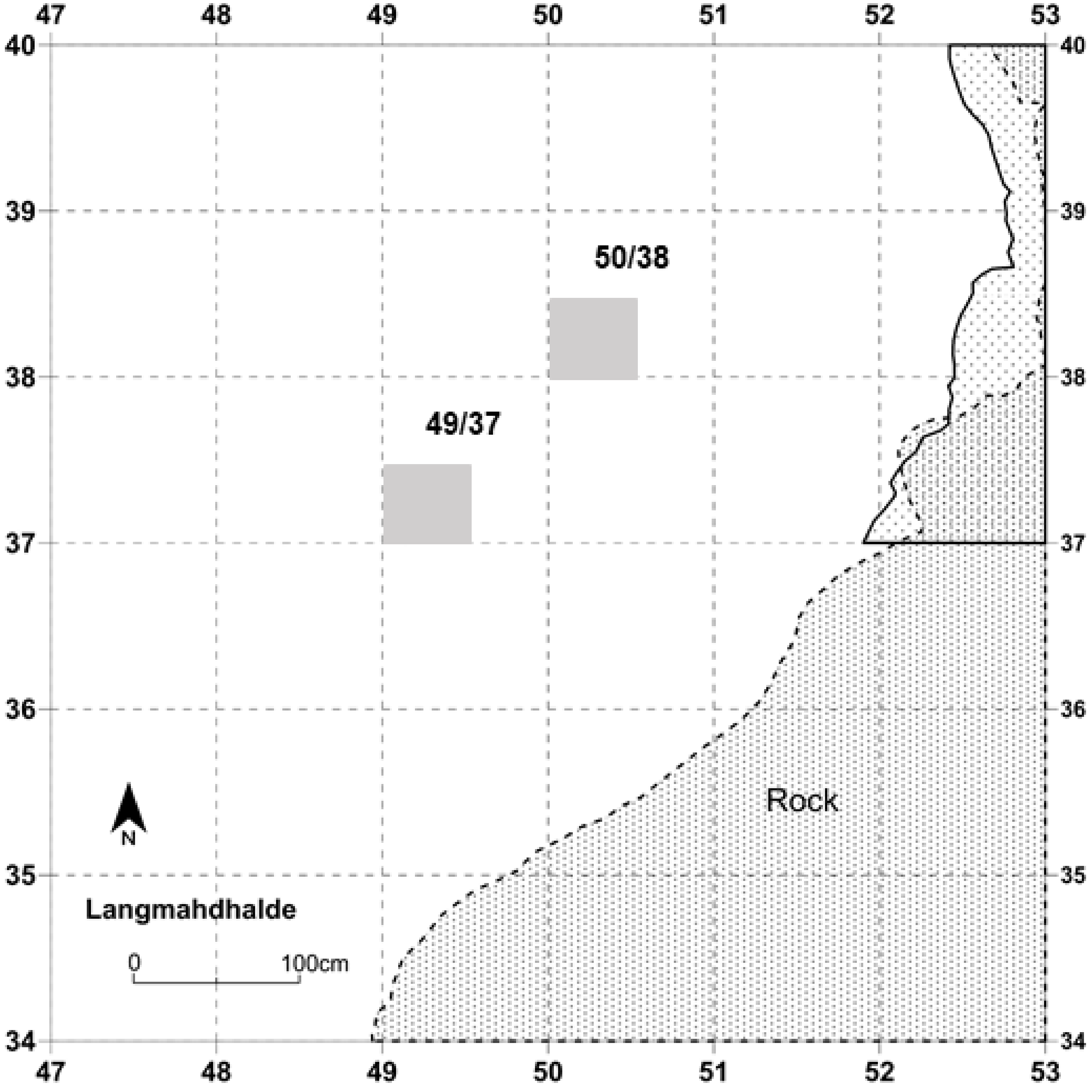
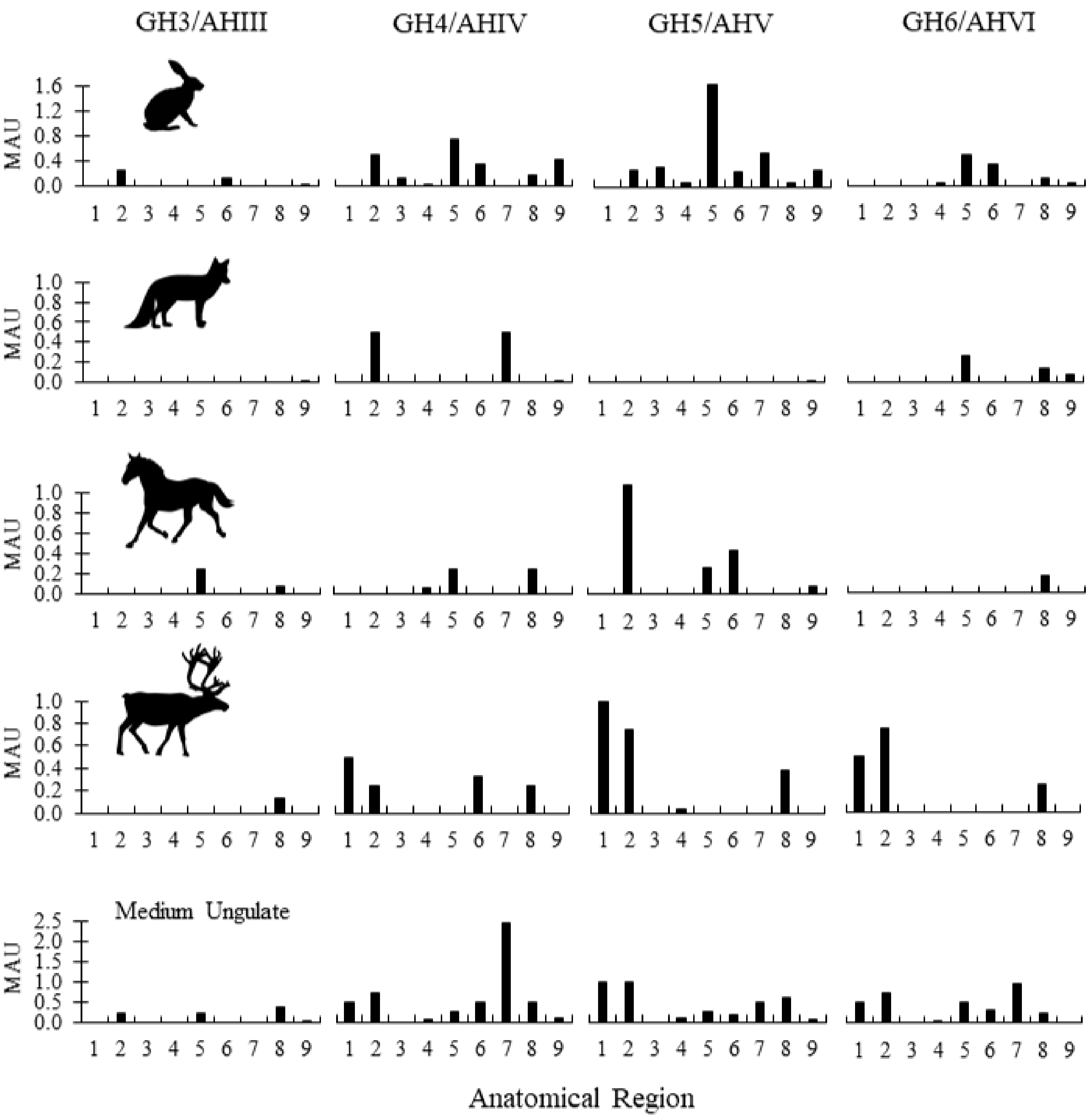
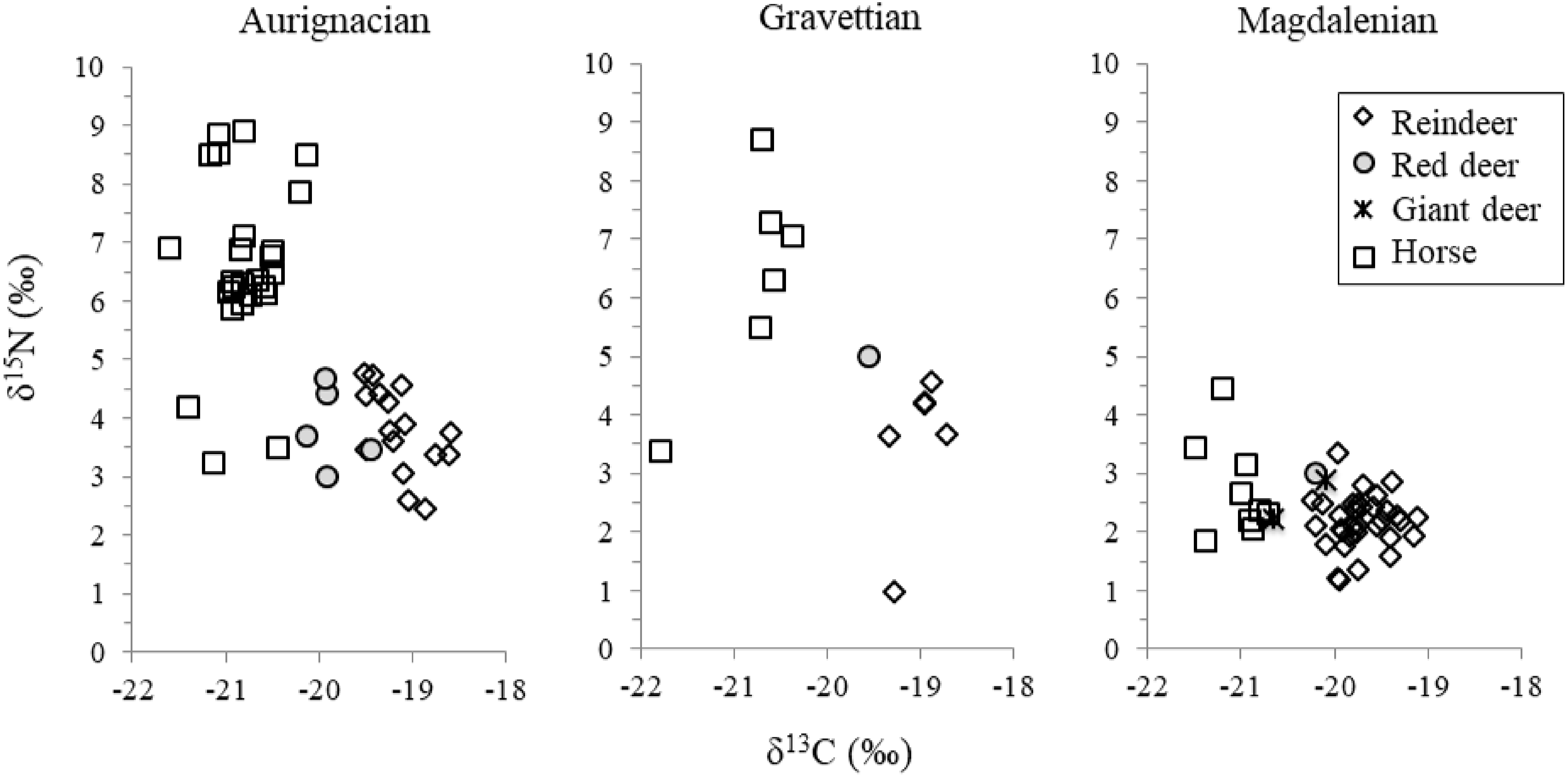

N
Heidenheim
2
1
Lone
Danube
Ulm
Blaubeuren
6
5
Ach
Schelklingen
3
4
Stuttgart
Tübingen
Sigmaringen
0
10
20 km


47
48
49
50
51
52
53
40
39
38
37
36
35
34
50/38
49/37
Rock
N
Langmahdhalde
0
100cm


10 cm


GH3/AHIII
GH4/AHIV
GH5/AHV
GH6/AHVI
MAU
1.6
1.2
0.8
0.4
0.0
1.0
0.8
0.6
0.4
0.2
0.0
2.5
2.0
1.5
1.0
0.5
0.0
1 2 3 4 5 6 7 8 9
Medium Ungulate
Anatomical Region


Aurignacian
Gravettian
Magdalenian
δ15N (‰)
10
9
8
7
6
5
4
3
2
1
0
-22
-21
-20
-19
-18
δ13C (‰)
◇ Reindeer
● Red deer
✶ Giant deer
□ Horse

GH	AH	Cultural Affiliation	Dates (cal yr BP)	Source of Dates
1	I	Modern humus layer		
2	II	Ceramics & lithics from Neolithic, metal ages, early middle ages	2,680 - 2,354	1;2
2a	IIa	Mesolithic	6,483 - 5,071	4
3	III	Mostly archaeologically sterile	14,653 - 14,034	1;2
4	IV	Magdalenian	15,447 - 13,934 (overlapping dates)	1;2;3;4
5	V			
6	VI			

Table 1. Stratigraphic information for Langmahdhalde including the dating and cultural affiliation of each horizon. GH = Geological Horizon; AH = Archaeological Horizon. 1 = Conard et al. 2017; 2 = Wong et al. 2020; 3 = Conard et al. 2018; 4 = Conard et al. 2019.

Taxon	GH3/AHIII		GH4/AHIV		GH5/AHV		GH6/AHVI	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Mammals								
European Hare (*Lepus europaeus*)			3	1	1	1	3	1
Mountain Hare (*Lepus timidus*)			6	3	1	1	2	1
Hare (*Lepus* sp.)	5	1	80	2	49	2	16	2
Lagomorpha	2		27	2	16	1	14	2
Fox (*Vulpes* sp.)	8	1	18	2	18	2	3	1
Arctic Fox (*Vulpes lagopus*)			1	1				
Pine Marten (*Martes martes*)					1	1		
(*Mustela erminea*)							1	1
Polecat (*Mustela putorius*)					1	1		
Weasel/Polecat (*Mustela* sp.)			2	1				
small Mustelid (*Mustela nivalis* or *erminea*)			13	2	16	3	6	1
Carnivore			1					
Small Carnivore	1		6		10		89	
Large Carnivore	2		1					
Cave Lion (*Panthera spelea*)	4	2	3	1	2	1		
Mammoth (*Mammuthus primigenius*) ivory					1		2	
Wild Cattle or Bison (*Bos/Bison* sp.)			1	1	1	1		
Horse (*Equus ferus*)	2	1	11	4	38	2	3	1
Ibex (*Capra ibex*)	1	1			1	1	2	1
Chamois (*Rupicapra rupicapra*)	1	1			3	1	1	1
European Elk/Moose (*Alces alces*)			1	1				
Red Deer (*Cervus elaphus*)	2	1	5	2	3	1	3	1
Reindeer (*Rangifer tarandus*)	2	1	18	2	49	2	22	2
Roe deer (*Capreolus capreolus*)	1	1						
Large Deer (e.g. *Cervus* or *Rangifer*)	2		18		31		6	
Deer (Cervidae)			2		4			
Ungulate			2		5			
Small Ungulate	1				1			
Small/Medium Ungulate	1		1		1		1	
Medium Ungulate	5		10		8		7	
Medium/Large Ungulate			5		1			
Large Ungulate			11		5			
Small Mammal	46		411		369		82	
Small/Medium Mammal	10		229		194		161	
Medium Mammal	15		297		281		108	
Medium/Large Mammal	5		55		81		34	
Large Mammal			7		3		2	
Mammal	3		34		21		6	
TOTAL Mammal NISP	119		1279		1216		574	
Birds								
Ptarmigen (*Lagopus* sp.)			22	3	13	4	3	1
Hazel Grouse (*Tetrastes bonasia*)			2	1				
Black Grouse (*Tetrao tetrix*)			1	1				
Common Teal (*Anas crecca*)			2	1				
Dabbling duck (*Anas* sp.)	1	1	1	1				
Goose (*Anser* sp.)			2	1				
Eurasian Golden Plover (*Pluvialis apricaria*)			2	1			1	1
White Stork (*Ciconia ciconia*)			1	1				
Black Stork (*Ciconia nigra*)			1	1				
Snowy, horned, eagle, & fish owls (*Bubo* sp.)							1	1

Tawny Owl (*Strix aluco*)							2	1
Accipitridae							1	
Columbidae			1	1				
Phasianidae	1		1		2			
Podicipedidae			1					
Charadriidae					1			
Passeriformes			8		1			
Charadriiformes			2		1			
Small Bird			21		12		1	
Small/Medium Bird	2		14		5		1	
Medium Bird	1		81		81		37	
Medium/Large Bird	1		6		8		12	
Large Bird			9		2		1	
Large/Huge Bird	1							
Bird					1			
TOTAL Bird NISP	7		178		127		60	

Table 2. NISP and MNI values for the mammal and bird macrofaunal remains from Langmahdhalde, organized by horizon.

	N	**r_s**	***p* - value**
GH3/AHIII			
Hare	51	0.03	0.83
Medium Ungulate	102	0.13	0.19
GH4/AHIV			
Hare	51	0.12	0.40
Medium Ungulate	102	0.00	0.99
GH5/AHV			
Hare	51	-0.18	0.20
Medium Ungulate	102	0.12	0.22
GH6/AHVI			
Hare	51	-0.18	0.20
Medium Ungulate	102	-0.02	0.81

Table 3. Spearman's rank-order correlation between bone density values and % survivorship by horizon for the taxonomic groups "Hare" and "Medium Ungulate." Hare bone density values from snowshoe hare values reported in Pavao and Stahl (1999). Medium ungulate density values from reindeer values reported in Lam et al. (1999) without corrections for marrow cavities.

	Tooth MNE	**Bone MNE**	**Tooth:Bone MNE**
GH3/AHIII			
Horse	0	0	-
Medium Ungulate	1	1	1.00
Hare	1	1	1.00
Total	2	2	1.00
GH4/AHIV			
Horse	1	0	-
Medium Ungulate	3	2	1.50
Hare	6	1	6.00
Total	10	3	3.33
GH5/AHV			
Horse	3	3	1.00
Medium Ungulate	3	3	1.00
Hare	2	1	2.00
Total	8	7	1.14
GH6/AHVI			
Horse	0	0	-
Medium Ungulate	1	1	1.00
Hare	1	0	-
Total	2	1	2.00

Table 4. MNE values of teeth and crania and the ratio of tooth MNE to cranial MNE for the taxonomic categories horse, medium ungulate, hare, and fox organized by horizon. The final row for each horizon ("Total") presents these MNE values summed. The medium ungulate group includes specimens identified as ibex, red deer, reindeer, large deer, and medium ungulate. The hare group includes specimens identified as European hare and mountain hare, as well as specimens assigned to the genus *Lepus*. The fox group includes specimens identified as artic fox and assigned to the genus *Vulpes*.

	GH3/AHIII (NISP = 126)	**GH4/AHIV (NISP = 1457)**	**GH5/AHV (NISP = 1343)**	**GH6/AHVI (NISP = 634)**
Chemical Weathering				
NISP	4	37	52	1
%NISP	3.2	2.5	3.9	0.2
Root Etching				
NISP	21	284	235	110
%NISP	16.7	19.5	17.5	17.4
Burning				
NISP	12	47	10	0
%NISP	9.5	3.2	0.7	0
Cone Fractures				
NISP	0	2	0	2
Bone Negatives				
NISP	0	1	1	0
Cut Marks				
NISP	1	24	24	4
%NISP	0.8	1.6	1.8	0.6
Spiral Fractures				
NISP	9	39	52	24
%NISP	7.1	2.7	3.9	3.8
Carnivore Gnawing/Bite Marks				
NISP	0	7	7	5
%NISP	0	0.5	0.5	0.8
Digestion				
NISP	0	0	0	3

Table 5. Summary of taphonomic modifications on macrofaunal specimens (mammal and bird) from Langmahdhalde organized by horizon. Total NISP for each horizon included in the column header.

	NSP	**NISP**
Feature 1	713	2
Feature 2	0	0
Feature 3		
Feature 4	32	0
Feature 5		
Feature 6	280	33

Table 6. Number of Specimens (NSP) and NISP associated of the macrofaunal assemblage of Langmahdhalde that are associated with features and burned. All features are in GH5/AHV. Specimens included in NSP counts are both diagnostic and not diagnostic.

	Maxilla	Mandible	Scapula	Humerus	Radius	Ulna	Innominate	Femur	Tibia	Calcaneus	Astragalus	Vertebra	Isolated Incisor	In situ Incisor	Isolated Molar	In situ Molar	Phalanx	Metapodial	Total NISP
GH2/AHII (MNI = 16)																			
actual #	7	17	1	10	1	3	1	6	7	1	0	2	64	1	167	6	6	11	311
expected #	32	32	32	32	32	32	32	32	32	32	32	624	64		192		960	320	-
% relative abundance	21.9	53.1	3.1	31.3	3.1	9.4	3.1	18.8	21.9	3.1	0.0	0.3	100.0		87.0		0.6	3.4	-
GH2a/AHIIa (MNI = 2)																			
actual #	0	0	0	3	0	1	0	1	0	0	0	0	5	0	17	0	0	0	27
expected #	4	4	4	4	4	4	4	4	4	4	4	78	8		24		120	40	-
% relative abundance	0.0	0.0	0.0	75.0	0.0	25.0	0.0	25.0	0.0	0.0	0.0	0.0	62.5		70.8		0.0	0.0	-
GH3/AHIII (MNI = 1)																			
actual #	0	1	0	0	0	1	0	2	0	0	0	0	3	0	5	0	0	0	12
expected #	2	2	2	2	2	2	2	2	2	2	2	39	4		12		60	20	-
% relative abundance	0.0	50.0	0.0	0.0	0.0	50.0	0.0	100.0	0.0	0.0	0.0	0.0	75.0		41.7		0.0	0.0	-
GH4/AHIV (MNI = 93)																			
actual #	31	95	14	163	62	126	57	136	185	5	1	23	166	1	327	0	5	97	1494
expected #	186	186	186	186	186	186	186	186	186	186	186	3627	372		1116		5580	1860	-
% relative abundance	16.7	51.1	7.5	87.6	33.3	67.7	30.6	73.1	99.5	2.7	0.5	0.6	44.6		29.3		0.1	5.2	-
GH5/AHV sub-layer 2 (MNI = 11)																			
actual #	4	5	0	10	1	6	1	9	13	0	0	5	9	1	42	1	0	4	111
expected #	22	22	22	22	22	22	22	22	22	22	22	429	44		132		660	220	-
% relative abundance	18.2	22.7	0.0	45.5	4.5	27.3	4.5	40.9	59.1	0.0	0.0	1.2	20.5		31.8		0.0	1.8	-
GH5/AHV sub-layer 3 (MNI = 22)																			
actual #	2	20	10	31	26	27	18	40	44	2	0	13	38	3	88	1	1	7	371
expected #	44	44	44	44	44	44	44	44	44	44	44	858	88		264		1320	440	-
% relative abundance	4.5	45.5	22.7	70.5	59.1	61.4	40.9	90.9	100.0	4.5	0.0	1.5	43.2		33.3		0.1	1.6	-
GH5/AHV sub-layer 4 (MNI =79)																			
actual #	12	50	40	110	69	113	69	100	157	7	1	54	121	3	270	0	8	98	1282
expected #	158	158	158	158	158	158	158	158	158	158	158	3081	316		948		4740	1580	-
% relative abundance	7.6	31.6	25.3	69.6	43.7	71.5	43.7	63.3	99.4	4.4	0.6	1.8	38.3		28.5		0.2	6.2	-
GH5/AHV sub-layer 5 (MNI = 51)																			
actual #	4	24	21	101	39	90	31	95	87	18	8	37	80	4	150	1	12	108	910

expected #	102	102	102	102	102	102	102	102	102	102	102	1989	204		612		3060	1020	-
% relative abundance	3.9	23.5	20.6	99.0	38.2	88.2	30.4	93.1	85.3	17.6	7.8	1.9	39.2		24.5		0.4	10.6	-
GH5/AHV sub-layer 6 (MNI =41)																			
actual #	3	18	14	55	42	42	29	62	81	33	30	38	50	4	127	1	129	209	967
expected #	82	82	82	82	82	82	82	82	82	82	82	1599	164		492		2460	820	-
% relative abundance	3.7	22.0	17.1	67.1	51.2	51.2	35.4	75.6	98.8	40.2	36.6	2.4	30.5		25.8		5.2	25.5	-
GH6/AHVI sub-layer 1 (MNI = 40)																			
actual #	0	7	11	51	49	50	25	56	79	13	8	31	30	0	34	0	29	135	608
expected #	80	80	80	80	80	80	80	80	80	80	80	1560	160		480		2400	800	-
% relative abundance	0.0	8.8	13.8	63.8	61.3	62.5	31.3	70.0	98.8	16.3	10.0	2.0	18.8		7.1		1.2	16.9	-
GH6/AHVI sub-layer 2 (MNI = 62)																			
actual #	8	23	20	83	46	71	49	81	124	15	6	30	78	8	143	0	21	137	943
expected #	124	124	124	124	124	124	124	124	124	124	124	2418	248		744		3720	1240	-
% relative abundance	6.5	18.5	16.1	66.9	37.1	57.3	39.5	65.3	100.0	12.1	4.8	1.2	31.5		19.2		0.6	11.0	-
GH6/AHVI sub-layer 3 (MNI = 48)																			
actual #	10	38	8	83	38	53	62	91	96	0	0	48	76	4	172	0	1	45	825
expected #	96	96	96	96	96	96	96	96	96	96	96	1872	192		576		2880	960	-
% relative abundance	10.4	39.6	8.3	86.5	39.6	55.2	64.6	94.8	100.0	0.0	0.0	2.6	39.6		29.9		0.0	4.7	-

Table 7. The % relative abundance of each element and total NISP by horizon and sub-layer of the microfaunal assemblage at Langmahdhalde. MNI values for each horizon or sub-layer are based on all rodent and insectivore remains from the horizon or sub-layer and are reported in the table. We did not calculate the % relative abundance of in situ (in bone) teeth. Actual # = the actual number of that element represented in the assemblage of that horizon or sub-layer. Expected # = the number of that element we would expect in the horizon based on the MNI of the horizon. % relative abundance is calculated by multiplying "actual #" by 100 and dividing the result by the "expected #" (Andrews 1990: 46-47).

	Burning		Oxide Staining	
	NISP	**Burn Stage**	**NISP**	**%NISP**
GH2/AHII	1	4	56	18
GH2a/AHIIa	1	4	7	25.9
GH3/AHIII			3	25
GH4/AHIV			604	40.4
GH5/AHV	1	3	623	17.1
GH6/AHVI			313	13.2

Table 8. Information on specimens in the microfaunal assemblage of Langmahdhalde that show evidence of burning or oxide staining. The burn stages follow Stiner et al. (1995). The burned specimen in GH5/AHV is from sub-layer 3.

Horizon	**Predator**	**tau**	***p*-value**
GH2/AHII	hen harrier (*Circus cyaneus*)	0.771	<0.001*
GH2a/AHIIa	pine marten (*Martes martes*)	0.585	0.005*
GH3/AHIII	red fox (*Vulpes vulpes*)	0.588	0.005*
GH4/AHIV	little owl (*Athene noctua*)	0.746	<0.001*
GH5/AHV sub-layer 2	red fox (*Vulpes vulpes*)	0.708	<0.001*
GH5/AHV sub-layer 3	little owl (*Athene noctua*)	0.698	<0.001*
GH5/AHV sub-layer 4	little owl (*Athene noctua*)	0.655	<0.001*
GH5/AHV sub-layer 5	Eurasian eagle owl (*Bubo bubo*)	0.661	<0.001*
GH5/AHV sub-layer 6	short-eared owl (*Asio flammeus*)	0.42	0.024*
GH6/AHVI sub-layer 1	short-eared owl (*Asio flammeus*)	0.511	0.006*
GH6/AHVI sub-layer 2	little owl (*Athene noctua*)	0.661	<0.001*
GH6/AHVI sub-layer 3	great grey owl (*Strix nebulosa*)	0.718	<0.001*

Table 9. The results of the Kendall's tau b correlation between the horizons and sub-layers at Langmahdhalde and the modern predator assemblages reported in Andrews (1990:213). In this table, we show only the results from the predator with the highest tau value for each horizon. Correlation results for the remaining predators for each horizon and sub-layer can be found in Supplementary Table 3. * = statistically significant (≤0.05).

	GH2/AHII		**GH2a/AHIIa**		**GH3/AHIII**		**GH4/AHIV**		**GH5/AHV sub-layer 2**		**GH5/AHV sub-layer 3**		**GH5/AHV sub-layer 4**		**GH5/AHV sub-layer 5**		**GH5/AHV sub-layer 6**		**GH6/AHVI sub-layer 1**		**GH6/AHVI sub-layer 2**		**GH6/AHVI sub-layer 3**	
	NISP	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**	**NISP**	**%NISP**
Humerus																								
Complete	0	0.0	0	0.0	0	0.0	25	15.3	2	20.0	2	6.5	19	17.3	10	9.9	5	9.1	4	7.8	10	12.0	23	27.7
Proximal	2	20.0	0	0.0	0	0.0	32	19.6	1	10.0	10	32.3	22	20.0	37	36.6	20	36.4	20	39.2	23	27.7	12	14.5
Shaft	0	0.0	0	0.0	0	0.0	39	23.9	2	20.0	16	51.6	15	13.6	7	6.9	3	5.5	6	11.8	8	9.6	11	13.3
Distal	8	80.0	3	100.0	0	0.0	67	41.1	5	50.0	3	9.7	54	49.1	47	46.5	27	49.1	21	41.2	42	50.6	37	44.6
Total	10	100.0	3	100.0	0	0.0	163	100.0	10	100.0	31	100.0	110	100.0	101	100.0	55	100.0	51	100.0	83	100.0	83	100.0
Radius																								
Complete	0	0.0	0	0.0	0	0.0	8	12.9	0	0.0	3	11.5	5	7.2	4	10.3	5	11.9	1	2.0	5	10.9	16	42.1
Proximal	1	100.0	0	0.0	0	0.0	28	45.2	1	100.0	6	23.1	31	44.9	24	61.5	21	50.0	26	53.1	25	54.3	12	31.6
Shaft	0	0.0	0	0.0	0	0.0	7	11.3	0	0.0	7	26.9	14	20.3	1	2.6	6	14.3	8	16.3	3	6.5	4	10.5
Distal	0	0.0	0	0.0	0	0.0	19	30.6	0	0.0	10	38.5	19	27.5	10	25.6	10	23.8	14	28.6	13	28.3	6	15.8
Total	1	100.0	0	0.0	0	0.0	62	100.0	1	100.0	26	100.0	69	100.0	39	100.0	42	100.0	49	100.0	46	100.0	38	100.0
Ulna																								
Complete	0	0.0	0	0.0	0	0.0	2	1.6	1	16.7	0	0.0	4	3.5	1	1.1	0	0.0	0	0.0	6	8.5	4	7.5
Proximal	3	100.0	0	0.0	1	100.0	74	58.7	1	16.7	14	51.9	57	50.4	47	52.2	29	69.0	24	48.0	40	56.3	31	58.5
Shaft	0	0.0	0	0.0	0	0.0	22	17.5	1	16.7	2	7.4	10	8.8	13	14.4	1	2.4	6	12.0	5	7.0	7	13.2
Distal	0	0.0	1	100.0	0	0.0	28	22.2	3	50.0	11	40.7	42	37.2	29	32.2	12	28.6	20	40.0	20	28.2	11	20.8
Total	3	100.0	1	100.0	1	100.0	126	100.0	6	100.0	27	100.0	113	100.0	90	100.0	42	100.0	50	100.0	71	100.0	53	100.0
Femur																								
Complete	0	0.0	0	0.0	0	0.0	25	18.4	0	0.0	1	2.5	12	12.0	4	4.2	0	0.0	2	3.6	2	2.5	17	18.7
Proximal	4	66.7	1	100.0	1	50.0	72	52.9	6	66.7	24	60.0	50	50.0	48	50.5	31	50.0	21	37.5	43	53.1	46	50.5
Shaft	0	0.0	0	0.0	1	50.0	12	8.8	1	11.1	2	5.0	7	7.0	5	5.3	4	6.5	9	16.1	6	7.4	2	2.2
Distal	2	33.3	0	0.0	0	0.0	27	19.9	2	22.2	13	32.5	31	31.0	38	40.0	27	43.5	24	42.9	30	37.0	26	28.6
Total	6	100.0	1	100.0	2	100.0	136	100.0	9	100.0	40	100.0	100	100.0	95	100.0	62	100.0	56	100.0	81	100.0	91	100.0
Tibia																								
Complete	0	0.0	0	0.0	0	0.0	8	4.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	1.3	1	0.8	6	6.3
Proximal	1	14.3	0	0.0	0	0.0	35	18.9	2	15.4	11	25.0	49	31.2	32	36.8	27	33.3	17	21.5	25	20.2	27	28.1
Shaft	2	28.6	0	0.0	0	0.0	68	36.8	7	53.8	14	31.8	42	26.8	15	17.2	16	19.8	31	39.2	38	30.6	14	14.6
Distal	4	57.1	0	0.0	0	0.0	74	40.0	4	30.8	19	43.2	66	42.0	40	46.0	38	46.9	30	38.0	60	48.4	49	51.0
Total	7	100.0	0	0.0	0	0.0	185	100.0	13	100.0	44	100.0	157	100.0	87	100.0	81	100.0	79	100.0	124	100.0	96	100.0
Total																								
Complete	0	0.0	0	0.0	0	0.0	68	10.1	3	7.7	6	3.6	40	7.3	19	4.6	10	3.5	8	2.8	24	5.9	66	18.3
Proximal	11	40.7	1	20.0	2	66.7	241	35.9	11	28.2	65	38.7	209	38.1	188	45.6	128	45.4	108	37.9	156	38.5	128	35.5
Shaft	2	7.4	0	0.0	1	33.3	148	22.0	11	28.2	41	24.4	88	16.0	41	10.0	30	10.6	60	21.1	60	14.8	38	10.5

Distal	14	51.9	4	80.0	0	0.0	215	32.0	14	35.9	56	33.3	212	38.6	164	39.8	114	40.4	109	38.2	165	40.7	129	35.7
Total	27	100.0	5	100.0	3	100.0	672	100.0	39	100.0	168	100.0	549	100.0	412	100.0	282	100.0	285	100.0	405	100.0	361	100.0

Table 10. Representation of long bone portions of microfauna from Langmahdhalde by horizon and sub-layer, following Andrews (1990: 50-52).

	Maxilla					Mandible									
	retaining zygomatic arch	without zygomatic arch	total maxillae	molar loss	incisor loss	complete	ascending ramus broken	ascending ramus missing	inferior border broken	further breakage	total mandibles	molar loss	incisor loss	% isolated molars	% isolated incisors
GH2/AHII															
N	2	5	7	3	0	0	2	1	11	3	17	14	2		
%	28.6	71.4	100.0	14.3	0.0	0.0	11.8	5.9	64.7	17.6	100.0	27.5	11.8	309.3	278.3
GH2a/AHIIa															
N	0	0	0	0	0	0	0	0	0	0	0	0	0		
%	-	-	-	0.0	0.0	-	-	-	-	-	-	0.0	0.0	-	-
GH3/AHIII															
N	0	0	0	0	0	0	0	0	1	0	1	1	0		
%	-	-	-	0.0	0.0	0.0	0.0	0.0	100.0	0.0	100.0	33.3	0.0	166.7	300.0
GH4/AHIV															
N	1	30	31	23	0	1	5	23	51	15	95	67	24		
%	3.2	96.8	100.0	24.7	0.0	1.1	5.3	24.2	53.7	15.8	100.0	23.5	25.3	87.0	132.8
GH5/AHV sub-layer 2															
N	0	4	4	1	0	0	0	3	2	0	5	9	3		
%	0.0	100.0	100.0	8.3	0.0	0.0	0.0	60.0	40.0	0.0	100.0	60.0	60.0	182.6	112.5
GH5/AHV sub-layer 3															
N	0	2	2	3	0	0	1	16	3	0	20	28	9		
%	0.0	100.0	100.0	50.0	0.0	0.0	5.0	80.0	15.0	0.0	100.0	46.7	45.0	144.3	200
GH5/AHV sub-layer 4															
N	0	12	12	11	0	2	2	40	6	0	50	43	13		
%	0.0	100.0	100.0	30.6	0.0	4.0	4.0	80.0	12.0	0.0	100.0	28.7	26.0	153.4	205.1
GH5/AHV sub-layer 5															
N	0	4	4	4	0	0	1	16	7	0	24	28	13		
%	0.0	100.0	100.0	33.3	0.0	0.0	4.2	66.7	29.2	0.0	100.0	38.9	54.2	189.9	333.3
GH5/AHV sub-layer 6															

N	0	3	3	3	0	0	3	7	8	0	18	15	7		
%	0.0	100.0	100.0	33.3	0.0	0.0	16.7	38.9	44.4	0.0	100.0	27.8	38.9	226.8	294.1
GH6/AHVI sub-layer 1															
N	0	0	0	0	0	0	0	3	4	0	7	12	4		
%	-	-	-	0.0	0.0	0.0	0.0	42.9	57.1	0.0	100.0	57.1	57.1	161.9	428.6
GH6/AHVI sub-layer 2															
N	0	8	8	4	0	0	1	16	6	0	23	23	8		
%	0.0	100.0	100.0	16.7	0.0	0.0	4.3	69.6	26.1	0.0	100.0	33.3	34.8	164.4	339.1
GH6/AHVI sub-layer 3															
N	0	10	10	7	0	0	1	21	16	0	38	22	9		
%	0.0	100.0	100.0	23.3	0.0	0.0	2.6	55.3	42.1	0.0	100.0	19.3	23.7	209.8	271.4

Table 11. Breakage of mandibles and maxillae in the microfauna assemblage at Langmahdhalde by horizon and sub-layer (following Andrews 1990). No maxillae were present in skulls in the sampled Langmahdhalde microfaunal material. Molar and incisor loss is defined by the number of empty alveolar sockets. The % molar or incisor loss is calculated by multiplying tooth loss by 100 and dividing by the expected number of teeth. The expected number of teeth is the total number of teeth that should be present in the number of mandibles or maxillae present in the assemblage, we use three molars and one incisor for each quadrant on the mouth to calculate the expected number. The relative proportion of isolated teeth ("% isolated molars" and "% isolated incisors") is calculated by multiplying the number of isolated teeth by 100 and dividing by the number of teeth missing, where the number of teeth missing is calculated by subtracting the number of in situ teeth from the number of expected teeth.

	Distal Humerus									Proximal Ulna									Proximal Femur									Total								
	None	Light	Light/ Moderate	Moderate	Moderate/ Heavy	Heavy	Extreme	Total	Total Digested	None	Light	Light/ Moderate	Moderate	Moderate/ Heavy	Heavy	Extreme	Total	Total Digested	None	Light	Light/ Moderate	Moderate	Moderate/ Heavy	Heavy	Extreme	Total	Total Digested	None	Light	Light/ Moderate	Moderate	Moderate/ Heavy	Heavy	Extreme	Total long bones	Total Digested
GH2/AHII																																				
NISP	3	3	0	2	0	0	0	8	5	0	0	0	3	0	0	0	3	3	1	1	0	2	0	0	0	4	3	4	4	0	7	0	0	0	15	11
%NISP	37.5	37.5	0.0	25.0	0.0	0.0	0.0	100.0	62.5	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0	100.0	25.0	25.0	0.0	50.0	0.0	0.0	0.0	100.0	75.0	26.7	26.7	0.0	46.7	0.0	0.0	0.0		73.3
GH2a/AHIIa																																				
NISP	2	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2	1	0	1	0	0	0	4	2
%NISP	66.7	33.3	0.0	0.0	0.0	0.0	0.0	100.0	33.3	-	-	-	-	-	-	-	-	-	0.0	0.0	0.0	100.0	0.0	0.0	0.0	100.0	100.0	50.0	25.0	0.0	25.0	0.0	0.0	0.0		50.0
GH3/AHIII																																				
NISP	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	2	0
%NISP	-	-	-	-	-	-	-	-	-	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0		0.0
GH4/AHIV																																				
NISP	47	24	3	15	0	3	0	92	45	58	10	1	7	0	0	0	76	18	58	20	1	11	0	7	0	97	39	163	54	5	33	0	10	0	265	102
%NISP	51.1	26.1	3.3	16.3	0.0	3.3	0.0	100.0	48.9	76.3	13.2	1.3	9.2	0.0	0.0	0.0	100.0	23.7	59.8	20.6	1.0	11.3	0.0	7.2	0.0	100.0	40.2	61.5	20.4	1.9	12.5	0.0	3.8	0.0		38.5
GH5/AHV sub-layer 2																																				
NISP	2	2	0	1	0	0	0	5	3	0	1	0	0	0	0	0	1	1	4	1	0	1	0	0	0	6	2	6	4	0	2	0	0	0	12	6
%NISP	40.0	40.0	0.0	20.0	0.0	0.0	0.0	100.0	60.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	100.0	100.0	66.7	16.7	0.0	16.7	0.0	0.0	0.0	100.0	33.3	50.0	33.3	0.0	16.7	0.0	0.0	0.0		50.0
GH5/AHV sub-layer 3																																				
NISP	8	1	0	7	0	0	0	16	8	12	0	0	2	0	0	0	14	2	16	4	0	2	0	2	0	24	8	36	5	0	11	0	2	0	54	18
%NISP	50.0	6.3	0.0	43.8	0.0	0.0	0.0	100.0	50.0	85.7	0.0	0.0	14.3	0.0	0.0	0.0	100.0	14.3	66.7	16.7	0.0	8.3	0.0	8.3	0.0	100.0	33.3	66.7	9.3	0.0	20.4	0.0	3.7	0.0		33.3
GH5/AHV sub-layer 4																																				
NISP	35	8	0	9	1	1	0	54	19	49	4	1	2	0	1	0	57	8	35	7	0	6	0	2	0	50	15	119	19	1	17	1	4	0	161	42
%NISP	64.8	14.8	0.0	16.7	1.9	1.9	0.0	100.0	35.2	86.0	7.0	1.8	3.5	0.0	1.8	0.0	100.0	14.0	70.0	14.0	0.0	12.0	0.0	4.0	0.0	100.0	30.0	73.9	11.8	0.6	10.6	0.6	2.5	0.0		26.1
GH5/AHV sub-layer 5																																				
NISP	32	10	0	4	0	1	0	47	15	38	4	0	4	0	1	0	47	9	29	13	0	4	0	2	0	48	19	99	27	0	12	0	4	0	142	43
%NISP	68.1	21.3	0.0	8.5	0.0	2.1	0.0	100.0	31.9	80.9	8.5	0.0	8.5	0.0	2.1	0.0	100.0	19.1	60.4	27.1	0.0	8.3	0.0	4.2	0.0	100.0	39.6	69.7	19.0	0.0	8.5	0.0	2.8	0.0		30.3
GH5/AHV sub-layer 6																																				
NISP	16	5	0	4	1	1	0	27	11	22	2	0	5	0	0	0	29	7	23	5	0	2	0	1	0	31	8	61	12	0	11	1	2	0	87	26
%NISP	59.3	18.5	0.0	14.8	3.7	3.7	0.0	100.0	40.7	75.9	6.9	0.0	17.2	0.0	0.0	0.0	100.0	24.1	74.2	16.1	0.0	6.5	0.0	3.2	0.0	100.0	25.8	70.1	13.8	0.0	12.6	1.1	2.3	0.0		29.9
GH6/AHVI sub-layer 1																																				
NISP	11	5	0	5	0	0	0	21	10	23	0	0	0	0	1	0	24	1	15	3	0	1	0	2	0	21	6	49	8	0	6	0	3	0	66	17
%NISP	52.4	23.8	0.0	23.8	0.0	0.0	0.0	100.0	47.6	95.8	0.0	0.0	0.0	0.0	4.2	0.0	100.0	4.2	71.4	14.3	0.0	4.8	0.0	9.5	0.0	100.0	28.6	74.2	12.1	0.0	9.1	0.0	4.5	0.0		25.8
GH6/AHVI sub-layer 2																																				
NISP	23	4	2	10	1	2	0	42	19	27	7	0	3	2	1	0	40	13	25	12	1	2	0	3	0	43	18	75	23	3	15	3	6	0	125	50

%NISP	54.8	9.5	4.8	23.8	2.4	4.8	0.0	100.0	45.2	67.5	17.5	0.0	7.5	5.0	2.5	0.0	100.0	32.5	58.1	27.9	2.3	4.7	0.0	7.0	0.0	100.0	41.9	60.0	18.4	2.4	12.0	2.4	4.8	0.0		40.0
GH6/AHVI sub-layer 3																																					
NISP	20	9	1	7	0	0	0	37	17	27	2	0	1	0	1	0	31	4	27	12	1	4	0	2	0	46	19	74	23	2	12	0	3	0	114	40
%NISP	54.1	24.3	2.7	18.9	0.0	0.0	0.0	100.0	45.9	87.1	6.5	0.0	3.2	0.0	3.2	0.0	100.0	12.9	58.7	26.1	2.2	8.7	0.0	4.3	0.0	100.0	41.3	64.9	20.2	1.8	10.5	0.0	2.6	0.0		35.1

Table 12. Long bone digestion in the rodent and insectivore remains at Langmahdhalde by horizon and sub-layer.

Incisor Digestion	**None**	**Light**	**Light/ Moderate**	**Moderate**	**Moderate/ Heavy**	**Heavy**	**Extreme**	**Total Incisors**	**Total Digested**	**Digested in situ incisors**	**Total in situ incisors**	**Digested isolated incisors**	**Total isolated incisors**
GH2/AHII													
NISP	49	9	0	6	0	1	0	65	16	0	1	16	64
%NISP	75.4	13.8	0.0	9.2	0.0	1.5	0.0	100.0	24.6	0.0	-	25.0	-
GH2a/AHIIa													
NISP	3	1	0	1	0	0	0	5	2	0	0	2	5
%NISP	60.0	20.0	0.0	20.0	0.0	0.0	0.0	100.0	40.0		-	40.0	-
GH3/AHIII													
NISP	3	0	0	0	0	0	0	3	0	0	0	0	3
%NISP	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0		-	0.0	-
GH4/AHIV													
NISP	144	13	0	4	0	5	1	167	23	0	1	23	166
%NISP	86.2	7.8	0.0	2.4	0.0	3.0	0.6	100.0	13.8	0.0	-	13.9	-
GH5/AHV sub-layer 2													
NISP	8	2	0	0	0	0	0	10	2	0	1	2	9
%NISP	80.0	20.0	0.0	0.0	0.0	0.0	0.0	100.0	20.0	0.0	-	22.2	-
GH5/AHV sub-layer 3													
NISP	34	4	0	2	0	1	0	41	7	0	3	7	38
%NISP	82.9	9.8	0.0	4.9	0.0	2.4	0.0	100.0	17.1	0.0	-	18.4	-
GH5/AHV sub-layer 4													
NISP	110	4	0	4	0	6	0	124	14	0	3	14	121
%NISP	88.7	3.2	0.0	3.2	0.0	4.8	0.0	100.0	11.3	0.0	-	11.6	-
GH5/AHV sub-layer 5													
NISP	62	16	3	1	0	2	0	84	22	0	4	22	80
%NISP	73.8	19.0	3.6	1.2	0.0	2.4	0.0	100.0	26.2	0.0	-	27.5	-
GH5/AHV sub-layer 6													

NISP	45	3	0	3	0	1	3	54	9	0	4	9	50
%NISP	83.3	5.6	0.0	5.6	0.0	1.9	5.6	100.0	16.7	0.0	-	18.0	-
GH6/AHVI sub-layer 1													
NISP	25	3	0	0	0	2	0	30	5	0	0	5	30
%NISP	83.3	10.0	0.0	0.0	0.0	6.7	0.0	100.0	16.7		-	16.7	-
GH6/AHVI sub-layer 2													
NISP	76	2	0	4	1	3	0	86	10	0	8	10	78
%NISP	88.4	2.3	0.0	4.7	1.2	3.5	0.0	100.0	11.6	0.0	-	12.8	-
GH6/AHVI sub-layer 3													
NISP	70	4	0	6	0	0	0	80	10	0	4	10	76
%NISP	87.5	5.0	0.0	7.5	0.0	0.0	0.0	100.0	12.5	0.0	-	13.2	-

Table 13. Incisor digestion in the microfaunal assemblage of Langmahdhalde by horizon and sub-layer. The %NISP for each level of digestion is calculated using the total number of incisors in the horizon or sub-layer. The %NISP of isolated or in situ incisors is calculated using the total number of isolated or in situ incisors in the horizon or sub-layer. The %NISP for total isolated or in situ incisors in calculated using the total number of incisors in the horizon or sub-layer.

Molar Digestion	**None**	**Light**	**Light/ Moderate**	**Moderate**	**Moderate/ Heavy**	**Heavy**	**Extreme**	**Total Molars**	**Total Digested**	**digested in situ molars**	**total in situ molars**	**digested isolated molars**	**total isolated molars**
GH2/AHII													
NISP	87	45	10	12	0	0	0	154	67	5	6	61	148
%NISP	56.5	29.2	6.5	7.8	0.0	0.0	0.0	-	43.5	83.3	-	41.2	-
GH2a/AHIIa													
NISP	6	3	0	0	0	0	0	9	3	0	0	3	9
%NISP	66.7	33.3	0.0	0.0	0.0	0.0	0.0	-	33.3	0.0	-	33.3	-
GH3/AHIII													
NISP	3	1	0	0	1	0	0	5	2	0	0	2	5
%NISP	60.0	20.0	0.0	0.0	20.0	0.0	0.0	-	40.0	0.0	-	40.0	-
GH4/AHIV													
NISP	241	26	2	3	0	3	0	275	34	0	0	34	275
%NISP	87.6	9.5	0.7	1.1	0.0	1.1	0.0	-	12.4	0.0	-	12.4	-
GH5/AHV sub-layer 2													
NISP	21	3	0	0	0	1	0	25	4	0	1	4	24
%NISP	84.0	12.0	0.0	0.0	0.0	4.0	0.0	-	16.0	0.0	-	16.7	-
GH5/AHV sub-layer 3													
NISP	11	4	1	4	0	0	0	20	9	0	1	9	19
%NISP	55.0	20.0	5.0	20.0	0.0	0.0	0.0	-	45.0	0.0	-	47.4	-
GH5/AHV sub-layer 4													
NISP	135	14	0	2	0	2	1	154	19	0	0	19	154
%NISP	87.7	9.1	0.0	1.3	0.0	1.3	0.6	-	12.3	0.0	-	12.3	-
GH5/AHV sub-layer 5													
NISP	64	14	0	1	0	0	0	79	15	0	1	15	78
%NISP	81.0	17.7	0.0	1.3	0.0	0.0	0.0	-	19.0	0.0	-	19.2	-
GH5/AHV sub-layer 6													

NISP	79	13	0	5	0	1	1	89	20	0	1	20	88
%NISP	88.8	14.6	0.0	5.6	0.0	1.1	1.1	-	22.5	0.0	-	22.7	-
GH6/AHVI sub-layer 1													
NISP	14	3	0	1	0	0	0	18	4	0	0	4	18
%NISP	77.8	16.7	0.0	5.6	0.0	0.0	0.0	-	22.2	0.0	-	22.2	-
GH6/AHVI sub-layer 2													
NISP	58	18	1	5	1	3	1	87	29	0	0	29	87
%NISP	66.7	20.7	1.1	5.7	1.1	3.4	1.1	-	33.3	0.0	-	33.3	-
GH6/AHVI sub-layer 3													
NISP	78	22	0	2	0	0	0	102	24	0	0	78	102
%NISP	76.5	21.6	0.0	2.0	0.0	0.0	0.0	-	23.5	0.0	-	76.5	-

Table 14. Molar digestion on Arvicolids in in the microfaunal assemblage of Langmahdhalde by horizon and sub-layer, excluding lemmings (genera Dicrostonyx and Lemmus). The % NISP for each level of digestion is calculated using the total number of molars in the horizon or sub-layer. The % NISP of isolated or in situ molars is calculated using the total number of isolated or in situ molars. The % NISP for total isolated or in situ molars in calculated using the total number of molars.

Taxon	GH3/AHIII MNI	GH4/AHIV MNI	GH5/AHV MNI	GH6/AHVI MNI
Hare	1	5	2	2
Medium Ungulate	1	4	3	3

Supplementary Materials 1. MNI values for the aggregated taxonomic groups "Hare" and "Medium Ungulate" organized by horizon. We use these values to calculate %MAU. The hare group includes specimens identified as European hare and mountain hare, as well as specimens assigned to the genus *Lepus* . The medium ungulate group includes specimens identified as ibex, red deer, reindeer, large deer, and medium ungulate.

Taxon	Element	Age	Age category	Aging Source
GH3/AHIII				
Reindeer	1 fully fused proximal first phalanx	> 6-18 months	juvenile or older	1
Ibex	wear stage F	3-4 years	adult	2
Ungulate	pelvis (both sides)	fetal	fetal	
GH4/AHIV				
Medium Bird	9 unfused bones			
Fox	1 deciduous upper P4	< 1 year	juvenile	3
Reindeer	1 fully fused distal first phalanx	> 6-18 months	juvenile or older	1
Reindeer	1 fully fused calcaneus	> 18-42 months	juvenile or older	1
Reindeer	1 metarsal shaft fragment with woven bone	juvenile	juvenile	
Reindeer	1 unerupted upper M1 or M2	< 3-10 months	juvenile	4
Reindeer	1 lower P4 Severinghaus wear stage 12	3.5-4 years	adult	4;5
Horse	1 fully fused nearly complete pelvis	> 4.5-5 years	prime adult or older	6
GH5/AHV				
Medium Bird	1 unfused bone			
Hare	4 unfused postcranial remains	< 1 year	juvenile	3
Fox	5 unerupted premolars or molars	< 1 year	juvenile	3
Reindeer	1 unfused distal metatarsal	< 18-30 months	subadult	1
Reindeer	1 fully fused distal first phalanx	> 6-18 months	juvenile or older	1
Horse	lower P2-P4 in mandible	tooth eruption: > 3.5 years	prime adult or older	6
Horse	lower P2-M4 and C in mandible	tooth eruption: > 4.5 years	prime adult or older	6
Horse	articulated: 1 unerupted P or M, 1 upper P2, 1 deciduous upper P2	tooth eruption: < 2.5 years	juvenile	6
Horse	1 unerupted lower I3	< 5-9 months	juvenile	6
Horse	2 unerupted upper I3s	< 5-9 months	juvenile	6
Horse	1 unerupted upper I2	< 3-4 weeks	juvenile	6
Horse	2 lower I3s worn with oval infundibulum	5-9 years	prime/old	7
Horse	1 unknown I extremely worn	10-40 years	old	7
GH6/AHVI				
Medium Bird	2 unfused bones			
Hare	2 unfused long bones	< 1 year	juvenile	3
Reindeer	1 fully fused calcaneus	> 18-42 months	juvenile or older	1
Reindeer	deciduous upper P2-P4	< 18-21 months	juvenile	4

Supplementary Materials 2. Aging information for macrofaunal remains at Langmahdhalde, organized by horizon. I = incisor, C = canine, P = premolar, and M = molar. Age categories for reindeer are based on Miller (1974: 72) who defines juveniles as 0 to 25 months old, subadults as 27 to 39 months old, and adults as 41 months and older. Age categories for horse are based on those used by Turner (2002: 40) who defines juvenile horses as 0 to 2 years old, prime adults as 3 to 6 years old, and old horses as 7 years or older. Aging sources: 1 = Hufthammer 1995; 2 = Payne 1973; 3 = Habermehl 1985; 4 = Miller 1974; 5 = Severinghaus 1949; 6 = Silver 1969; 7 = Levine 1979 and 1982.

		GH2/AHII	**GH2a/AHIIa**	**GH3/AHIII**	**GH4/AHIV**	**GH5/AHV sub-layer 2**	**GH5/AHV sub-layer 3**	**GH5/AHV sub-layer 4**	**GH5/AHV sub-layer 5**	**GH5/AHV sub-layer 6**	**GH6/AHVI sub-layer 1**	**GH6/AHVI sub-layer 2**	**GH6/AHVI sub-layer 3**
Barn Owl	tau	0.249	-0.069	-0.023	0.450	0.404	0.427	0.427	0.267	0.243	0.267	0.283	0.445
Tyto alba	*p* -value	0.187	0.740	0.912	0.015*	0.033*	0.022*	0.022*	0.165	0.191	0.165	0.041*	0.018*
Snowy Owl	tau	-0.017	-0.138	-0.103	0.260	0.207	0.437	0.387	0.326	0.387	0.393	0.444	0.447
Bubo scandiacus	*p* -value	0.928	0.507	0.619	0.053	0.275	0.019*	0.038*	0.079	0.038*	0.034*	0.017*	0.018*
Northern Long-eared Owl	tau	0.266	-0.091	0.069	0.500	0.386	0.511	0.444	0.317	0.259	0.350	0.400	0.564
Asio otus	*p* -value	0.159	0.658	0.740	0.006*	0.041*	0.006*	0.017*	0.096	0.162	0.064	0.033*	0.003*
Short-eared Owl	tau	0.379	0.183	0.252	0.661	0.492	0.639	0.552	0.577	0.420	0.511	0.594	0.584
Asio flammeus	*p* -value	0.045*	0.376	0.224	<0.001*	0.010*	0.001*	0.002*	0.002*	0.024*	0.006*	0.001*	0.002*
Eurasian Eagle Owl	tau	0.466	0.367	0.481	0.711	0.621	0.689	0.588	0.661	0.370	0.393	0.611	0.695
Bubo bubo	*p* -value	0.014*	0.077	0.020*	<0.001*	0.001*	<0.001*	0.002*	<0.001*	0.047*	0.034*	0.001*	<0.001*
Great Grey Owl	tau	0.507	0.137	0.228	0.700	0.610	0.644	0.644	0.483	0.293	0.417	0.600	0.718
Stix nebulosa	*p* -value	0.007*	0.507	0.269	<0.001*	0.001*	0.001*	0.001*	0.009*	0.115	0.026*	0.001*	<0.001*
Tawny Owl	tau	0.476	0.138	0.299	0.672	0.563	0.684	0.616	0.521	0.363	0.471	0.605	0.690
Strix aluco	*p* -value	0.012*	0.507	0.150	<0.001*	0.003*	<0.001*	0.001*	0.005*	0.052	0.012*	0.001*	<0.001*
Little Owl	tau	0.611	0.429	0.522	0.746	0.673	0.698	0.655	0.610	0.400	0.475	0.661	0.678
Athene noctua	*p* -value	0.001*	0.040*	0.013*	<0.001*	<0.001*	<0.001*	<0.001*	0.001*	0.333	0.011*	<0.001*	<0.001*
Kestrel	tau	0.610	0.342	0.411	0.700	0.575	0.577	0.561	0.583	0.293	0.350	0.533	0.581
Falco tinnunculus	*p* -value	0.001*	0.097	0.047*	<0.001*	0.002*	0.002*	0.003*	0.001*	0.115	0.064	0.003*	0.002*
Hen Harrier	tau	0.771	0.414	0.414	0.487	0.494	0.397	0.346	0.387	0.127	0.168	0.319	0.362
Circus cyaneus	*p* -value	<0.001*	0.046*	0.046*	0.009*	0.009*	0.034*	0.064	0.038*	0.498	0.367	0.086	0.056
Red Fox	tau	0.646	0.541	0.588	0.678	0.708	0.630	0.578	0.610	0.414	0.472	0.575	0.626
Vulpes vulpes	*p* -value	0.001*	0.010*	0.005*	<0.001*	<0.001*	0.001*	0.002*	0.001*	0.029*	0.012*	0.002*	0.001*
Arctic Fox	tau	0.235	0.012	-0.048	0.088	0.253	-0.009	0.009	-0.070	-0.035	-0.158	-0.035	0.036
Vulpes lagopus	*p* -value	0.230	0.955	0.823	0.647	0.196	0.964	0.964	0.714	0.855	0.410	0.855	0.854
Pine Marten	tau	0.617	0.585	0.480	0.445	0.449	0.352	0.378	0.359	-0.009	0.085	0.291	0.412
Martes martes	*p* -value	0.001*	0.005*	0.023*	0.018*	0.020*	0.063	0.046*	0.057	0.964	0.650	0.123	0.032*

Supplementary Materials 3. The results of the Kendall's tau b correlation between the horizons and sub-layers at Langmahdhalde and the modern predator assemblages reported in Andrews (1990: 213). * = statistically significant (≤0.05). Cells highlighted in grey represent the correlations with the highest tau correlation coefficient for each horizon or sub-layer.

Site	Lab number	Species	Element	Excavation number	Stratigraphic Horizon	Cultural Period	C_{coll} (%)	N_{coll} (%)	$C:N_{coll}$	$d^{13}C_{coll}$ (‰)	$d^{15}N_{coll}$ (‰)	^{14}C age (uncal yr BP)	Ref ^{14}C	Source ^{14}C	Source $^{13}C^{15}N$
Hohle Fels	HF-15	Giant deer	metatarsal	HF/65/100		Magdalenian	31.5	11.2	3.3	-20.1	2.9	12370±30	MAMS-16557	4	4
Hohlenstein Stadel	HST-28	Giant deer	tibia	ST/213/203/144		Magdalenian	22.5	7.8	3.4	-20.7	2.2	12175±50	ETH-41223	4	4
Geißenklösterle	EQ-GK 316	Horse	humerus	GH9 88 644	Ib	Gravettian	41.5	14.6	3.3	-20.6	7.3				3
Geißenklösterle	EQ-GK 317	Horse	femur	GH9 56 364	Ib	Gravettian	36.3	13.5	3.1	-20.7	5.5				3
Geißenklösterle	EQ-GK 318	Horse	tibia	GH9 57 508	Ib	Gravettian	42.8	14.3	3.5	-21.8	3.4				3
Geißenklösterle	EQ-GK 321	Horse	tibia	GH12 58 170	IIa	Aurignacian	37.8	13.9	3.1	-20.1	8.5				3
Geißenklösterle	EQ-GK 322	Horse	tibia	GH12 45 60	IIa	Aurignacian	36.3	13.7	3.1	-20.8	6.3				3
Geißenklösterle	EQ-GK 323	Horse	tibia	GH12 336/ 366 138	IIa	Aurignacian	36.1	13.6	3.1	-20.7	6.1				3
Geißenklösterle	EQ-GK 325	Horse	tibia	GH12 76 435	IIa	Aurignacian	41.6	14.4	3.3	-20.8	7.1				3
Geißenklösterle	EQ-GK 326	Horse		GH13 36 188	IIb	Aurignacian	42.9	15.3	3.2	-21.0	6.1				3
Geißenklösterle	EQ-GK 327	Horse		GH13 57 650	IIb	Aurignacian	41.6	15.0	3.2	-20.9	5.9				3
Geißenklösterle	EQ-GK 329	Horse		GH13 46+46 523 511	IIb	Aurignacian	40.7	15.5	3.0	-20.8	6.9				3
Geißenklösterle	EQ-GK 330	Horse		GH13 67 1111	IIb	Aurignacian	28.6	10.9	3.0	-21.6	6.9				3
Geißenklösterle	EQ-GK 331	Horse		GH15 49 33	IIIa	Aurignacian	43.8	16.2	3.1	-20.6	6.1				3
Geißenklösterle	GK13/EQ-GK314	Horse	tibia	GK88 GH7 99 557	It	Gravettian	43.2	15.7	3.2	-20.7	8.7				3
Geißenklösterle	GK14	Horse	radius	GK90 GH6 24 225	Ib	Gravettian	41.1	14.6	3.3	-20.6	6.3				7
Geißenklösterle	GK15	Horse	radius	GK82 GH6 55 36	Is	Gravettian	39.3	14.0	3.3	-20.4	7.1				7
Geißenklösterle	GK16/TUB-78	Horse		GH13 67 931	IIb	Aurignacian	39.7	14.2	3.3	-21.2	8.5	34800±600	OxA-21742	6	3
Geißenklösterle	GK18/EQ-GK319	Horse	tibia	GH12 56 495	IIa	Aurignacian	42.2	14.8	3.3	-21.4	4.2				3
Geißenklösterle	GK19/TUB-77	Horse		GK01 GH15 78 1408	IIIb	Aurignacian	39.3	14.6	3.1	-21.1	3.2	36490+350-340	KIA-17303	10	3
Geißenklösterle	GK21	Horse	tibia	GK74 GH14 47 344	IIc	Aurignacian	42.9	15.4	3.2	-21.1	8.5				this work
Geißenklösterle	OxA-5158	Horse							3.2	-20.9	2.2	12450±120	OxA-5158	5	5
Geißenklösterle	P-21810	Horse	scapula	GH12 0 131	IIa	Aurignacian	45.2	15.7	3.4	-20.8	8.9	33000±500	OxA-21656	6	7
Geißenklösterle	P-22978	Horse	(retoucher)	GH14 55 319	IId	Aurignacian	44.1	15.4	3.3	-20.2	7.9	34200±550	OxA-21726	6	9
Geißenklösterle	P-22980	Horse	humerus	GH13 0 143	IIb	Aurignacian	44.4	15.5	3.3	-20.9	6.3	34900±600	OxA-21738	6	7
Geißenklösterle	GK20(OxA-21722)	Horse[c]	femur distal	GK91 GH15 66 1144	III	Aurignacian	46.0	16.1	3.3	-20.4	3.5	38900±530	OxA-21722	6	this work
Geißenklösterle	GK4	Horse[c]	humerus	GK83 GH13 67 968	IIb	Aurignacian	42.0	15.0	3.3	-20.8	6.0				9
Hohle Fels	HF-10	Horse	tibia	HF08 GH8b 30 1240	Vb	Aurignacian	41.6	14.9	3.2	-20.5	6.5				9
Hohle Fels	HF-5	Horse	pelvis	HF01 GH5 68 2399	IIe	Aurignacian	39.9	14.1	3.3	-21.1	8.8				8
Hohle Fels	HF-6	Horse	rib	HF08 GH8 30 1204	Vb	Aurignacian	41.0	14.7	3.2	-20.5	6.8				9
Hohle Fels	HF-7	Horse	tibia/radius	HF07 GH7a 10 946	Va	Aurignacian	44.3	16.2	3.2	-20.7	6.3				9
Hohle Fels	HF-8	Horse	rib	HF07 GH7a24 1564	Va	Aurignacian	44.2	15.7	3.3	-20.9	6.2				9
Hohle Fels	HF-9	Horse	radius	HF07 GH7a 24 1604	Va	Aurignacian	44.0	15.8	3.3	-20.5	6.9				9
Hohle Fels	TUB-80	Horse		GH7 79 2542	IV	Aurignacian	37.7	13.7	3.2	-20.6	6.2				3
Langmahdhalde	LGN-11	Horse	radius	LH 50/39_171	GH5/AHV	Magdalenian	36.8	13.1	3.3	-21.0	2.7				2
Langmahdhalde	LGN-4	Horse	humerus right	LH 48/38_170	GH5/AHV	Magdalenian	39.0	13.8	3.3	-20.9	3.1	12636±47	ETH-84042	2	2
Langmahdhalde	LGN-5	Horse	metatarsal right	LH 47/37_124	GH4/AHIV	Magdalenian	38.0	13.5	3.3	-20.7	2.3				2
Langmahdhalde	LGN-7	Horse	metatarsal right	LH 47/38_129	GH4/AHIV	Magdalenian	35.6	12.5	3.3	-20.9	2.1				2
Langmahdhalde	LGN-8	Horse	metacarpal	LH 47/38_142	GH5/AHV	Magdalenian	31.8	11.5	3.2	-20.8	2.4				2
Schussenquelle	SCH-10	Horse	metatarsal distal left	Nr.4816.14		Magdalenian	40.1	15.4	3.0	-21.2	4.5	12250±50	GrA-45305	2	2
Schussenquelle	SCH-12	Horse	mandible	Nr.4816.6		Magdalenian	44.3	15.9	3.3	-21.4	1.9				this work
Schussenquelle	SCH-13	Horse	cranial	Nr.4816.2+3		Magdalenian	43.0	15.5	3.2	-21.5	3.4				this work
Geißenklösterle	GK1	Red deer	cranium	GK91 GH8/12 33 35	I/II	Gravettian	43.4	15.4	3.3	-19.5	5.0	29220±500	OxA-5706	11	9
Geißenklösterle	GK2	Red deer		GK81 GH12 79 581	IIa	Aurignacian	39.0	13.4	3.4	-19.9	4.7				9
Geißenklösterle	GK6	Red deer		GK87 GH15 88 923	III	Aurignacian	37.3	12.5	3.5	-19.9	3.0				9
Hohle Fels	HF-1	Red deer	ulna	HF06 GH7 98 1837	IV	Aurignacian	41.0	14.7	3.3	-19.9	4.4				9
Hohle Fels	HF-2	Red deer	carpal	HF04 GH7 55 1681	IV	Aurignacian	41.8	15.0	3.2	-20.1	3.7				9
Hohle Fels	HF-3	Red deer	metacarpal	HF01 GH8 79 2648	V	Aurignacian	41.4	14.7	3.3	-19.4	3.5				9
Schussenquelle	SCH-6	Red deer[a]	tibia distal	Nr.33714.3	Schuler 1994	Magdalenian	45.5	15.6	3.4	-20.2	3.0	12355±45	GrA-39505	3	3
Fellställe	FLS-7	Reindeer	mandible	Q8 Nr1515	AH3	Late Magdalenian	35.4	12.4	3.3	-19.8	2.1				1
Fellställe	FLS-8	Reindeer	mandible	Q304 Nr59 Nr54+43	AH3a	Late Magdalenian	34.5	12.3	3.3	-19.3	2.2				1

Fellställe	FLS-9	Reindeer	mandible	Q300 Nr352+365	AH3b	Late Magdalenian	33.4	11.7	3.3	-20.2	2.1				1
Geißenklösterle	P-21813	Reindeer	tibia	GH15 77 627	III	Aurignacian	45.5	15.7	3.4	-19.4	4.4	35050±600	OxA-21659	6	this work
Geißenklösterle	P-21815	Reindeer	metacarpal	GH10 86 122	Ic	Gravettian	44.2	16.4	3.1	-18.9	4.6	32900±450	OxA-21661	6	7
Geißenklösterle	P-22985	Reindeer		GH15 67 1655	IIIb	Aurignacian	46.6	16.0	3.4	-19.2	3.6	36100±700	OxA-21743	6	this work
Geißenklösterle	P-22987	Reindeer	tibia	GH15 66 1073	IIIa	Aurignacian	46.6	16.1	3.4	-19.5	3.5	36650±750	OxA-21745	6	this work
Geißenklösterle	P-22988	Reindeer	tibia	GH15 67 1453	IIIa	Aurignacian	46.9	16.2	3.4	-19.2	4.3	36850±800	OxA-21746	6	this work
Geißenklösterle	RA-GK 294	Reindeer	metatarsal	GH7 79 501	It	Gravettian	43.4	15.5	3.2	-19.0	4.2				3
Geißenklösterle	RA-GK 295	Reindeer	tibia	GH7 99 331	It	Gravettian	43.6	16.0	3.2	-19.3	3.7				3
Geißenklösterle	RA-GK 296	Reindeer	tibia	GH7 130 336	It	Gravettian	44.0	15.5	3.3	-19.0	4.2				3
Geißenklösterle	RA-GK 298	Reindeer	tibia left	GH9 88 620	Ib	Gravettian	42.0	14.6	3.3	-19.3	1.0				3
Geißenklösterle	RA-GK 299	Reindeer	astragalus	GH12 76 392	IIa	Aurignacian	41.7	14.5	3.3	-19.2	3.8				3
Geißenklösterle	RA-GK 300	Reindeer	humerus	GH12 110 415	IIa	Aurignacian	40.6	14.3	3.3	-18.6	3.8				3
Geißenklösterle	RA-GK 302	Reindeer	metatarsal	GH12 59 195	IIa	Aurignacian	39.6	14.8	3.1	-19.1	4.6				3
Geißenklösterle	RA-GK 303	Reindeer	tibia	GH15 57a 1891	IIIa	Aurignacian	41.9	15.3	3.2	-18.9	2.4				3
Geißenklösterle	RA-GK 304	Reindeer	humerus	GH13 57 628	IIb	Aurignacian	36.2	12.9	3.2	-19.5	4.4				3
Geißenklösterle	RA-GK 306	Reindeer	astragalus	GH13 68 376	IIb	Aurignacian	43.1	14.9	3.3	-19.4	4.7				3
Geißenklösterle	RA-GK 308	Reindeer	tibia	GH15 47 300	IIIa	Aurignacian	41.7	14.4	3.3	-18.7	3.4				3
Geißenklösterle	RA-GK 309	Reindeer	tibia	GH15 57 1017	IIIa	Aurignacian	35.7	13.2	3.1	-19.1	3.9				3
Geißenklösterle	RA-GK 311	Reindeer	tibia	GH15 57 99	IIIa	Aurignacian	43.2	14.5	3.4	-18.6	3.4				3
Geißenklösterle	RA-GK 312	Reindeer	tibia	GH15 67 2017	IIIa	Aurignacian	41.8	15.3	3.2	-19.0	2.6				3
Hohle Fels	KIA-35462	Reindeer	vertebra		Va	Aurignacien	44.6	14.7	3.5	-19.5	4.8				9
Langmahdhalde	LGN-10	Reindeer	mandible right	LH 50/38_297	GH5/AHV	Magdalenian	38.2	13.5	3.3	-19.9	1.8				2
Langmahdhalde	LGN-12	Reindeer	mandible right	LH 51/37_201	GH5/AHV	Magdalenian	40.6	14.4	3.3	-19.8	2.0				2
Langmahdhalde	LGN-13	Reindeer	metatarsal	LH 52/38_100	GH5/AHV	Magdalenian	36.5	12.9	3.3	-19.8	2.0				2
Langmahdhalde	LGN-14	Reindeer	metatarsal	LH 50/39_133	GH4/AHIV	Magdalenian	42.1	14.8	3.3	-20.1	2.5				2
Langmahdhalde	LGN-6	Reindeer	tibia right	LH 47/37_156	GH5/AHV	Magdalenian	42.5	14.9	3.3	-19.4	1.6				2
Langmahdhalde	LGN-9	Reindeer	metatarsal	LH 48/39_129	GH4/AHIV	Magdalenian	37.3	13.1	3.3	-19.9	2.0				2
Petersfels	RA-PTF 363	Reindeer	metapodial left		P1 AH2	Magdalenian	45.2	15.3	3.4	-19.8	2.4				1
Petersfels	RA-PTF 364	Reindeer	metapodial right		P1 AH2	Magdalenian	45.6	15.6	3.4	-19.6	2.1				1
Petersfels	RA-PTF 365	Reindeer	calcaneus right		P1 AH2	Magdalenian	42.5	14.4	3.4	-19.9	2.3				1
Petersfels	RA-PTF 366	Reindeer	astragalus right		P1 AH2	Magdalenian	34.6	12.5	3.2	-20.0	1.2				1
Petersfels	RA-PTF 367	Reindeer	tibia right		P1 AH2	Magdalenian	31.8	11.6	3.2	-19.9	1.2				1
Petersfels	RA-PTF 368	Reindeer	calcaneus left		P1 AH3	Magdalenian	43.5	15.3	3.3	-19.4	2.4				1
Petersfels	RA-PTF 369	Reindeer	astragalus left		P1 AH3	Magdalenian	39.4	13.8	3.3	-20.2	2.6				1
Petersfels	RA-PTF 370	Reindeer	tibia left		P1 AH3	Magdalenian	40.6	13.9	3.4	-19.1	2.3				1
Petersfels	RA-PTF 371	Reindeer	calcaneus left		P1 AH3	Magdalenian	45.9	15.5	3.5	-19.7	2.1				1
Petersfels	RA-PTF 373	Reindeer	tibia left		P1 AH3	Magdalenian	43.7	14.9	3.4	-19.7	2.5				1
Petersfels	RA-PTF 374	Reindeer	tibia left		P1 AH3	Magdalenian	41.5	14.2	3.4	-19.7	1.4				1
Petersfels	RA-PTF 375	Reindeer	tibia left		P1 AH3	Magdalenian	42.1	14.4	3.4	-20.0	3.3				1
Petersfels	RA-PTF 376	Reindeer	tibia left		P1 AH3	Magdalenian	44.1	15.1	3.4	-19.7	2.4				1
Petersfels	RA-PTF 377	Reindeer	tibia left		P1 AH3	Magdalenian	42.8	14.8	3.4	-19.9	2.0				1
Petersfels	RA-PTF 379	Reindeer	tibia left		P1 AH3	Magdalenian	41.8	14.1	3.5	-19.5	2.6				1
Petersfels	RA-PTF 380	Reindeer	metapodial right		P1 AH4	Magdalenian	44.6	14.3	3.6	-19.6	2.4				1
Petersfels	RA-PTF 381	Reindeer	metapodial right		P1 AH4	Magdalenian	44.4	14.5	3.6	-19.3	2.3				1
Petersfels	RA-PTF 382	Reindeer	metapodial right		P1 AH4	Magdalenian	43.6	15.0	3.4	-19.1	1.9				1
Petersfels	RA-PTF 383	Reindeer	tibia right		P1 AH4	Magdalenian	44.3	14.5	3.6	-19.4	2.9				1
Schussenquelle	SCH-1	Reindeer	femur right			Magdalenian	44.7	15.5	3.4	-19.8	2.5				1
Schussenquelle	SCH-2	Reindeer	femur right			Magdalenian	44.5	15.9	3.3	-19.7	2.8				1
Schussenquelle	SCH-3	Reindeer	femur right			Magdalenian	45.1	15.5	3.4	-20.1	1.8				1
Schussenquelle	SCH-4	Reindeer	femur right			Magdalenian	44.0	15.7	3.3	-19.4	1.9				1
Schussenquelle	SCH-5	Reindeer	femur right			Magdalenian	45.8	15.4	3.5	-19.5	2.2				1
Geißenklösterle	(EQ)-GK 315	Reindeer[b]	long bone	24d 131	Ia/b	Gravettian	39.5	15.4	3.0	-18.7	3.7				3
Geißenklösterle	GK5	Reindeer[c]		GK01 GH15 78 1372	IIIb	Aurignacian	36.5	12.8	3.3	-19.1	3.1				7

Supplementary Materials 4. The stable isotope data and sources used for Figure 5. a = initially identified as European elk/moose but lately shown to be deer based on genetic sequence (Immel, personal communication 2015); b = initially identified as horse, lately re-attributed to reindeer; c = taxonomic identification revised/confirmed based on ZooMS analysis. 1 = Drucker et al. 2011; 2 = Wong et al. 2020; 3 = Bocherens et al. 2011; 4 = Immel et al. 2015; 5 = Stevens and Hedges 2004; 6 = Higham et al. 2012; 7 = Drucker et al. 2015; 8 = Fellows Yates et al. 2017; 9 = Münzel et al. 2017; 10 = Conard and Bolus 2008; 11 = Richter et al. 2000. The methods associated with specimens first reported in this work can be found in Supplementary Materials 5.

Supplementary Materials 5: The methods used for stable isotope analysis of specimens presented in this paper for the first time

From “New perspectives on human subsistence during the Magdalenian in the Swabian Jura, Germany” by G. L. Wong, B. M. Starkovich, D. G. Drucker, and N. J. Conard

For this paper, we have compiled isotopic data from published sources (Drucker et al., 2011; Wong et al., 2020; Bocherens et al., 2011; Immel et al., 2015; Stevens and Hedges, 2004; Drucker et al., 2015; Münzel et al., 2016; Fellows et al., 2017), as well as the results from eight bone samples from reindeer (n=4) and horses (n=4) from the sites of Geißenklösterle and Schussenquelle (Supplementary Table 4). Except for one horse sample from Geißenklösterle (GK20/OxA-21722), the extraction of collagen was conducted at the Department of Geosciences at the University of Tübingen (Germany) following a protocol based on Longin (1971) and modified by Bocherens et al. (1997). The extraction process includes a step of soaking in 0.125 M NaOH between the demineralization and solubilization steps to achieve the elimination of lipids and humic substances. The sample GK20/OxA-21722 was treated in Oxford following a protocol described in Bronk Ramsey et al. (2004) that includes a step of separation of lower molecular weight components from the gelatin extracted from bones using Longin’s (1971) method.

The elemental analysis (C_{coll} and N_{coll}) and isotopic analysis ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) were performed at the Geochemical unit of the Department of Geosciences at the University of Tübingen using an elemental analyzer NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer for all collagen. The only exception is a horse tibia from Geißenklösterle (GK21) that was submitted to elemental analyses and isotopic measurements in duplicate at the Institute of Environmental Science and Technology of the Universitat Autònoma de Barcelona (ICTA-UAB) using a Thermo Flash 1112 (Thermo ScientificVC) elemental analyzer coupled to a Thermo Delta V Advantage mass spectrometer with a Conflo III interface. The isotopic ratios are expressed using the “δ” (delta) value as follows: ($\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard}-1]$ x1000‰ and ($\delta^{15}N=[(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{standard}-1]$ x 1000‰. The measurements were calibrated in reference to the international standards (V-PDB for carbon and AIR for nitrogen) using USGS-24 ($\delta^{13}C = -16.0$‰), IAEA 305A ($\delta^{15}N=+39.8$‰) at Tübingen, IAEA 600 ($\delta^{13}C = -27.8$‰), ($\delta^{15}N=+1.0$‰) at Barcelona and in-house reference materials (modern collagen of camel and elk) at both places. Analytical precision, based on within-run replicate measurement of laboratory standards (egg albumin, keratin, alanine amino acid, modern collagen), was ±0.1‰ for $\delta^{13}C$, and ±0.2‰ for $\delta^{15}N$ at Tübingen and below ±0.2‰ at Barcelona. The reproducibility error for the amounts of C and N was lower than 5% at Tübingen and lower than 2% at Barcelona. The biochemical reliability of the collagen was estimated by considering the chemical composition of collagen, with C/N atomic ratio (C:N_{coll}) ranging from 2.9 to 3.6 (DeNiro 1985) and contents of C_{coll} and N_{coll} above 8% and 3% respectively (Ambrose 1990).

See Supplementary Materials 6 for a summary of the locations where collagen extraction and stable isotope analyses of the previously unpublished data were performed.

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Site	Lab number	Species	Excavation number	Location of collagen extraction	Location of stable isotope analyses
Schussenquelle	SCH-12	Horse	Nr.4816.6	Tübingen	Tübingen
Schussenquelle	SCH-13	Horse	Nr.4816.2+3	Tübingen	Tübingen
Geissenklösterle	P-21813	Reindeer	GH15 77 627	Tübingen	Tübingen
Geissenklösterle	P-22987	Reindeer	GH15 66 1073	Tübingen	Tübingen
Geissenklösterle	P-22988	Reindeer	GH15 67 1453	Tübingen	Tübingen
Geissenklösterle	P-22985	Reindeer	GH15 67 1655	Tübingen	Tübingen
Geissenklösterle	GK21	Horse	GK74 GH14 47 344	Tübingen	Barcelona
Geissenklösterle	GK20(OxA-21722)	Horse	GK91 GH15 66 1144	Oxford	Tübingen

Supplementary Materials 6. Summary of the locations where collagen extraction and stable isotope analyses of unpublished data were performed.