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ORIGINAL PAPER

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 1860s. While there is a rich tradition of research on the Magdalenian, many of the best-known sites were not excavated using modern methods, 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 compared to regions to the west.

Keywords Zooarchaeology · Taphonomy · Paleoenvironment · Late Glacial · Human subsistence · Magdalenian

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

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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 have indicated that the most commonly hunted animals were large migratory game, such as reindeer (*Rangifer tarandus*) and horse (*Equus ferus*), 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 found 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 argued, 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 called 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 have 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.

Notable archaeological sites dating to the Magdalenian in the Swabian Jura include the cave sites of Schussenquelle (Fraas 1867; Schuler 1994), Brillenhöhle (Riek 1973b), and Hohle Fels (Napierala et al. 2014; Taller 2014), and the rock shelter Felsställe (Kind 1987). However, several Magdalenian sites in the Swabian Jura are poorly preserved, severely affected by taphonomic processes, or are in contexts that are mixed with early Holocene materials. Further, 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 Langmahdhalde, a rock shelter in the Lone Valley, which revealed intact archaeological horizons dating to the Magdalenian, prompting annual excavations (Conard et al. 2017, 2018, 2019). Our recent study 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 (Wong et al. 2017). This previous 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, p. 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 microfaunal data because they can indicate which nonhuman 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.

Langmahdhalde

Langmahdhalde (48° 34′ 0.84″ N, 10° 12′ 47.88″ E) is a limestone rock shelter located on the edge of the Lone River valley, approximately 2 km from the well-known archaeological site Vogelherd (Fig. 1). Our 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). Figure 2 presents a stratigraphic profile from the site and we summarize the cultural affiliations and dating for each horizon 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. In GH4/AHIV, GH5/AHV, and GH6/AHVI, excavators have found lithics from one horizon that refit with those from another horizon. These three horizons are also 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 excavated the site by 1/4m2 within 1x1 m quadrants named by the coordinates of their southwestern corner (Fig. 3). The team excavated GH5/AHV and GH6/AHVI in 2 to 3 cm deep sublayers 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 sublayer. 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 × 50 cm subquadrant from each 1 × 1 m quadrant. All other horizons discussed in this study had all sediment water-screened. This may result in the under-representation of small taxa and elements that are usually recovered during water-screening, as opposed to during excavation, in GH3/AHIII.

Methods

We define macrofauna as those specimens that belong to medium- to large-sized animals and were likely deposited at the site as a result of human or large carnivore activity. 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.). In the current context, 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”

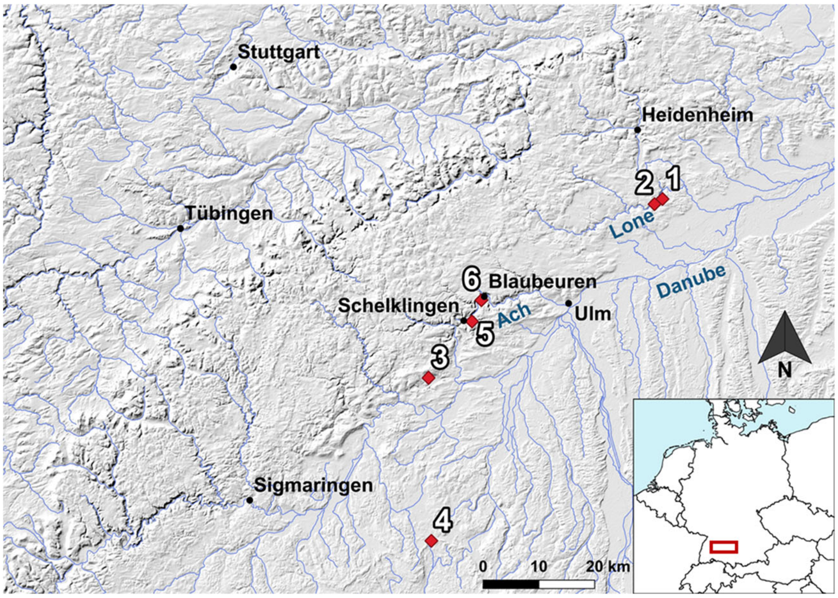

Fig. 1 Map of Langmahdhalde and other archeological sites mentioned in the text. 1 = Langmahdhalde; 2 = Vogelherd; 3 = Felsställe; 4 = Schussenquelle; 5 = Hohle Fels; 6 = Brillenhöhle. Map made in QGIS version 3.4 with topographic data from SRTM NASA version 3, hydrology data from the Landesanstalt für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

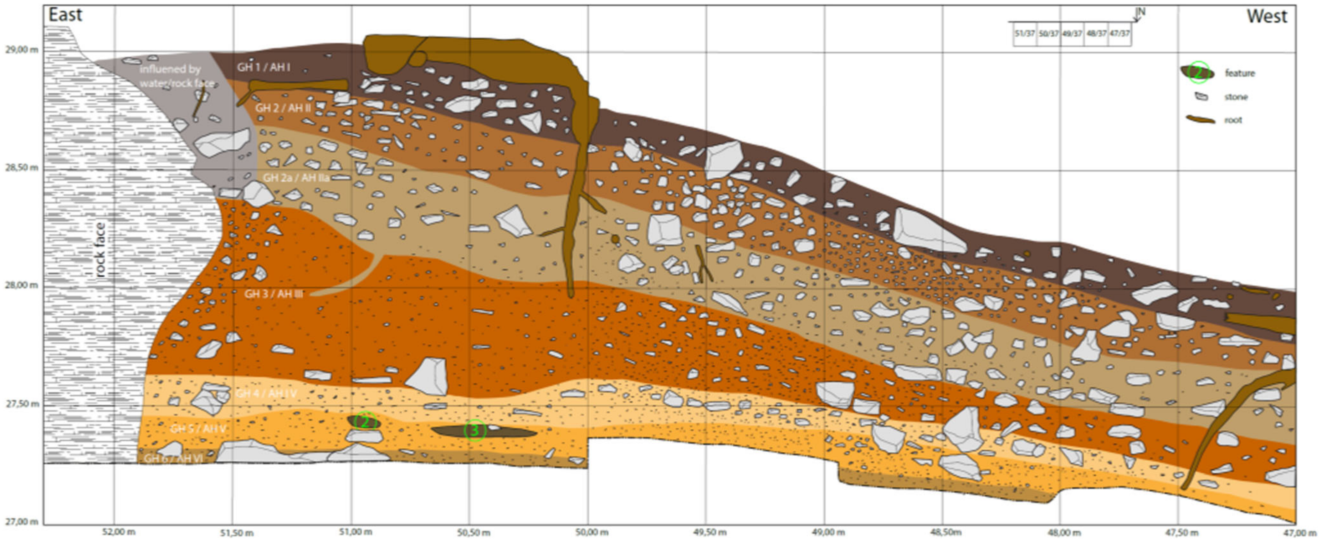

Fig. 2 The stratigraphy of Langmahdhalde from excavation years 2016 to 2018. This is the southern profile of the site at the *y*-coordinate 37 (which runs east to west). Combustion features, stones, and roots can be identified using the key in the upper right. Further information can be found in Table 1. GH = geological horizon; AH = archaeological horizon. Figure by A. Janas

throughout the paper). Of course, these two groups are not mutually exclusive, and there is likely to be overlap in the species brought to the site by different agents. However, micromammal assemblages (including rodents and insectivores) are almost always deposited by nonhuman predators, such as small mammalian carnivores or predatory birds (Fernández-Jalvo et al. 2016).

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;

Table 1 Stratigraphic information for Langmahdhalde including the dating and cultural affiliation of each horizon

GH	AH	Cultural affiliation	Dates (cal yr BP)	Source of dates
1	I	Modern humus layer		
2	II	Ceramics and lithics from Neolithic, metal ages, early Middle ages	2680–2354	1; 2
2a	IIa	Mesolithic	6483–5071	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			

1 = Conard et al. (2017); 2 = Wong et al. (2020); 3 = Conard et al. (2018); 4 = Conard et al. (2019)

GH = geological horizon; AH = archaeological horizon

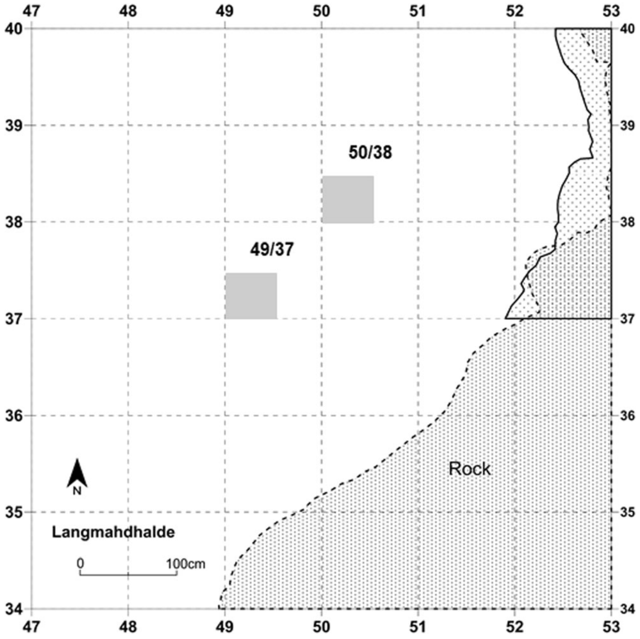

Fig. 3 Overview of the excavation quadrants at Langmahdhalde. Each quadrant is 1 × 1 m in dimension and named based on the coordinates of its southwestern corner. The dotted areas on the right side of the figure indicate the rock shelter. The 50 × 50 cm southwestern subquadrants, highlighted in gray, are the subquadrants selected for the taphonomic analysis of the microfauna (49/37 for GH3 and 50/38 for all other horizons). Figure by M. Zeidi

Fernández-Jalvo and Andrews 2016). We define spiral fractures following Shipman et al. (1981). When discussing "cone fractures," we are referring to fracturing as a result of dynamic loading and direct percussion, referred to as "flake scars" by Lyman (1987) and the "impact point" by Johnson (1987). This type of fracture often causes pieces of bone to flake off; we refer to these as "cone negatives." There has been much discussion regarding the reliability of identifications of cut marks in the archaeological record (see Lyman 1994, p. 297–299 and Domínguez-Rodrigo et al. 2017 for discussions). We identified cut marks based on their placement and orientation and the following morphological attributes: V-shaped in cross-section, elongate, and the presence of "shoulder effects." Potential cut marks were examined under a Zeiss SteREO Discovery V8 microscope before being classified as such.

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 based on 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 the 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 element (MNE; Lyman 1994) values. Tooth enamel, though, has a higher mineral content than bone, so teeth are more likely to preserve in the archeological record (Lyman 1994; Hillson 2005). If the ratio of tooth MNE to cranial bone MNE is higher than one, teeth are more common in the record than bone and it is possible that this is a result of their higher mineral content, not the actual number of teeth and bones deposited at the site. If this is the case, 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).

Microfauna

For all horizons of the site, the microfaunal remains are more densely distributed along the dripline of the rock shelter, which generally corresponds to the units with east–west values of 49, 50, and 51 (see Fig. 3). 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 (Fig. 3). There is one exception to this: excavators did not save any sediment from GH3/AHIII for water-screening from quadrant 50/38, and we therefore analyzed the taphonomy of the microfauna from the southwest corner of quadrant 49/37 (Fig. 3) for GH3/AHIII. We included GH2/AHII and GH2a/AH2a in this analysis to provide context for GH3/AHIII to GH6/AHVI. We also present the taxonomic identifications from this sample (Wong et al. 2020 includes further taxonomic identifications from all subquadrants of quadrants 49/37, 50/38, and 50/39). We used several identification guides (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 in the Institute for Archaeological Sciences at the University of Tübingen to make these identifications. In order to classify specimens in the genera *Sorex* and *Apodemus* to the species-level, we followed measuring criteria from Niethammer and Krapp (1978, p. 326, 338, 361), Ziegler (1995), and Maul (2001). We took measurements at the Institute for Archaeological Sciences at the University of Tübingen using a Keyence Digital Microscope VHX-500F. We calculated the NISP and MNI for each taxonomic category (Grayson 1984; Lyman 2008). We did not include specimens identifiable only to Rodentia in our taxonomic identifications and we gave specimens that articulate a total NISP value of one. We do differentiate common and field voles (*Microtus arvalis* and *agrestis*) in this study, although, as we reported in Wong et al. (2020), both species are present in every horizon and sublayer of the site.

We identified burning in the microfaunal assemblage following visual criteria discussed in Stiner et al. (1995). We differentiated between burning and oxide staining with a visual inspection using a Zeiss Stemi 305 EDU microscope, where burning is actual blackening and calcination, as opposed to shades of brown that are more likely to be staining.

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, p. 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 sublayer based on the MNI value of the entire horizon or sublayer. 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 sublayer by 100 and dividing by the number of that element that we would expect in the horizon based on the MNI (Andrews 1990, p. 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).

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

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

where the number of missing teeth 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 destruction during consumption and post-depositional taphonomic processes, such as trampling or screening. This index assumes that teeth are in their alveolar sockets when an individual is consumed by a predator. 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 destruction 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:

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

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). To avoid overcounting, we recorded digestion on incisor tips only and did not include small fragmented pieces of incisor tips in our counts. We also only recorded digestion on molars that are ≥ 60% complete.

Results

Macrofauna

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 archeological horizons, hare, reindeer, horse, ptarmigan, and small carnivores are the most common 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 (Fig. 4) and another has an intact base, indicating that it was collected after it was shed. Both are from AHV. 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 (Table 2). 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-sized 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).

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.

Taphonomy

We summarize the taphonomic modifications on the macrofaunal remains from Langmahdhalde in Tables 5 and 6. Many

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

Taxon	GH3/AHIII		GH4/AHIV		GH5/AHV		GH6/AHVI	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Mammals								
Chamois (*Rupicapra rupicapra*)	1	1			3	1	1	1
Ibex (*Capra ibex*)	1	1			1	1	2	1
Wild bison or cattle (*Bison*/*Bos* sp.)			1	1	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
Large deer (e.g., *Cervus* or *Rangifer*)	2		18		31		6	
Roe deer (*Capreolus capreolus*)	1	1						
European elk/moose (*Alces alces*)			1	1				
Deer (Cervidae)			2		4			
Horse (*Equus ferus*)	2	1	11	4	38	2	3	1
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			
Ungulate			2		5			
Stoat (*Mustela erminea*)							1	1
Polecate (*Mustela putorius*)					1	1		
Small mustelid (*Mustela nivalis* or *erminea*)			13	2	16	3	6	1
Weasel/polecat (*Mustela* sp.)			2	1				
Pine marten (*Martes martes*)					1	1		
Arctic fox (*Vulpes lagopus*)			1	1				
Fox (*Vulpes* sp.)	8	1	18	2	18	2	3	1
Cave lion (*Panthera spelea*)	4	2	3	1	2	1		
Small carnivore	1		6		10		89	
Large carnivore	2		1					
Carnivore			1					
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
Mammoth (*Mammuthus primigenius*) ivory					1		2	
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								
Goose (*Anser* sp.)			2	1				
Common teal (*Anas crecca*)			2	1				
Dabbling duck (*Anas* sp.)	1	1	1	1				
Black grouse (*Tetrao tetrix*)			1	1				
Hazel grouse (*Tetrastes bonasia*)			2	1				
Ptarmigen (*Lagopus* sp.)			22	3	13	4	3	1

Table 2 (continued)

Taxon	GH3/AHIII		GH4/AHIV		GH5/AHV		GH6/AHVI	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Phasianidae	1		1		2			
Podicipedidae			1					
Columbidae			1	1				
Eurasian golden plover (*Pluvialis apricaria*)			2	1			1	1
Charadriidae					1			
Charadriiformes			2		1			
White stork (*Ciconia ciconia*)			1	1				
Black stork (*Ciconia nigra*)			1	1				
Accipitridae							1	
Snowy, horned, eagle, and fish owls (*Bubo* sp.)							1	1
Tawny owl (*Strix aluco*)							2	1
Passeriformes			8		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	

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

Fig. 4 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

Table 3 Spearman's rank-order correlation between bone density values and % survivorship by horizon for the taxonomic groups "hare" and "medium ungulate"

	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

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

	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

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

	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

Total NISP for each horizon included in the column header

display cone fractures and two specimens are 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 cut marks on 0.6 to 1.8% of the specimens, depending on the horizon (Table 5). The majority of the specimens displaying

Table 6 Number of specimens (NSP) and NISP associated of the macrofaunal assemblage of Langmahdhalde that are associated with features and burned

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

All features are in GH5/AHV. Specimens included in NSP counts are both diagnostic and nondiagnostic 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 suggests it was skinned, probably for its fur (Binford 1981, p. 47; Wong et al. 2017). We observed cut marks on horse and reindeer specimens in GH5/AHV and on horse specimens in GH6/AHVI. Another observed human modification on the faunal remains is a small (approximately 3.5 cm long) antler fragment, from GH6/AHVI, that has been grooved. The abovementioned reindeer antler from GH5/AHV that is connected to the braincase has a notch close to the base (Fig. 4) that, based on its placement and morphology, is likely anthropogenic, although the poor preservation of the antler's surface makes this difficult to confirm.

In general, there are very few diagnostic burned remains at the site; most burned faunal remains are small, unidentifiable fragments weighing less than 0.1 g (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. On five hare (*Lepus* sp.) specimens, we observed bite marks or punctures. Four of these specimens are from GH4/AHIV: one is a calcaneus with carnivore gnawing and a puncture mark approximately 4.3 mm in diameter, one is a first phalanx with a small circular puncture mark, one is a second phalanx with a small circular puncture mark, and one is a humerus fragment with a bite mark and carnivore gnawing. The final specimen is from GH6/AHVI and has five bite marks that measure an average of 1.4 mm in diameter, as well as evidence of carnivore gnawing on one end.

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.

Skeletal element representation

In Fig. 5, 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 present. 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.

Microfauna taphonomy

The taphonomic analysis of the microfaunal remains included 7921 specimens. In Table 7, we report the total number of microfaunal specimens in our taphonomic analysis by horizon and sublayer. Table 7 also includes the relative abundance of each skeletal element and the overall MNI value for each horizon and sublayer. No microfaunal remains that are identifiable to element were observed in GH5/AHV sublayer 1 of our sample, so we exclude this sublayer from our taphonomic analysis. We present the taxonomic identifications in Table 8. All horizons of the assemblage are dominated by Arvicolids, with common and field voles present in every horizon and sublayer. In the Holocene horizons, red-backed voles (*Myodes glareolus*) are the most common taxon, while in the Late Glacial horizons, collared lemmings (*Dicrostonyx* sp.) dominate and narrow-headed voles (*Lasiopodomys gregalis*) are represented in numbers similar to common and field voles. Insectivores are rare in the assemblage and are primarily in GH2/AHII, although there are three shrew specimens in GH5/AHV sublayer 4.

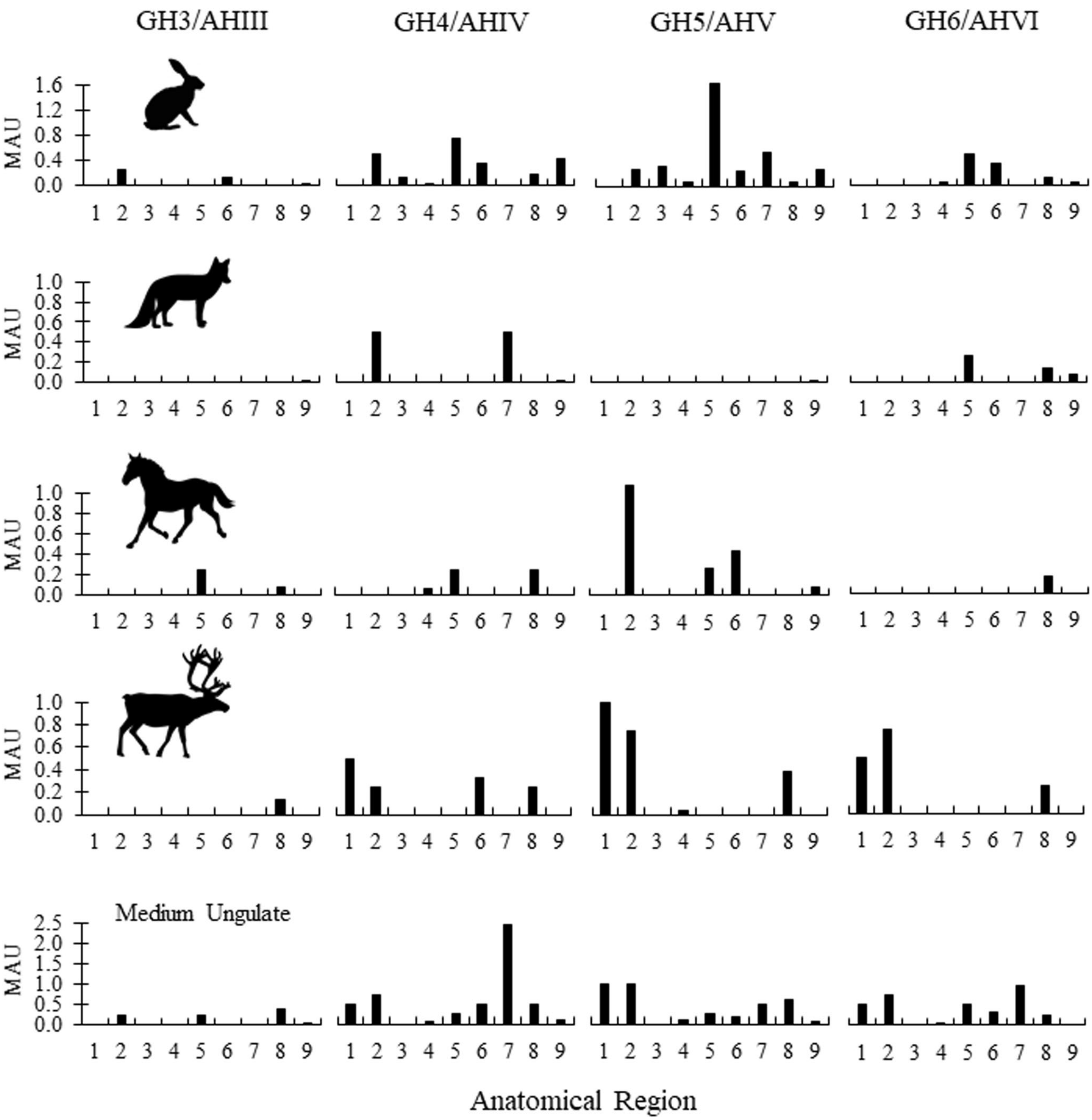

Fig. 5 Skeletal element representation of hare (top), fox, horse, reindeer, and medium ungulate (bottom) remains at Langmahdhalde by horizon. The anatomical region is on the *x*-axis (after Stiner 1991) and MAU values are on the *y*-axis. For the anatomical regions, region 1 = horn/antler, 2 = head, 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 of the same scale

In Table 9, 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%).

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 sublayer 2 has the highest percentage of complete long bones (humeri, 20%). There are no complete long bones in the Holocene horizons of GH3/AHIII. In GH2/

Table 7 The % relative abundance of each element and total NISP by horizon and sublayer of the microfaunal assemblage at Langmahdhalde

	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	156	18	6	11	312
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		81.3		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	2	5	97	1496
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 sublayer 2 (MNI = 11)																			
Actual #	4	5	0	10	1	6	1	9	13	0	0	5	9	1	42	4	0	4	114
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 sublayer 3 (MNI = 22)																			
Actual #	2	20	10	31	26	27	18	40	44	2	0	13	38	3	88	5	1	7	375
Expected #	44	44	44	44	44	44	44	44	44	44	44	858	88		264		1320	440	–
	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	–

Table 7 (continued)

	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
% relative abundance																			
GH5/AHV sublayer 4 (MNI = 79)																			
Actual #	12	50	40	110	69	113	69	100	157	7	1	54	121	3	270	10	8	98	1292
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 sublayer 5 (MNI = 51)																			
Actual #	4	24	21	101	39	90	31	95	87	18	8	37	80	4	150	5	12	108	914
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 sublayer 6 (MNI = 41)																			
Actual #	3	18	14	55	42	42	29	62	81	33	30	38	50	4	137	7	129	209	983
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		27.8		5.2	25.5	–
GH6/AHVI sublayer 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 sublayer 2 (MNI = 62)																			
Actual #	8	23	20	83	46	71	49	81	124	15	6	30	78	8	143	6	21	137	949
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 sublayer 3 (MNI = 48)																			
actual #	10	38	8	83	38	53	62	91	96	0	0	48	76	4	172	14	1	45	839

Table 7 (continued)

	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
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	–

MNI values for each horizon or sublayer are based on all rodent and insectivore remains from the horizon or sublayer 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 sublayer. 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, p. 46–47)

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 sublayers 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 sublayers 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 288.9% 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 sublayers 1 and 2 have the highest values (428.6% and 339.1%, respectively).

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 sublayers from GH4/AHIV to GH6/AHVI, except GH5/AHV sublayer 2, there are specimens that have light, medium, and heavy digestion. In GH4/AHIV, approximately 40% of the long bones are digested, with light and medium digestion being the most common. All sublayers 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

Table 8 Taxonomic identifications of the microfaunal remains from Langmahdhalde

Common name	Taxon	GH2/AHII		GH2a/ AHIIa		GH3/ AHIII		GH4/ AHIV		GH5/AHV sublayer 2		GH5/AHV sublayer 3		GH5/AHV sublayer 4		GH5/AHV sublayer 5		GH5/AHV sublayer 6		GH6/ AHVI sublayer 1		GH6/ AHVI sublayer 2		GH6/ AHVI sublayer 3	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Moles	*Talpa* sp.	3	1																						
Shrews	Soricidae indet.	3	1											1	1										
Red-toothed shrews	Soricinae indet.	3	2																						
Long-tailed shrews	*Sorex* sp.													1	1										
Common shrew	*Sorex araneus*	1	1											1	1										
Dormice and hazel mice	Gliridae indet.	1	1																						
Edible dormouse	*Glis glis*	6	1																						
Yellow-necked/wood mouse	*Apodemus flavicollis/sylvaticus*	7	2																						
Yellow-necked mouse	*Apodemus flavicollis*	7	2					1	1																
Common/field vole	*Microtus arvalis/agrestis*	17	9	1	1	1	1	39	21	9	5	8	6	20	14	12	7	10	6	1	1	28	15	24	14
Common/field vole or narrow-headed vole	*Microtus arvalis/agrestis* or *Lasiopodomys gregalis*							1	1			1	1	6	3									2	1
Narrow-headed vole	*Lasiopodomys gregalis*					1	1	27	15	1	1	1	1	19	12	7	4	7	6			9	5	19	11
Tundra vole	*Microtus oeconomus*							3	2	2	2														
Terricola group	Genus *Microtus*	3	2																						
Eurasian snow vole	*Chionomys nivalis*	4	3					3	3																
Collared lemming	*Dicrostonyx* sp.							53	11	20	2	73	12	122	17	76	13	46	10	16	5	62	13	81	20
Water vole	*Arvicola amphibius*	7	3	3	2																				
Red-backed vole	*Myodes glareolus*	74	12	4	2	2	1	1	1																
Lemmings and voles	Arvicolinae indet. (excluding the genera *Lemmus*, *Dicrostonyx*, *Myodes*, and *Arvicola*)	46	9	1	1	1	1	201	35	13	4	10	3	109	18	60	11	72	13	17	5	50	8	57	15
	Total	182	49	9	6	5	4	329	90	45	14	93	23	279	67	155	35	135	35	34	11	149	41	183	61

We do not include specimens identified to the order Rodentia. For GH3/AHIII, specimens are from the southwestern subquadrant of 49/37. For all other horizons, specimens are from the southwestern subquadrant of 50/38

Table 9 Information on specimens in the microfaunal assemblage of Langmahdhalde that show evidence of burning or oxide staining

	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

The burn stages follow Stiner et al. (1995). The burned specimen in GH5/AHV is from sublayer 3

proportions of digestion-level categories (light to extreme), across all sublayers: 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 sublayer 6) and three molars (from GH5/AHV sublayers 4 and 6 and GH6/AHVI sublayer 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.

Discussion

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 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. 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 primarily on using the percentage of long bones, molars, and incisors that have been digested to present the likely predator(s) responsible for depositing the assemblage in each horizon and sublayer. To do so, we rely on Andrews' (1990, p. 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. When discussing predators based on these two sources, we only use those species distributed in Central Europe during the Pleistocene and/or Holocene.

In GH2/AHII, the percentage of incisors that are digested (24.6%) falls in line with a category 2 predator, whereas the percentage of digested molars (40.8%) and long bones (73.3%) indicate a category 3 predator. This suggests that several predators likely deposited the microfauna from this horizon. Predators associated with category 2 incisor digestion are long-eared owls (*Asio otus*) and great gray owls (*Strix nebulosa*); predators associated with category 3 molar digestion are Eurasian eagle owls (*Bubo bubo*) and tawny owls (*Strix aluco*); and predators associated with category 3 long bone digestion are little owls (*Athene noctua*), kestrels (*Falco tinnunculus*), hen harriers (*Circus cyaneus*), and peregrine falcons (*Falco peregrinus*). Long-eared owls, great gray owls, and hen harriers prefer to feed on Arvicolids (Andrews 1990, p. 184, 190–191, 197), while Eurasian eagle owls and tawny owls are opportunist feeders (Andrews 1990, p. 189 and 193). Little owls, kestrels, and peregrine falcons are unlikely to greatly influence micromammal assemblages. Both little owls and peregrine falcons consume very few mammals; little owls prefer insects and peregrine falcons prefer birds (Andrews 1990, p. 193–196). Although kestrels prefer to consume voles, their pellets are not necessarily accurate representations of the individuals they have consumed as there is much loss of individual prey items due to digestion or the style of eating (Andrews 1990, p. 196). Arvicolids are, therefore, probably overrepresented in this horizon compared to their natural occurrence because of contributions from long-eared owls, great gray owls, and hen harriers, but the contributions of opportunistic predators as well indicate 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 sublayer 2 have similar digestion results. In both, the percentage of digested incisors and long bones implies a category 2 predator, while the percentage of digested molars suggests a category 3 predator. As mentioned above, predators associated with category 2 incisor digestion are long-eared owls and great gray owls, and predators associated with category 3 molar digestion are Eurasian eagle owls and tawny owls. Eurasian eagle owls and tawny owls are also associated with category 2 long bone digestion. These results, then, indicate that both opportunistic and specialist feeders likely accumulated the microfaunal assemblage in these horizons. We therefore find that, like in GH2/AHII, Arvicolids may be overrepresented in these two horizons compared to their relative abundance on the landscape but that presence/absence data for the taxa in the assemblage will

Table 10 Representation of long bone portions of microfauna from Langmahdhalde by horizon and sublayer, following Andrews (1990, p. 50–52)

	GH2/AHII		GH2a/AHIIa		GH3/AHIII		GH4/AHIV		GH5/AHV sublayer 2		GH5/AHV sublayer 3		GH5/AHV sublayer 4
	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
Proximal	2	20.0	0	0.0	0	0.0	32	19.6	1	10.0	10	32.3	22
Shaft	0	0.0	0	0.0	0	0.0	39	23.9	2	20.0	16	51.6	15
Distal	8	80.0	3	100.0	0	0.0	67	41.1	5	50.0	3	9.7	54
Total	10	100.0	3	100.0	0	0.0	163	100.0	10	100.0	31	100.0	110
Radius													
Complete	0	0.0	0	0.0	0	0.0	8	12.9	0	0.0	3	11.5	5
Proximal	1	100.0	0	0.0	0	0.0	28	45.2	1	100.0	6	23.1	31
Shaft	0	0.0	0	0.0	0	0.0	7	11.3	0	0.0	7	26.9	14
Distal	0	0.0	0	0.0	0	0.0	19	30.6	0	0.0	10	38.5	19
Total	1	100.0	0	0.0	0	0.0	62	100.0	1	100.0	26	100.0	69
Ulna													
Complete	0	0.0	0	0.0	0	0.0	2	1.6	1	16.7	0	0.0	4
Proximal	3	100.0	0	0.0	1	100.0	74	58.7	1	16.7	14	51.9	57
Shaft	0	0.0	0	0.0	0	0.0	22	17.5	1	16.7	2	7.4	10
Distal	0	0.0	1	100.0	0	0.0	28	22.2	3	50.0	11	40.7	42
Total	3	100.0	1	100.0	1	100.0	126	100.0	6	100.0	27	100.0	113
Femur													
Complete	0	0.0	0	0.0	0	0.0	25	18.4	0	0.0	1	2.5	12
Proximal	4	66.7	1	100.0	1	50.0	72	52.9	6	66.7	24	60.0	50
Shaft	0	0.0	0	0.0	1	50.0	12	8.8	1	11.1	2	5.0	7
Distal	2	33.3	0	0.0	0	0.0	27	19.9	2	22.2	13	32.5	31
Total	6	100.0	1	100.0	2	100.0	136	100.0	9	100.0	40	100.0	100
Tibia													
Complete	0	0.0	0	0.0	0	0.0	8	4.3	0	0.0	0	0.0	0
Proximal	1	14.3	0	0.0	0	0.0	35	18.9	2	15.4	11	25.0	49
Shaft	2	28.6	0	0.0	0	0.0	68	36.8	7	53.8	14	31.8	42
Distal	4	57.1	0	0.0	0	0.0	74	40.0	4	30.8	19	43.2	66
Total	7	100.0	0	0.0	0	0.0	185	100.0	13	100.0	44	100.0	157
Total													
Complete	0	0.0	0	0.0	0	0.0	68	10.1	3	7.7	6	3.6	40
Proximal	11	40.7	1	20.0	2	66.7	241	35.9	11	28.2	65	38.7	209
Shaft	2	7.4	0	0.0	1	33.3	148	22.0	11	28.2	41	24.4	88
Distal	14	51.9	4	80.0	0	0.0	215	32.0	14	35.9	56	33.3	212
Total	27	100.0	5	100.0	3	100.0	672	100.0	39	100.0	168	100.0	549

	GH5/AHV sublayer 4	GH5/AHV sublayer 5		GH5/AHV sublayer 6		GH6/AHVI sublayer 1		GH6/AHVI sublayer 2		GH6/AHVI sublayer 3	
	%NISP	NISP	%NISP	NISP	%NISP	NISP	%NISP	NISP	%NISP	NISP	%NISP

Table 10 (continued)

Humerus											
Complete	17.3	10	9.9	5	9.1	4	7.8	10	12.0	23	27.7
Proximal	20.0	37	36.6	20	36.4	20	39.2	23	27.7	12	14.5
Shaft	13.6	7	6.9	3	5.5	6	11.8	8	9.6	11	13.3
Distal	49.1	47	46.5	27	49.1	21	41.2	42	50.6	37	44.6
Total	100.0	101	100.0	55	100.0	51	100.0	83	100.0	83	100.0
Radius											
Complete	7.2	4	10.3	5	11.9	1	2.0	5	10.9	16	42.1
Proximal	44.9	24	61.5	21	50.0	26	53.1	25	54.3	12	31.6
Shaft	20.3	1	2.6	6	14.3	8	16.3	3	6.5	4	10.5
Distal	27.5	10	25.6	10	23.8	14	28.6	13	28.3	6	15.8
Total	100.0	39	100.0	42	100.0	49	100.0	46	100.0	38	100.0
Ulna											
Complete	3.5	1	1.1	0	0.0	0	0.0	6	8.5	4	7.5
Proximal	50.4	47	52.2	29	69.0	24	48.0	40	56.3	31	58.5
Shaft	8.8	13	14.4	1	2.4	6	12.0	5	7.0	7	13.2
Distal	37.2	29	32.2	12	28.6	20	40.0	20	28.2	11	20.8
Total	100.0	90	100.0	42	100.0	50	100.0	71	100.0	53	100.0
Femur											
Complete	12.0	4	4.2	0	0.0	2	3.6	2	2.5	17	18.7
Proximal	50.0	48	50.5	31	50.0	21	37.5	43	53.1	46	50.5
Shaft	7.0	5	5.3	4	6.5	9	16.1	6	7.4	2	2.2
Distal	31.0	38	40.0	27	43.5	24	42.9	30	37.0	26	28.6
Total	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	1	1.3	1	0.8	6	6.3
Proximal	31.2	32	36.8	27	33.3	17	21.5	25	20.2	27	28.1
Shaft	26.8	15	17.2	16	19.8	31	39.2	38	30.6	14	14.6
Distal	42.0	40	46.0	38	46.9	30	38.0	60	48.4	49	51.0
Total	100.0	87	100.0	81	100.0	79	100.0	124	100.0	96	100.0
Total											
Complete	7.3	19	4.6	10	3.5	8	2.8	24	5.9	66	18.3
Proximal	38.1	188	45.6	128	45.4	108	37.9	156	38.5	128	35.5
Shaft	16.0	41	10.0	30	10.6	60	21.1	60	14.8	38	10.5
Distal	38.6	164	39.8	114	40.4	109	38.2	165	40.7	129	35.7
Total	100.0	412	100.0	282	100.0	285	100.0	405	100.0	361	100.0

Table 11 Breakage of mandibles and maxillae in the microfauna assemblage at Langmahdhalde by horizon and sublayer (following Andrews 1990)

	Maxilla					Mandible								% isolated molars	% isolated incisors
	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		
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	288.9	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 sublayer 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 sublayer 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 sublayer 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 sublayer 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 sublayer 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	244.6	294.1
GH6/AHVI sublayer 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 sublayer 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

Table 11 (continued)

Maxilla					Mandible								% isolated molars	% isolated incisors
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		
GH6/AHVI sublayer 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

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 missing teeth, where the number of missing teeth is calculated by subtracting the number of in situ teeth from the number of expected teeth

probably reflect the presence/absence of most taxa on the landscape.

GH3/AHIII and GH6AHVI sublayer 2 have similar results in terms of which category of predator the levels of digestion on the microfaunal remains indicate. 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 predator. Predators associated with category 1 digestion on incisors are barn owls (*Tyto alba*), short-eared owls (*Asio flammeus*), and snowy owls (*Bubo scandiacus*); predators associated with category 1 digestion on long bones are barn owls, short-eared owls, snowy owls, long-eared owls, and great gray owls. Again, Eurasian eagle owls and tawny owls are associated with category 3 digestion on molars. Like long-eared owls and great gray owls, short-eared owls and snowy owls prefer Arvicolid prey (Andrews 1990, p. 181–182, 185). Barn owls are more similar to Eurasian eagle owls and tawny owls in this respect; they prefer Arvicolids, Murids, and Soricids as prey items (Andrews 1990, p. 179–180) and are, therefore, for the purposes of this study, considered generalists.

GH4/AHIV and GH5/AHV sublayers 4 and 6 have similar proportions of digestion on the teeth and long bones in their samples. The percentage of digested incisors suggests a category 1 predator, while the percentage of digested molars and long bones are indicative of a category 2 predator. As discussed above, barn owls, short-eared owls, and snowy owls are category 1 predators for percent digested incisors, while Eurasian eagle owls and tawny owls are category 2 predators for percent digestion on long bones. Snowy owls and great gray owls are category 2 predators associated with percent digestion on molars.

In GH5/AHV sublayer 3 and GH6/AHVI sublayers 1 and 3, there are few digested incisors (less than 20%), supporting the actions of a category 1 predator, such as a barn owl, short-eared owl, or snowy owl. Further, the percentage of digested molars in these sublayers indicates a category 3 predator and the percentage of digested long bones indicates a category 2 predator, both associated with Eurasian eagle owls and tawny owls. Lastly, in GH5/AHV sublayer 5, the percentage of digested molars, incisors, and long bones all indicate a category 2 predator: long-eared owls, great gray owls, snowy owls, Eurasian eagle owls, and tawny owls.

There are teeth with extreme levels of digestion in GH4/AHIV, GH5/AHV sublayer 4, and GH6/AHVI sublayer 2. Predators associated with extreme digestion are usually mammalian carnivores or hen harriers (Andrews 1990), but juvenile barn owls also produce higher levels of digestion in their pellet assemblages (Andrews 1990; Fernández-Jalvo et al. 2016). As the Langmahdhalde assemblage was deposited by several different owl species and there are no other indications that mammalian predators or hen harriers contributed to the

Table 12 Long bone digestion in the rodent and insectivore remains at Langmahdhalde by horizon and sublayer

	Distal humerus									Proximal ulna								
	None	Light	Light/ moderate	Moderate	Moderate/ heavy	Heavy	Extreme	Total	Total digested	None	Light	Light/ moderate	Moderate	Moderate/ heavy	Heavy	Extreme	Total	Total digested
GH2/AHII																		
NISP	3	3	0	2	0	0	0	8	5	0	0	0	3	0	0	0	3	3
%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
GH2a/AHIIa																		
NISP	2	1	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0
%NISP	66.7	33.3	0.0	0.0	0.0	0.0	0.0	100.0	33.3	–	–	–	–	–	–	–	–	–
GH3/AHIII																		
NISP	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
%NISP	–	–	–	–	–	–	–	–	–	100.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
GH4/AHIV																		
NISP	47	24	3	15	0	3	0	92	45	58	10	1	7	0	0	0	76	18
%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
GH5/AHV sublayer 2																		
NISP	2	2	0	1	0	0	0	5	3	0	1	0	0	0	0	0	1	1
%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
GH5/AHV sublayer 3																		
NISP	8	1	0	7	0	0	0	16	8	12	0	0	2	0	0	0	14	2
%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
GH5/AHV sublayer 4																		
NISP	35	8	0	9	1	1	0	54	19	49	4	1	2	0	1	0	57	8
%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
GH5/AHV sublayer 5																		
NISP	32	10	0	4	0	1	0	47	15	38	4	0	4	0	1	0	47	9
%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
GH5/AHV sublayer 6																		
NISP	16	5	0	4	1	1	0	27	11	22	2	0	5	0	0	0	29	7
%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
GH6/AHVI sublayer 1																		
NISP	11	5	0	5	0	0	0	21	10	23	0	0	0	0	1	0	24	1
%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
GH6/AHVI sublayer 2																		
NISP	23	4	2	10	1	2	0	42	19	27	7	0	3	2	1	0	40	13
%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
GH6/AHVI sublayer 3																		
NISP	20	9	1	7	0	0	0	37	17	27	2	0	1	0	1	0	31	4
%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

	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 long bones	Total digested
GH2/AHII																		

Table 12 (continued)

NISP	1	1	0	2	0	0	0	4	3	4	4	0	7	0	0	0	15	11
%NISP	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	0	0	0	1	0	0	0	1	1	2	1	0	1	0	0	0	4	2
%NISP	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	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		0.0
GH4/AHIV																		
NISP	58	20	1	11	0	7	0	97	39	163	54	5	33	0	10	0	265	102
%NISP	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 sublayer 2																		
NISP	4	1	0	1	0	0	0	6	2	6	4	0	2	0	0	0	12	6
%NISP	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 sublayer 3																		
NISP	16	4	0	2	0	2	0	24	8	36	5	0	11	0	2	0	54	18
%NISP	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 sublayer 4																		
NISP	35	7	0	6	0	2	0	50	15	119	19	1	17	1	4	0	161	42
%NISP	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 sublayer 5																		
NISP	29	13	0	4	0	2	0	48	19	99	27	0	12	0	4	0	142	43
%NISP	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 sublayer 6																		
NISP	23	5	0	2	0	1	0	31	8	61	12	0	11	1	2	0	87	26
%NISP	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 sublayer 1																		
NISP	15	3	0	1	0	2	0	21	6	49	8	0	6	0	3	0	66	17
%NISP	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 sublayer 2																		
NISP	25	12	1	2	0	3	0	43	18	75	23	3	15	3	6	0	125	50
%NISP	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 sublayer 3																		
NISP	27	12	1	4	0	2	0	46	19	74	23	2	12	0	3	0	114	40
%NISP	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 13 Incisor digestion in the microfaunal assemblage of Langmahdhalde by horizon and sublayer

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 sublayer 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 sublayer 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 sublayer 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 sublayer 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 sublayer 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 sublayer 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 sublayer 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 sublayer 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	–

The %NISP for each level of digestion is calculated using the total number of incisors in the horizon or sublayer. The %NISP of isolated or in situ incisors is calculated using the total number of isolated or in situ incisors in the horizon or sublayer. The %NISP for total isolated or in situ incisors is calculated using the total number of incisors in the horizon or sublayer

assemblage otherwise, we find that it is unlikely that these predators were involved (except in GH2/AHII where hen harriers are suggested by the percentage of digested long bones). This taphonomic analysis indicates 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, and peregrine falcons, potential contributors to GH2/AHII, eat primarily birds (Andrews 1990). Further, several owls, including the Eurasian eagle owl, hunt Lagomorphs (Andrews 1990). The hare specimens from GH4/AHIV and GH6/AHVI that

Table 14 Molar digestion in the microfaunal assemblage of Langmahdhalde by horizon and sublayer

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	103	45	10	13	3	0	0	174	71	9	18	62	156
%NISP	59.2	25.9	5.7	7.5	1.7	0.0	0.0	–	40.8	50.0	–	39.7	–
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	284	36	3	3	0	3	0	329	45	0	2	45	327
%NISP	86.3	10.9	0.9	0.9	0.0	0.9	0.0	–	13.7	0.0	–	13.8	–
GH5/AHV sublayer 2													
NISP	36	6	3	0	0	1	0	46	10	2	4	8	42
%NISP	78.3	13.0	6.5	0.0	0.0	2.2	0.0	–	21.7	50.0	–	19.0	–
GH5/AHV sublayer 3													
NISP	75	8	3	7	0	0	0	93	18	0	5	18	88
%NISP	80.6	8.6	3.2	7.5	0.0	0.0	0.0	–	19.4	0.0	–	20.5	–
GH5/AHV sublayer 4													
NISP	254	17	1	5	0	2	1	280	26	0	10	26	270
%NISP	90.7	6.1	0.4	1.8	0.0	0.7	0.4	–	9.3	0.0	–	9.6	–
GH5/AHV sublayer 5													
NISP	134	19	0	2	0	0	0	155	21	0	5	21	150
%NISP	86.5	12.3	0.0	1.3	0.0	0.0	0.0	–	13.5	0.0	–	14.0	–
GH5/AHV sublayer 6													
NISP	121	16	0	5	0	1	1	144	23	0	7	23	137
%NISP	84.0	11.1	0.0	3.5	0.0	0.7	0.7	–	16.0	0.0	–	16.8	–
GH6/AHVI sublayer 1													
NISP	28	4	0	2	0	0	0	34	6	0	0	6	34
%NISP	82.4	11.8	0.0	5.9	0.0	0.0	0.0	–	17.6	0.0	–	17.6	–
GH6/AHVI sublayer 2													
NISP	105	28	2	9	1	3	1	149	44	0	6	44	143
%NISP	70.5	18.8	1.3	6.0	0.7	2.0	0.7	–	29.5	0.0	–	30.8	–
GH6/AHVI sublayer 3													
NISP	152	30	0	4	0	0	0	186	34	0	14	34	172
%NISP	81.7	16.1	0.0	2.2	0.0	0.0	0.0	–	18.3	0.0	–	19.8	–

The %NISP for each level of digestion is calculated using the total number of molars in the horizon or sublayer. 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 is calculated using the total number of molars

have bite marks or punctures on them suggest that, at least in these horizons, a small mammalian carnivore likely contributed to the Langmahdhalde faunal assemblage.

Based on the taphonomic analysis of the microfaunal assemblage from Langmahdhalde, we hypothesize that in all of the horizons and sublayers 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.

Finally, our reconstructions of the primary accumulators of the microfaunal assemblage at Langmahdhalde have implications for the scale of paleoenvironmental reconstructions that use the microfaunal remains from the site. Long-eared owls, tawny owls, and short-eared owls have home ranges that are less than 10 km^2 (Andrews 1990, p. 182, 192), while hen harriers, Eurasian eagle owls, and barn owls have ranges between approximately 10 and 30 km^2 (Haller 1978; Picozzi 1978; Mikkola 1983; Arroyo et al. 2005; Martin et al. 2008). Finally, the predators with the largest home ranges are snowy owls and great gray owls, with ranges between 50 and 70 km^2 (Bull et al. 1988; Chang and Wiebe 2018). As all horizons and sublayers in the assemblage, except GH5/AH5 sublayer 3 and GH6/AHVI sublayers 1 and 3, seem to be associated with great gray owls, paleoenvironmental reconstructions from Langmahdhalde apply to within 70 km^2 of the rock shelter for these horizons. For GH5/AH5 sublayer 3 and GH6/AHVI sublayers 1 and 3, barn owls have the largest hunting ranges of the likely accumulators, meaning that paleoenvironmental reconstructions probably apply to within 55 km^2. For context, we note that the Lone Valley is approximately 44 km long.

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. Based on the presence of cut marks, cone fractures, and cone negatives in the assemblage, we find evidence that butchering and marrow extraction took place at the site. Further, needle-making and antler working were also probably performed, as demonstrated by the needle blank (Wong et al. 2017) and the worked antler pieces. As we have found no evidence of human modifications on the cave lion remains in Langmahdhalde, it is unclear whether lions used the site when humans were not present, or if their deposition at the site was anthropogenic.

The macrofaunal assemblage provides little evidence for which season(s) humans occupied the rock shelter, although the ungulate fetal pelvis in GH3/AHIII suggests that it may have been 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 (Fig. 5), it is possible that for all horizons hunter-gatherers transported only certain portions of reindeer and horse 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 (which includes reindeer) 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 people exploited a mix of ages, with more juveniles being represented in the assemblage, although this is difficult to interpret due to small sample sizes.

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 the use or abandonment of the rock shelter by humans. The absence of significant amounts of lithics and other artifacts in this horizon suggests this is a likely scenario, although a geoarcheological 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 archeological 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.

Paleoecology

Our previously published reconstructions of the environment during the Late Glacial, based on the bioclimatic analysis and stable isotope analysis of bone collagen of reindeer and horse from the site, suggest that the environment surrounding Langmahdhalde was generally open tundra (Wong et al. 2020). With the addition of the above taphonomic analysis of the microfauna, we can say, additionally, that this reconstruction probably applies to within 70 km^2 of the site for all horizons and sublayers except GH5/AH5 sublayer 3 and GH6/AHVI sublayers 1 and 3, where reconstructions are likely within 55 km^2 of the site.

In Wong et al. (2020), we found that the tundra in this area 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, p. 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 the westernmost part of the excavation, where the reduced 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, p. 1402; Spiess 1979, p. 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 δ^{13}C and δ^{15}N values from bone collagen of horse and deer specimens. In Fig. 6, 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 3 for the stable isotope data and sources and Supplementary materials 4 and 5 for the methods associated with these values). This probably meant that these species were in increasingly direct competition with each other for resources.

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). Although the size of the groups remains unclear, Langmahdhalde documents therepeated occupation of the Lone Valley by Magdalenian people. 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, such as horse and deer, whose dietary niches were shifting and beginning to overlap. Paleoenvironmental reconstructions based on faunal remains from Langmahdhalde have shown that the tundra environments in the region were more heterogeneous and diverse than previously thought. Additionally, our taphonomic analysis of the microfauna from the site indicates that this environmental reconstruction applies specifically to the Lone Valley and its surroundings (within 55 to 70 km^2 of the site); further studies are necessary to determine whether this reconstruction is true throughout the Swabian Jura.

Overall, our work with the faunal remains from Langmahdhalde has combined traditional zooarcheological analysis, microfaunal analyses, and stable isotope analysis of bone collagen (in this paper and in Wong et al. 2017, Wong et al. 2020). This combination of studies has allowed us to examine human use of the rock shelter and the Lone Valley within the context of the local ecology. Based on all of our work, we suggest that the vegetative situation of the Swabian Jura during the Late Glacial may have made it an attractive place to settle for Magdalenian peoples moving into

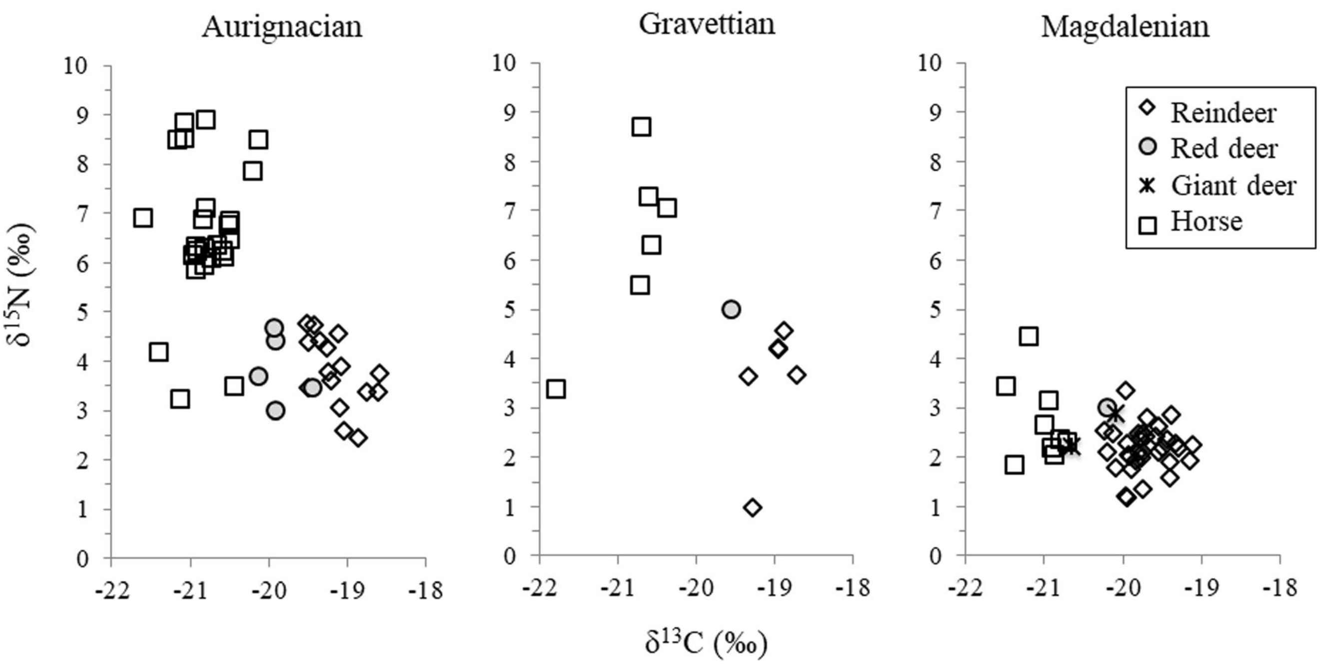

Fig. 6 Stable isotope values on bone collagen from reindeer (*Rangifer tarandus*), red deer (*Cervus elaphus*), giant deer (*Megaloceros giganteus*), and horse (*Equus ferus*) remains from the Upper Paleolithic of the Swabian Jura. The symbol key for the graphs of all three periods is in the upper right. Values are from the following archeological sites: Fellställe, Geißenklösterle, Hohle Fels, Hohlenstein-Stadel, Langmahdhalde, Petersfels, and Schussenquelle. The stable isotope values and sources are listed in Supplementary materials 3. For those values that are not previously published, see Supplementary materials 4 for the methods associated with these values

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 southwest 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 find 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 suggests, then, that expansion into the Swabian Jura may not have been driven exclusively by adaptations to specific environments (Taller et al. 2014), but also by the availability of comparatively diverse resources in this region, further emphasizing the need for regional- and local-scale paleoenvironmental data.

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Data availability All newly published results and data are included in the manuscript. Archeological data from Langmahdhalde, including zooarcheological 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.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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