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RESEARCH

Magdalenian environments and ecosystems of the northern Alpine foreland: the case of Gnirshöhle and Petersfels

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Abstract

After the Last Glacial Maximum (LGM: ~ 26.5–19.0 ka cal BP), large-scale warming resulted in glacial retreat and climatic amelioration, prompting changes to local and regional ecosystems across Eurasia during the Late Glacial. Consequently, Magdalenian hunter-gatherers reoccupied parts of Central Europe that were mostly devoid of humans during the LGM. Petersfels and Gnirshöhle (~ 17.0–13.0 ka cal BP), two Magdalenian cave sites in the Hegau Jura of southwestern Germany, preserve the later stages of this recolonization and serve as archives of paleoenvironmental data. In this study, we examine carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotopes in horse (*Equus ferus*) and bovine (*Bos/Bison* sp.) tooth enamel carbonate from both sites to investigate the microenvironment of the northern Alpine foreland. We contextualize our results within a broader geographical framework by comparing the Hegau Jura to Verberie (Le Buisson Campin), a contemporaneous Magdalenian site in northern France (~ 16.0–14.0 ka cal BP). The apparent difference in $\delta^{18}O$ suggests that northern France was warmer with weaker seasonal climatic fluctuations than southwestern Germany. This difference likely affected cold-adapted fauna, such as reindeer (*Rangifer tarandus*), resulting in diverse animal ecologies that influenced hunter-gatherer subsistence behaviors across western and central Europe. Our exploration of Magdalenian landscapes reveals a mosaic of ecological variability, which likely influenced daily activities such as movement and food procurement, highlighting the interconnected relationship between environment and hunter-gatherer behavior during this period.

Keywords Magdalenian · Paleoenvironment · Climate · Herbivores · Stable isotopes · Carbon · Oxygen

Introduction

After the Last Glacial Maximum (LGM: ~ 26.5–19.0 ka cal BP), ameliorating climates facilitated the recolonization of Central Europe by Magdalenian groups during the Late Glacial (19.0–11.6 ka cal BP) (Albrecht and Engelhardt 1988; Street and Terberger 1999; Ivy-Ochs et al. 2008; Clark et al. 2009; Kretschmer 2015; Maier 2015; Leesch et al. 2019). This shift influenced local environments, altering human subsistence and ecological dynamics. During this period, Magdalenian groups reoccupied southwestern Germany, probably as early as 20.0 ka cal BP (Pasda 1998, 2019a, b) and more consistently after 16.0 ka cal BP (Taller 2014; Maier 2015). The sporadic nature of initial occupations suggests that recolonization did not occur in a single wave but was a discontinuous process of discovery, colonization, and establishment (Graves and Addison 1996; Jochim et al. 1999). It is also possible that parts of Central Europe were never entirely abandoned and that small, ephemeral

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groups persisted throughout the LGM (Street and Terberger 1999; Blockley et al. 2000). Regardless, the appearance of the Magdalenian represents the more significant return of hunter-gatherers to Central Europe.

This study offers a comprehensive paleoenvironmental reconstruction of the Hegau Jura, a region of the northern Alpine foreland in southwestern Germany, using carbonate from horse and bovine tooth enamel, expanding beyond previous regional analyses, which were limited to bone collagen. In particular, we focus on two Magdalenian sites, Petersfels (WGS84: N47°51′38.9"E8°48′15.1") and Gnirshöhle (WGS84: N47°51′33.8"E8°48′54.0"), dated to ~ 17.0–13.0 ka cal BP (Figs. 1–2) (Jaguttis-Emden 1983; Bronk Ramsey 2009, 2021; Albrecht et al. 2019; Reimer et al. 2020; Baumann et al. 2021). Both sites are located in the Bruderthal, a narrow valley under study since the early twentieth century (e.g., Peters 1930a, b). Here, we investigate the microenvironment of the valley via stable isotope analyses of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) in ungulate tooth enamel carbonate. Serial sampling of horse (*Equus ferus*, n = 7) and bovine (*Bos/Bison* sp., *n* = 1) tooth enamel provides a picture of animal diet and environment from the first 1–2 years of life (DeNiro and Epstein 1978; Lee-Thorp 1989; Balasse et al. 1999; Hoppe et al. 2004). Isotopic evidence from the Hegau Jura is compared with data from Verberie (Le Buisson Campin) (WGS84: N49°20′24.0"E2°45′00.0"), a contemporaneous (~ 16.0–14.0 ka cal BP) Magdalenian site in northern France. A single *Equus* sp. tooth (n = 1) from Verberie provides a comparative signal from Western Europe, which was more continuously occupied throughout the LGM than the northern Alpine foreland (Bignon-Lau et al. 2021). Despite the small sample size, which may well be an outlier, and the geographic and paleoecological differences between the Hegau Jura and Northern France, data from Verberie

Fig. 1 Map of western and central Europe and the studied sites in northern France (Verberie) and the Hegau Jura of southwestern Germany (Petersfels and Gnirshöhle). Modified maps from Wikipedia (CC BY-SA 3.0) and Apple Maps (Apple Maps 2023)

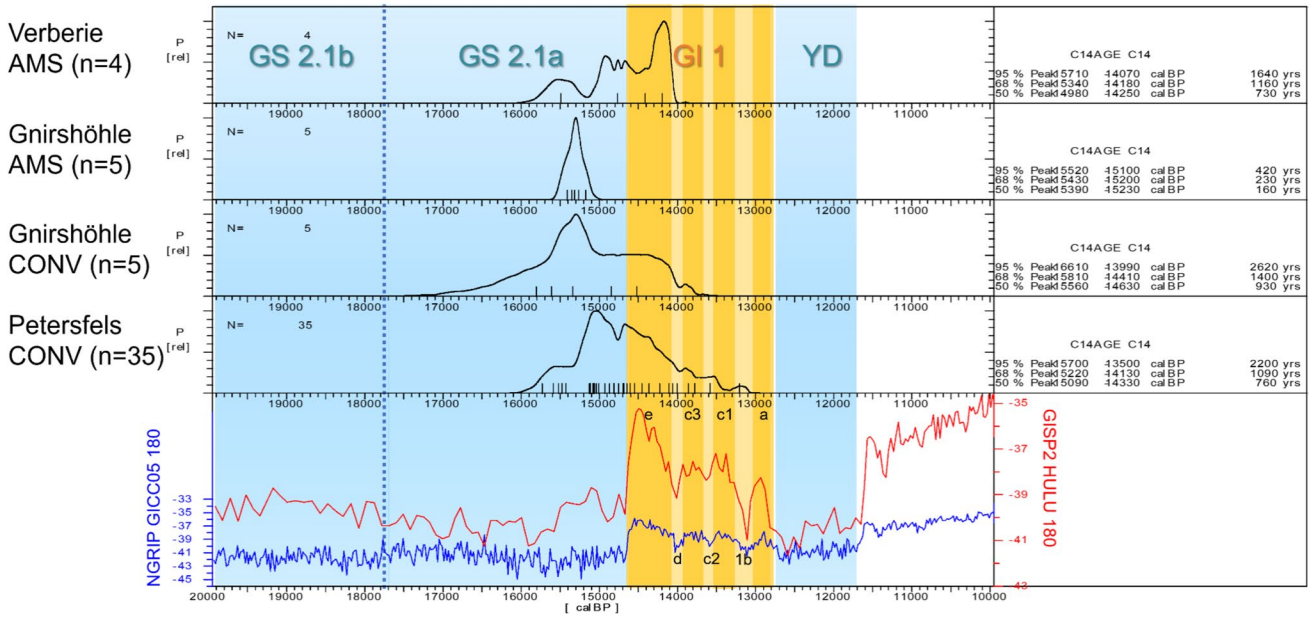

Fig. 2 Chronology of the studied sites. Recent dates for Verberie (Debout et al. 2012; Wild 2020) and Gnirshöhle (Baumann et al. 2021) via accelerator mass spectrometry (AMS), other dates for Gnirshöhle (Weniger 1982; Albrecht 2010) and Petersfels (Jaguttis-Emden 1983; Bronk Ramsey 2009, 2021; Reimer et al. 2020) via the conventional counting method (CONV). Data on Greenland stadial (blue) and interstadial (yellow) ranges were acquired from Rasmussen et al. (2014) and calibrated with CalPal version 2023.5 (Weninger and Jöris 2008)

facilitates a broader understanding of human settlement patterns and paleoecology during the Magdalenian.

Although previous paleoenvironmental studies provide valuable insights into the region (e.g., Stephan 1999; Drucker et al. 2011; Baumann et al. 2021), these were focused on reindeer and canids, and relied on the analysis of bone collagen. While informative, bone collagen provides an averaged signal of paleoenvironment from the last decade of an animal's life (Bocherens et al. 1997; Bocherens 2003; Krajcarz et al. 2018). In contrast, serially sampled tooth enamel records information from just the first few years of life and facilitates a finer resolution reconstruction of diet and environment (Pederzani and Britton 2019). By analyzing additional species, our work expands the scope of environmental reconstructions in the region, offering a more comprehensive understanding of the ecological conditions experienced by Magdalenian people during the Late Glacial.

Background information

Site descriptions

The Brudertal represents a glacial drainage canal shaped by the retreat of ice sheets after the LGM (Albrecht 1979; Albrecht et al. 1983, 2019; Laville 1983). According to conventional radiocarbon dates – mainly on bulk bone collagen samples – the Magdalenian occupations of Petersfels commenced around ~ 16.0 ka cal BP and lasted until at least 14.0 ka cal BP. Possible occupations during younger phases beyond Greenland Interstadial (GI) 1e are unconfirmed. The occupation of Gnirshöhle includes the earlier portion of this period, especially according to recent AMS dates concentrating around ~ 16.0–15.0 ka cal BP (Albrecht 1979; Albrecht et al. 1983; Jaguttis-Emden 1983; Bronk Ramsey 2009, 2021; Reimer et al. 2020; Baumann et al. 2021).

Petersfels is a high but narrow cave that continues into a small, currently inaccessible chamber. Occupation horizons from Magdalenian hunter-gatherers are preserved within the cave and the surrounding valley. The site was first discovered in 1924 and has since undergone numerous excavations, the longest of which were in the 1920–30s by Eduard Peters and the 1970–80s by Gerd Albrecht from the University of Tübingen (Peters 1930a; Peters and Toepfer 1932; Albrecht 1979; Albrecht et al. 1983). These campaigns were highly successful, revealing abundant lithics, fauna, osseous artifacts, personal ornaments, engravings, human remains, and female figurines (Peters 1930a, b; Peters and Toepfer 1932; Kraft 1939; Mauser 1970; Albrecht 1979; Albrecht et al. 1983, 1994; Berke 1987; Walter 2000; Pfeifer 2014, 2016; McCartin et al. 2023). Hunter-gatherers occupied the site during the fall-winter and focused on acquiring reindeer in peak nutritional condition (Albrecht et al. 1983; Berke 1987; Eriksen 1991; Weinstock 2000; McCartin et al. 2023).

Importantly, Petersfels is interpreted as a large-scale aggregation camp – a place where seasonally distant groups gathered to acquire and process resources, produce tools and symbolic objects, and cultivate the social relationships that connected Magdalenian groups across the Swabian Jura and, indirectly, across the rest of Central Europe (Hahn 1978; Conkey et al. 1980; Weniger 1987, 1989; Eriksen 1991).

Opposite Petersfels is Gnirshöhle, a cave with two chambers (GN1 and GN2) situated 15 m above the valley floor. Early excavations are poorly documented but likely began with Eduard Peters in 1927 (Peters 1930a), who only mentioned potential Magdalenian finds in an unpublished report from 1946 (Peters 1946). Gnirshöhle was then affected by speleological activities in 1976 that destroyed large parts of the intact archaeological layers. Subsequent systematic excavations were conducted by Gerd Albrecht and Claus-Joachim Kind in three campaigns between 1977 and 1979 (Albrecht et al. 1983). Important finds include jet beads and perforated mollusk shells alongside typical Magdalenian lithic, organic tools, and faunal remains. New radiocarbon dates suggest the two cave chambers were occupied coevally (Baumann et al. 2021). However, the quantity and diversity of finds are far less than at Petersfels, indicating the sites may present different occupation patterns. For example, during some periods, Petersfels was utilized for large-scale aggregations, while Gnirshöhle was likely occupied by smaller groups (Albrecht et al. 1977; Albrecht and Hahn 1991; McCartin et al. 2023). However, the question of differential site utilization remains the subject of ongoing research, including the exceptionally well-preserved neighboring site of Drexlerhöhle (Tafelmaier et al. 2022, 2024).

Faunal remains

Both sites present typical Magdalenian taxa and are dominated by reindeer (*Rangifer tarandus*), hare (*Lepus* sp.), and horse (*Equus ferus*). At Petersfels, ptarmigan (*Lagopus* sp.) is also well represented and other ungulates include chamois (*Rupicapra rupicapra*), roe deer (*Capreolus capreolus*), ibex (*Capra ibex*), red deer (*Cervus elaphus*), aurochs or steppe bison (*Bos primigenius* or *Bison priscus*), and wild boar (*Sus scrofa*). Carnivores are represented by various mustelids (Mustelidae), foxes (*Vulpes vulpes* and *V. lagopus*), felids (*Felis silvestris*, *Lynx lynx*, *Panthera spelaea*), wolf (*Canis lupus*), and brown bear (*Ursus arctos*) (Peters 1930a; Peters and Toepfer 1932; Berke 1987; Pasda 1998; McCartin et al. 2023). The faunal assemblage of Gnirshöhle is less diverse than Petersfels. Large felids, such as lynx, cave lion, and brown bear, are absent. At GN1, hares are the most frequent taxon, followed by reindeer, large canids, foxes, and badgers (*Meles meles*). At GN2, badgers are most abundant, followed by reindeer, horses, and hares, while large canids are present but rare (Albrecht et al. 1977, 2019; Weniger 1982, 1989; Albrecht and Hahn 1991; Baumann et al. 2021). Other differences between the two chambers include the exclusive presence of red deer and roe deer at GN1 and wildcat and wild boar at GN2. Badgers are particularly abundant at Gnirshöhle, and the presence of a large badger burrow at GN2 draws the stratigraphic integrity partly into question. This issue is currently under investigation.

The Petersfels faunal assemblage is highly anthropogenic, as evidenced by abundant cut marks, impacts, and green breaks, as well as the use of animal remains to produce thousands of tools (e.g., needles, projectile points, bâton percés) and symbolic objects (e.g., engravings, figurines, ornamentation). Humans occupied the site primarily during the fall-winter, although some spring–summer habitations are also likely (Peters 1930a, 1936; Peters and Toepfer 1932, p. 193; Mauser 1970; Albrecht 1979; Albrecht and Berke 1980; Albrecht et al. 1983, 1994; Berke 1987; Pfeifer 2016; McCartin et al. 2023). In comparison, Gnirshöhle presents some butchery modifications and osseous tools in both chambers, namely worked antlers, sewing needles, and projectile points; however, carnivore traces, likely produced by badgers, are very abundant, suggesting not only bioturbation (as the remains of human-hunted taxa were displaced) but also some non-human accumulations (Albrecht and Engelhardt 1988; Albrecht and Hahn 1991; Cattin 2018). Although carnivore damage is present at Petersfels, the abundance of anthropogenic traces suggests carnivores had secondary access to remains via the exploitation of human garbage (McCartin et al. 2023). This is consistent with regional evidence of commensal canids (Baumann et al. 2020b, a) and the likely presence of early wolf domestication at Gnirshöhle (Baumann et al. 2021), indicating that some carnivores regularly accessed human-constructed niches (Baumann 2023).

Prior paleoenvironmental reconstructions

Today, the paleoenvironmental conditions found in the Magdalenian no longer exist, and the elements that once composed them are distributed across three distinct ecosystems: steppe, tundra, and high mountains (Leesch et al. 2012). Although different, these environments are all characterized by cold and open landscapes with sparse vegetation and low primary productivity. Compared to the present, post-LGM environments were a mosaic of natural areas with diverse plant communities, which supported a variety of herbivore and carnivore species (Bliss and Richards 1982; Leesch et al. 2012; Drucker 2022).

Prior paleoenvironmental studies of the Hegau Jura are cursory; however, details from the macrofaunal assemblages, sedimentology, and isotopic analyses provide insights into the ecological and climatic conditions of the region during the Late Glacial. At Petersfels, ptarmigan and lark

(*Eremophilia alpestris*) indicate sparse vegetation with some areas of cover (Mourer-Chauvire 1983; Krönneck 2009). Mammals are typical of the Late Glacial (e.g., reindeer, horse) and primarily indicate steppe, tundra, and/or park-tundra landscapes. This is supported by the relative scarcity of species typically associated with warmer or forested environments, such as roe deer (Peters 1930a; Albrecht et al. 1983; Berke 1987; Eriksen 1991; Sommer and Nadachowski 2006; Sommer and Zachos 2009; McCartin et al. 2023). Stratigraphic and sedimentological analyses indicate at least two distinct periods, one warmer (perhaps Bølling/GI- 1e) and one cooler (perhaps Oldest Dryas/GS- 2.1a) (Laville 1983). This is also supported by radiocarbon dates and $\delta^{18}O$ values from reindeer bone collagen (Jaguttis-Emden 1983; Stephan 1999). Unfortunately, the pollen and small mammal assemblages were insufficient for conclusive analyses (Wille 1978; Albrecht et al. 1983; Storch 1983).

From the Petersfels assemblage, isotopic data from ungulate bone collagen was previously presented by Stephan (1999) and Drucker et al. (2011). Compared to northern Germany and southwestern France, the reindeer at Petersfels exhibit comparable $\delta^{13}C$ but lower $\delta^{15}N$ and $\delta^{18}O$ values. This suggests that the Petersfels reindeer occupied a colder environment (Stephan 1999) with less advanced soil maturation than in southwestern France (Drucker et al. 2011). At Gnirshöhle, prior isotopic analyses were conducted on canid bone collagen, and the results suggest significant niche partitioning between foxes and wolves in a potential early stage of domestication (Baumann et al. 2020b, 2021). It is likely that the above mentioned ecological separation reflects a heterogeneous environment with diverse prey availability. Although these studies provide some paleoenvironmental information, analyses focused on a narrow range of species and samples gathered from bone collagen. This paper thus provides a new and more holistic attempt at a paleoenvironmental reconstruction of the Hegau Jura using tooth carbonate from additional horses and a bovine.

Stable isotope analyses

Tooth bioapatite is often used to study past diets and environments by analyzing stable isotopes preserved in tooth enamel carbonate. Isotopic data are presented in delta notation (δ), which expresses the relative difference in isotopic ratios between a sample and an international standard. For example, a positive δ indicates the sample is enriched in the heavier isotope relative to the standard. This ratio is expressed as parts per mil (‰).

In herbivores, $\delta^{13}C$ reflects differences in the isotopic composition of consumed plants, which is primarily controlled by the plant's photosynthetic pathway and other environmental conditions (DeNiro and Epstein 1978; Tieszen 1991; Kohn 2010). There are two main photosynthetic pathways: C3 and C4. The former includes trees and herbaceous plants from temperate environments, which dominated Eurasian Pleistocene ecosystems (Bombin and Muehlenbachs 1985), while the latter corresponds to tropical grasses. In comparison to C4 plants, C3 plants are depleted in the heavier isotope (^{13}C) relative to the lighter isotope (^{12}C) and exhibit lower $\delta^{13}C$ values in the range of − 20 to − 35‰, averaging around − 26‰ (review in Kohn 2010). In tooth enamel, $\delta^{13}C$ values are also enriched relative to diet due to physiological fractionation. In large herbivores, this enrichment factor is approximately + 14‰. Thus, if an animal consumed primarily C3 plants with an average $\delta^{13}C$ of − 26‰, the $\delta^{13}C$ value of enamel carbonate would be − 12‰ (Cerling and Harris 1999; Diefendorf et al. 2010; Passey et al. 2005). In environments dominated by C3 resources, such as Pleistocene Eurasia, differentiation can occur due to the canopy effect, in which a plant's vertical position in the canopy influences the degree of isotopic fractionation. Higher $\delta^{13}C$ values are indicative of plants from the upper canopy, such as leaves and fruits, while lower values indicate lower canopy resources (Cerling et al. 2004; Drucker et al. 2008). Aridity also shapes $\delta^{13}C$ values. In particular, plants in dry environments exhibit higher water-use efficiency by reducing stomatal conductance, limiting the discrimination against ^{13}C resulting in elevated $\delta^{13}C$ values. As a result, C3 plants in arid environments exhibit elevated $\delta^{13}C$ values compared to the same species in more humid environments (Kohn 2010; Wang et al. 2010).

Turning to oxygen, $\delta^{18}O$ values in herbivore tooth enamel primarily reflect ingested meteoric water, which is derived from plant consumption, drinking water, and inhaled vapor (Dansgaard 1964; Kohn and Cerling 2002; Bocherens et al. 1996). These values are influenced by several climatic and ecological factors, including the $\delta^{18}O$ of local precipitation, which reflects climatic variables such as temperature, aridity, altitude, and rainfall (Dansgaard 1964; Higgins and MacFadden 2009; Kohn and Cerling 2002; Pederzani and Britton 2019; Reinhard et al. 1996). In herbivores, most oxygen enters the body through drinking water (Pederzani and Britton 2019; Reinhard et al. 1996) and water from plant consumption (Bocherens et al. 1996). The relative importance of these sources depends on whether the animal is an obligate or non-obligate drinker (Pederzani and Britton 2019 and references therein). Cold and high elevation environments generally result in lower $\delta^{18}O$ due to temperature-dependent fractionation (Higgins and MacFadden 2009; Gifford-Gonzalez 2018). Similarly, warmer environments and regions with greater summer rainfall will exhibit higher $\delta^{18}O$ values (Rivals et al. 2015; Pederzani and Britton 2019). Plant water is often enriched in $\delta^{18}O$ relative to other water sources due to evapotranspiration. Thus, herbivores that obtain greater proportions of water from plants will show higher $\delta^{18}O$ values (Bocherens et al. 1996; Gifford-Gonzalez 2018). These

factors make $\delta^{18}O$ values a valuable tool to reconstruct climate, seasonality, and mobility (Krajcarz and Krajcarz 2014; Gifford-Gonzalez 2018; Pederzani and Britton 2019).

Horses and bovines are often used for Pleistocene paleoenvironmental reconstructions, as serial sampling of their large, hypsodont (i.e., high-crowned) dentition can provide a relatively precise record of diet and climate (Pellegrini et al. 2008; Fabre et al. 2011; Julien et al. 2012; Rivals et al. 2015; Velivetskaya et al. 2016; Britton et al. 2023). However, it is essential to note that enamel only records information from the period of maturation, which spans the first years of an animal's life, not the entire lifespan (Brown et al. 1960, p. 1; Sharp and Cerling 1998; Hoppe et al. 2004). In horses, adult molars and premolars form within the first five years of life (Hoppe et al. 2004), while this period lasts approximately two years in bovines (Brown et al. 1960). During this time, enamel is first deposited (apposition) and then undergoes maturation, in which the mineral content of the tooth gradually increases over 3–4 to 6–7 months, progressing from the tooth crown towards the enamel root junction (ERJ) (Balasse 2002; Bryant et al. 1996; Hoppe et al. 2004; Czernielewski 2023; for criticism, see Wiedemann 2000). Apposition and maturation progress along different geometries, which contributes to the averaging of the isotopic signal (Green et al. 2017). Sequential sampling of horse and bovine tooth enamel can reveal the spatiotemporal, nutritional, and environmental changes that occurred during tooth mineralization, providing high-resolution insights into intra-specimen variability during early life (Hoppe et al. 2004; Pederzani and Britton 2019). Due to the nature and timing of enamel maturation, intra-tooth samples represent an averaged isotopic signal, not a discrete interval of time (Balasse 2002; Trayler and Kohn 2017; Blumenthal et al. 2019). Sampling bands are thus considered arbitrary units, not isotopic events (Pederzani and Britton 2019).

Materials and methods

Materials

For Petersfels, we reviewed all complete and mostly complete horse and bovine teeth from Albrecht's 1979 excavation of P6, a 16-square-meter area in front of the cave, considering their state of preservation and other relevant features (e.g., fractures). Four suitable horse molars (PTF-E1 – PTF-E4) and one suitable bovine molar (PTF-B1) were selected for serial sampling. Except for PTF-E2 and PTF-E3, all samples derive from different archaeological layers. Conversely, only three horse molars/premolars (GNI- 25, GNI- 53, and GNI- 54) were preserved from Gnirshöhle chamber 1 (GNI- 53) and chamber 2 (GNI- 25 and GNI- 54), all of which were sampled in this study. SCM conducted zooarchaeological identification of the Gnirshöhle samples and MJM and BMS of the Petersfels samples. We also conducted Zooarchaeology by Mass Spectrometry (ZooMS) on a portion of the Petersfels P6 faunal assemblage. Most notably, this included a morphologically ambiguous bovine mandible fragment associated with the sampled molar (PTF-B1), which we confirmed as either aurochs or steppe bison (*Bos/Bison* sp.), not musk ox (*Ovibos moschatus*). Additional information on the ZooMS sample, methods, and results are presented in Sup. Text. 1 and Sup. Figure 1.

Lastly, a single horse molar/premolar from the Magdalenian open-air site of Verberie (Le Buisson Campin) in the Paris Basin (VBR- 7) was also included in the isotopic dataset for comparative purposes. The tooth comes from level II.2 and was analyzed for intra-individual analysis (enamel $\delta^{13}C$ and $\delta^{18}O$) by DGD in collaboration with Françoise Audouze, the lead excavator (Audouze et al.

Table 1 Summary of average carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) values from Petersfels, Gnirshöhle, and Verberie

Tooth ID	Site ID	Position	AH	n	$\delta^{13}C$				$\delta^{18}O$			
					Mean	SD	Min	Max	Mean	SD	Min	Max
GNI- 25	Gn2, P/21–12	L M^1 or M^2	2a	21	− 11.9	0.2	− 12.2	− 11.6	20.8	1.0	19.0	22.0
GNI- 53	Gn1, E/52–33	M/P frag	5	8	− 11.7	0.1	− 11.9	− 11.6	19.7	1.0	18.8	21.2
GNI- 54	Gn2, P/21–119	M/P frag	2a	5	− 11.3	0.3	− 11.6	− 10.8	19.7	0.5	19.1	20.3
PTF-B1	P6, Z/29–725	L M_3	4	13	− 9.4	0.3	− 10.0	− 9.0	19.1	0.5	18.0	20.0
PTF-E1	P6, Z/28–1298	L M_3	3/4	15	− 12.3	0.2	− 12.7	− 11.8	21.3	0.5	20.2	22.0
PTF-E2	P6, Z/29–778	R M_3	NA	15	− 11.7	0.3	− 12.2	− 11.3	20.5	0.4	20.0	21.2
PTF-E3	P6, Z- 29–726	L M^3	NA	21	− 11.7	0.4	− 12.3	− 10.9	19.9	0.5	19.0	21.3
PTF-E4	P6, Z/27–1305	R M_1 or R M_2	2/3	17	− 11.6	0.4	− 12.0	− 10.6	19.8	0.4	19.0	20.6
VBR- 7	VBC94 202 C10.84	Upper M/P	II.2	22	− 11.6	0.1	− 11.8	− 11.4	22.3	0.6	21.2	23.3

Tooth ID = ID assigned during isotopic sampling; *Site ID* = archaeological ID; *Position: L* = left, *R* = right, *M* = molar, *P* = premolar, superscript = upper tooth number, subscript = lower tooth number; *AH* = archaeological horizon; *n* = number of samples from each tooth; *SD* = standard deviation from the mean

1981; Enloe and Audouze 2010; Drucker et al. 2015; Audouze and Enloe 2017). A summary of each sample is presented in Table 1, and images from before and after sampling are presented in Sup. Figure 2.

Methods

All steps of sample preparation, processing, and analysis were done in the laboratories of the Biogeology working group (Senckenberg Centre for Human Evolution and Palaeoenvironment and Department of Geosciences) at the University of Tübingen in Germany. The surface of each tooth was first cleaned to remove potential contaminants. Samples were then drilled in multiple horizontal bands placed 2–3 mm apart, moving from the occlusal end toward the ERJ. The distance to the ERJ (or occlusal surface when the ERJ was not present) was recorded from the center of each horizontal band. For some Petersfels specimens, the ERJ was not preserved. To standardize the values, we measured from the occlusal surface and inverted the measurements to reflect the earliest to the latest mineralization phase. We achieved this by rounding the greatest distance from the occlusal surface up to the nearest multiple of five to establish an approximate ERJ value and then subtracted all measurements from that value to calculate the distance from the approximate ERJ.

Pretreatment follows the protocol of Bocherens et al. (1996), including the removal of organic contamination by using NaOCl at 2.5% concentration. After samples were rinsed three times with Milli-Q H_2O, 1.35 ml of Ca/Hac-Buffer solution (pH 4.66) was added. Pretreated carbonate was reacted with 99% H_3PO_4 for four hours at 70 °C using a MultiFlow-Geo interfaced with the Elementar IsoPrime 100 IRMS. The international laboratory standards IAEA-603 ($\delta^{13}C = +2.46‰$, $\delta^{18}O = -2.37‰$) and NBS- 18 ($\delta^{13}C = -5.01‰$, $\delta^{18}O = -23.20‰$) were used for the two-point calibration of isotopic measurements. Additionally, three in-house reference materials (pure carbonate Laaser Marmor with $\delta^{13}C = +1.50‰$ and $\delta^{18}O = -5.20‰$, pre-treated fossil elephant enamel with $\delta^{13}C = -10.55‰$ and $\delta^{18}O = +1.80‰$, and pre-treated fossil hippo enamel with $\delta^{13}C = -3.80‰$ and $\delta^{18}O = -2.10‰$) were analyzed alongside the samples to monitor accuracy and precision for quality control purposes. IonOS software (Version 4.3) by Elementar was used to carry out multi-point standard isotope calibration by generating a trend line ($y = mx + c$) that maps measured versus expected isotopic results, which is then used to calibrate sample results. Measurement uncertainty was monitored using the three in-house standards. Overall analytical precision is higher than 0.1‰ for carbon and better than 0.2‰ for oxygen isotopic values. All commissioned laboratories measured the ratios of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ relative to VPDB reference material. The isotopic ratios were then expressed in per mill (‰) using the δ (delta) value as follows:

$$\delta^{13}C = \left(\left({}^{13}C/{}^{12}C \right)_{sample} / \left({}^{13}C/{}^{12}C \right)_{reference} - 1 \right) \times 1000$$

$$\delta^{18}O = \left(\left({}^{18}O/{}^{16}O \right)_{sample} / \left({}^{18}C/{}^{16}O \right)_{reference} - 1 \right) \times 1000$$

To test for diagenetic alteration or contamination, we monitored the carbonate ($CaCO_3$) content with an expected range of 2.3–5.2% in weight based on the analysis of modern enamel (Bocherens and Drucker 2007). Measurements of in-house standards, which underwent the same pretreatment as the archaeological samples, gave a weight percentage of carbonate from 3.8–5.7%. To facilitate future comparisons with water $\delta^{18}O$ values, following the convention used in previous studies, all $\delta^{18}O$ values were converted from VPDB to VSMOW following Coplen et al. (1983):

$$\delta^{18}O_{CO3(VSMOW)} = 1.03091 \times \delta^{18}O_{CO3(VPDB)} + 30.91$$

Statistical analyses

All statistical analyses were performed in R Version 4.3.3 (R Core Team 2024) using the Rstudio interface version 2023.12.1 (RStudio Team 2024). We used the package "psych" (Revelle 2024) for the descriptive analysis and "SIBER" (Jackson et al. 2019; Jackson and Parnell 2023) for the Layman metrics and the isotope-based niche calculation (Layman et al. 2007). The mean with standard deviation (SD) and the minimum and maximum values of $\delta^{13}C$ and $\delta^{18}O$ were calculated for the descriptive analysis.

The Layman metrics are used to quantify the structure and variability of isotopic niches in ecological communities (Layman et al. 2007) and include the range of $\delta^{13}C$ and $\delta^{18}O$, the total area (TA) occupied by individuals in the isotopic space, the mean distance to the centroid (CD), the distance to the nearest neighbor (NND), and the standard deviation of the distance to the nearest neighbor (SDNND). The above metrics provide information regarding the niche width, trophic diversity, and individual specialization within populations.

In addition, we calculated several measures of isotopic niche width based on ellipses fitted in two-dimensional isotope space. First is the standard ellipse area (SEA), representing the core isotopic niche and containing approximately 40% of the data points. Second is the standard ellipse area corrected for sample size (SEAc), which accounts for small sample sizes to improve comparability across groups. Lastly, we calculate the Bayesian standard ellipse area (SEAb), which uses Bayesian inference to estimate the niche width and facilitate probabilistic comparisons of niche overlap

and variation amongst groups (Jackson et al. 2011; Parnell et al. 2013). These metrics allow us to characterize both the breadth and structure of ecological and dietary niches and to evaluate the degrees of specialization among the taxa.

We also used additional packages in the production of figures: ggplot2 (Wickham 2016), dplyr (Wickham 2023), patchwork (Pedersen 2024), hrbrthemes (Rudis 2024), and ggpubr (Kassambara 2023). Graphic enhancement was performed with Affinity Designer 2 (version 2.5.5) and Adobe Photoshop (version 25.6.0).

Results

Table 1 summarizes the $\delta^{13}C$ and $\delta^{18}O$ values from each specimen. A full table of all measured values is given in the open access repository PANDORA (DOI: https://www.doi.org/https://doi.org/10.48493/3qd1-yq09). Plots of $\delta^{13}C$ and $\delta^{18}O$ across the sampled area are presented in Figs. 3 and 4, and Sup. Figure 3–4. There are clear differences between horses and the bovine and between some horse individuals in both carbon and oxygen values. Additionally, differences between Verberie and the two Hegau Jura sites are especially apparent in $\delta^{18}O$ values.

For the horses, $\delta^{18}O$ trendlines are broadly sinusoidal (Fig. 4), indicating seasonal changes in temperature and likely diet. The earliest recorded mineralization corresponds to spring in PTF-E1 and PTF-E2, lasting ~ 0.75 years, and summer in PTF-E3 and PTF-E4, lasting ~ 1.5 years. For Gnirshöhle, we focus on GNI- 25 since GNI-53 and GNI- 54 recorded a comparatively short period of life, although they are helpful for the discussion of niche reconstruction below. Like the Petersfels horses, GNI- 25 exhibits a sinusoidal pattern, likely related to climatic oscillations, and the earliest mineralization corresponds to winter and spans ~ 1 year. The Verberie individual (VBR-7) also records a seasonal signal, which begins and ends in winter and lasts for ~ 1 year. Horse carbon values are dissimilar between regions, although Verberie's range falls within the larger variation of Hegau Jura (range of $\delta^{13}C$: Verberie = − 11.8‰ to − 11.4‰, Hegau Jura = − 12.3‰ to − 10.6‰).

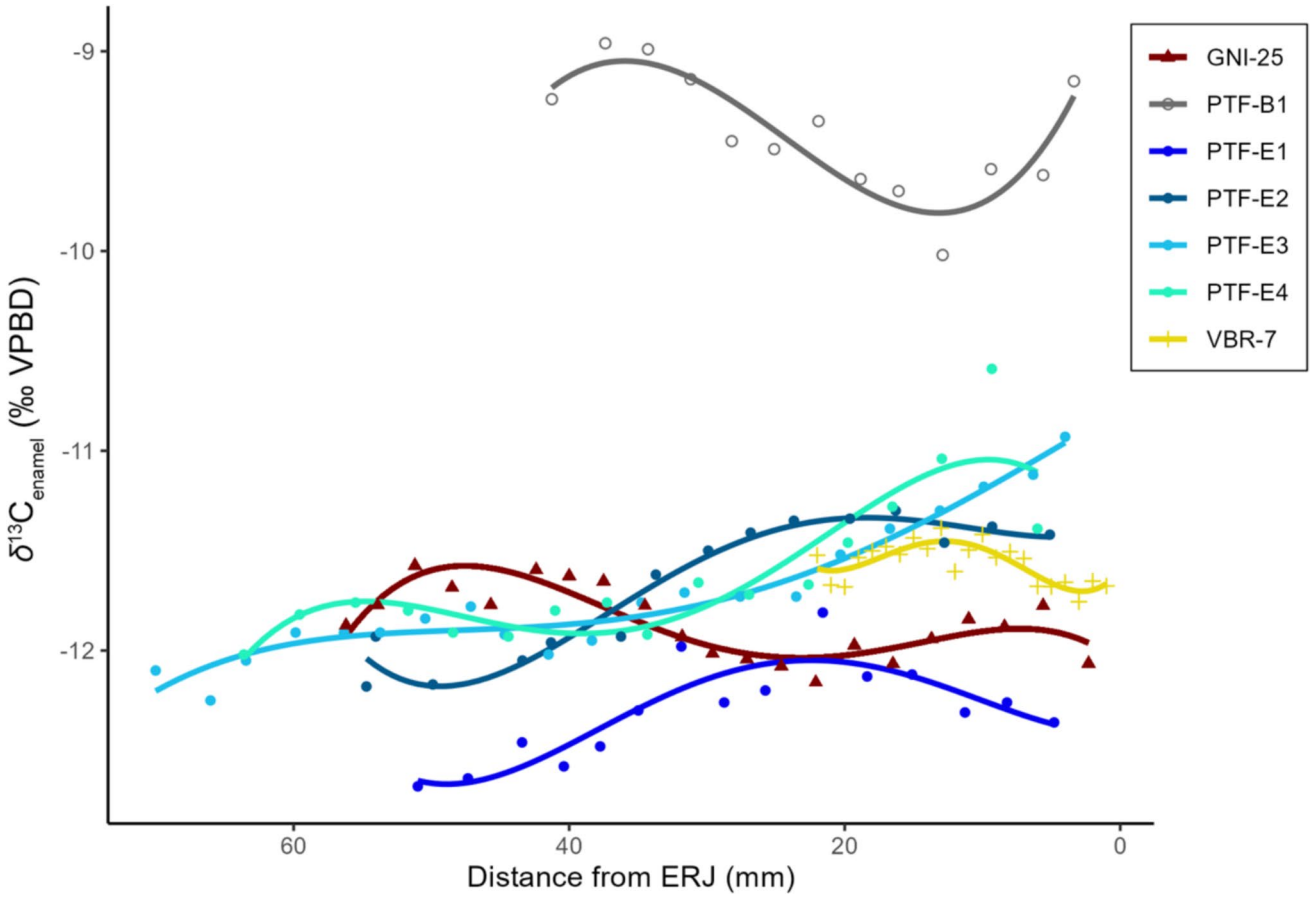

Fig. 3 Carbon ($\delta^{13}C$) values from horse and bovine enamel plotted along the distance from the ERJ (approximated for PTF-E2 and PTF-E3) from Petersfels (PTF), Gnirshöhle (GNI), and Verberie (VBR). Samples GNI- 53 and GNI- 54 are excluded here, given their short sampling area, but are presented in Sup. Figures 3–4. ERJ = enamel root junction. Trendlines are 5th order polynomial regression fits

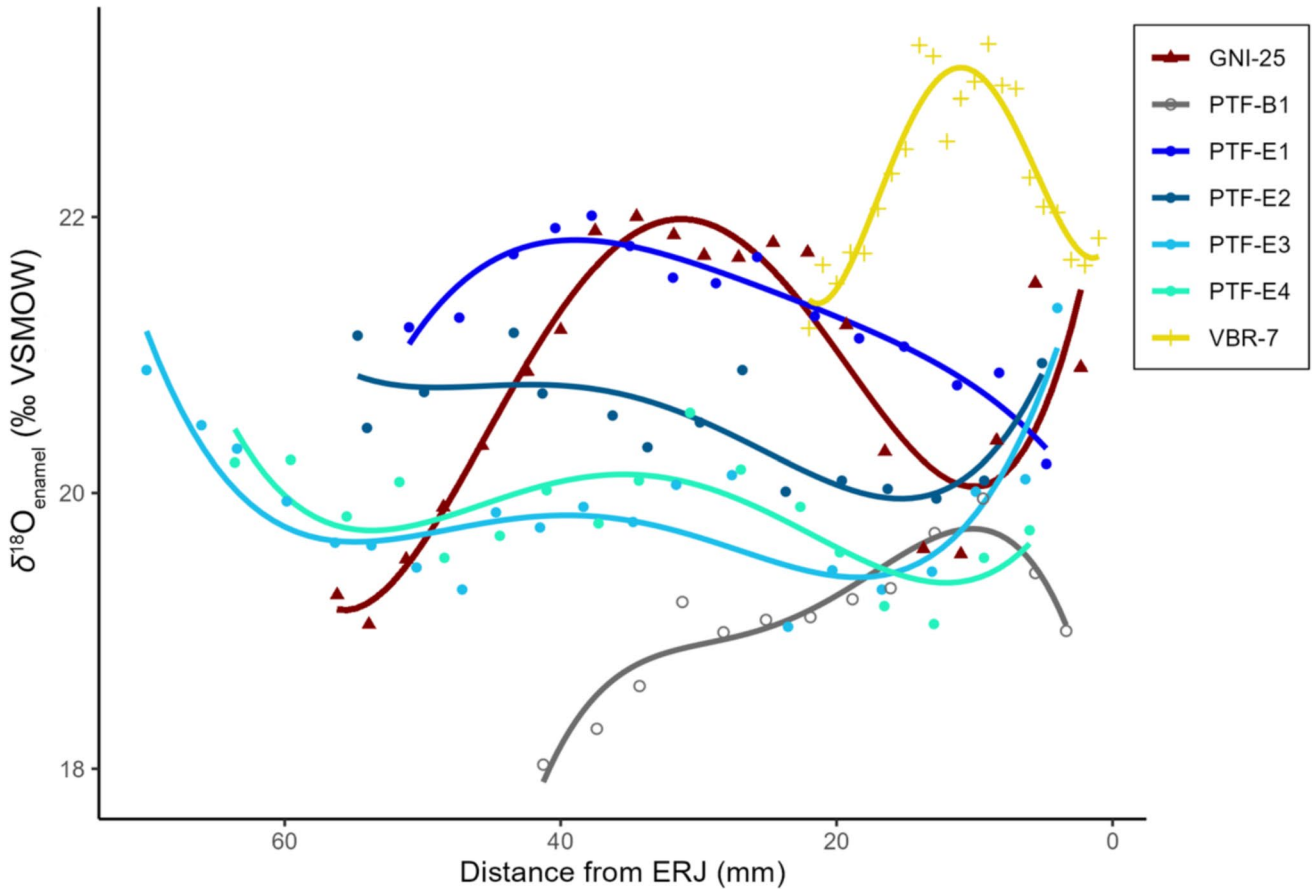

Fig. 4 Oxygen ($\delta^{18}O$) values from horse and bovine enamel plotted along the distance from the ERJ (approximated for PTF-E2 and PTF-E3) from Petersfels (PTF), Gnirshöhle (GNI), and Verberie (VBR). Given their short sampling area, samples GNI- 53 and GNI- 54 are excluded here but are presented in Sup. Figures 3–4. ERJ = enamel root junction. Trendlines are 5th order polynomial regression fits

For the Petersfels bovine (PTF-B1; Fig. 4), the sinusoidal shape of the $\delta^{13}C$ and $\delta^{18}O$ values indicates that diet and temperature varied seasonally, more so than in the horses. The earliest recorded signal of mineralization corresponds to the winter and lasts until fall (~ 0.75 years). The number of individuals limits the larger discussion of bovine diet and behavior in the region.

Figure 5 shows the carbon and oxygen isotopic space, or isospace (Robinson 2021), of all sampled individuals. This isospace, presented as the two-dimensional plot of $\delta^{13}C$ and $\delta^{18}O$ values, includes both convex hulls (illustrating the total isotopic range) and standard ellipses (corresponding to the core isotopic niche area), capturing different aspects of isotopic variability and ecological breadth (Parnell et al. 2013; Robinson 2021). Horses are characterized by a more significant variation in $\delta^{18}O$ values; however, distinct groups are still observed in $\delta^{13}C$ values. The greatest separation is observed between species, as horses and bovines exhibit distinct $\delta^{13}C$ values and minimally overlapping $\delta^{18}O$ values.

The PTF-E2 and GNI- 25 horses show the most significant niche expansion (TA of 1.80 and 1.22‰^{2}, and SEAc of 0.63 and 0.55‰^{2} respectively) (Table 2). This indicates strong seasonality during enamel formation. The high ranges of $\delta^{18}O$ values (2.31 and 2.96‰) also indicate large differences between winter and summer during the Magdalenian in the Hegau Jura. GNI- 53 also has a high $\delta^{18}O$ range (2.47‰) despite its relatively small core niche (SEAc = 0.34‰^{2}) and the fact that only a small fragment could be analyzed. Interestingly, this is not true for all horse teeth from the Hegau Jura, as the other five samples have lower $\delta^{18}O$ ranges (1.20 to 1.94‰) than the reference sample from Verberie (2.06‰). Nevertheless, all samples from the Hegau Jura have a larger core niche area than that of Verberie (SEAc of Hegau Jura = 0.34 to 0.55‰^{2}; SEAc of Verberie = 0.17‰^{2}). VBR- 7 also has the lowest NND and SDNND values (0.1 and 0.08‰), indicating a homogeneous, specialized ecological niche. The $\delta^{13}C$ ranges, which indicate dietary flexibility, are generally larger for the Hegau Jura samples (0.58 to 1.43‰) than for VBR-7 (0.37‰), except for GNI- 53, which has the smallest

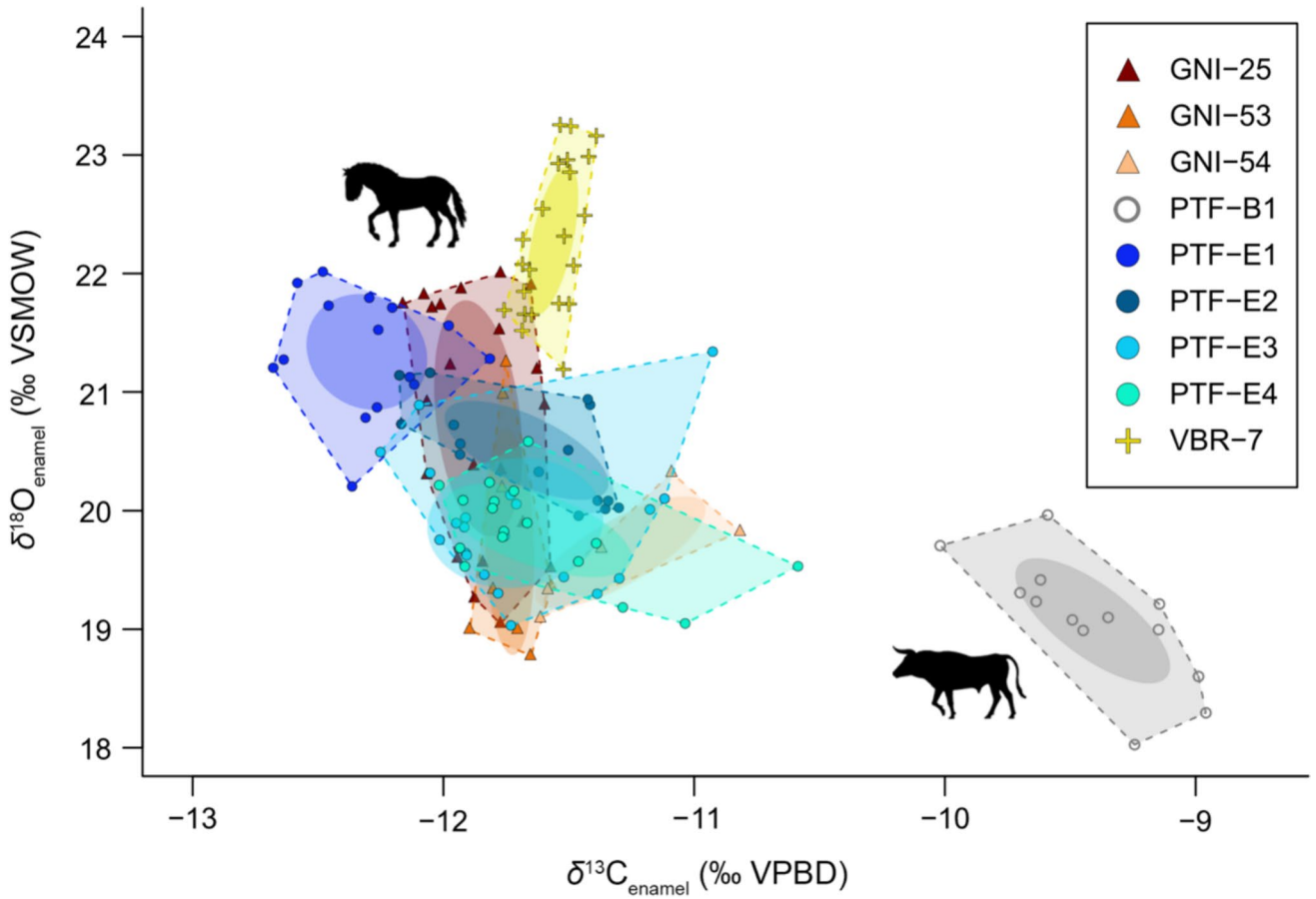

Fig. 5 Carbon (δ^{13}C) and oxygen (δ^{18}O) isospace of horses and the bovine from Petersfels, Gnirshöhle, and Verberie

Table 2 Summary of carbon (δ^{13}C) and oxygen (δ^{18}O) Layman metrics from Petersfels, Gnirshöhle, and Verberie

Tooth ID	δ^{18}O range	δ^{13}C range	TA	CD	NND	SDNND	SEA	SEAc
GNI- 25	2.96	0.58	1.22	0.90	0.19	0.10	0.53	0.55
GNI- 53	2.47	0.33	0.42	0.81	0.30	0.20	0.29	0.34
GNI- 54	1.22	0.80	0.34	0.47	0.40	0.17	0.33	0.44
PTF-B1	1.81	0.86	0.85	0.48	0.17	0.14	0.37	0.39
PTF-E1	1.20	0.87	0.61	0.48	0.11	0.07	0.32	0.35
PTF-E2	2.31	1.33	1.80	0.53	0.20	0.26	0.60	0.63
PTF-E3	1.53	1.43	1.16	0.44	0.18	0.15	0.37	0.40
PTF-E4	1.94	1.06	0.93	0.48	0.24	0.15	0.35	0.38
VBR- 7	2.06	0.37	0.40	0.55	0.10	0.08	0.16	0.17

TA = total area, *CD* = mean distance to the centroid, *NND* = mean nearest neighbor difference, *SDNND* = standard deviation of the nearest neighbor difference, *SEA* = standard ellipse area, *SEAc* = standard ellipse area corrected for sample size

range (0.33‰). Although the measured δ^{13}C values of the bovine individual (PTF-B1) differ strongly from those of the horses, the niche metrics are comparable to those of the Hegau Jura horses.

Discussion

Stable isotopes

Our isotopic results show clear differences in animal diet

and climate between the Hegau Jura and northern France, between horses in the Hegau Jura, and, more broadly, between species. Focusing on the horses, as they make up the majority of the assemblage, the range of $\delta^{18}O$ values (Fig. 4) suggests that the Gnirshöhle individuals occupied a slightly colder, more variable climate than those at Petersfels and that northern France was warmer than the Hegau Jura during the Late Glacial (range of $\delta^{18}O$: Hegau Jura = + 18.0‰ to + 22.0‰, Verberie = + 21.2‰ to + 23.3‰); this should be considered a preliminary hypothesis, given that we include only one individual from France in this analysis. The larger amplitude of the Gnirshöhle individuals indicates they experienced more pronounced seasonal variation and/or migrated between more climatically diverse environments. However, as horses exhibited rather limited seasonal movements than long-distance migrations during much of the late Pleistocene (Bignon and Eisenmann 2000; Bignon et al. 2005; Pellegrini et al. 2008), stronger seasonal extremes are a more parsimonious explanation. Additional isotopic data (e.g., Strontium and Sulfur) would help to test this hypothesis.

The horse $\delta^{13}C$ results (range of $\delta^{13}C$: Hegau Jura = − 12.3‰ to − 10.6‰, Verberie = − 11.8‰ to − 11.4‰) suggest that all individuals consumed a similar diet. This is expected, as Pleistocene horses were specialized grazers; although, some inter-individual variation can be explained by the occasional inclusion of other types of vegetation (e.g., Saarinen et al. 2016; Drucker 2022). The wider range of values at Petersfels and Gnirshöhle (Figs. 3 and 6) suggest that the Verberie horse consumed a particularly specialized diet. However, as Verberie is only represented by one sample, it is difficult to assess the full range of dietary behaviors. Lastly, all $\delta^{13}C$ trendlines exhibit a low-amplitude sinusoidal shape, indicating that, although seasonal dietary shifts occurred, they were minimal.

An interesting phenomenon in the Petersfels horses is the gradual decrease in $\delta^{18}O$ and increase in $\delta^{13}C$ over the first years of life in multiple individuals (Figs. 4 and 5). Since isotopic values vary between individuals and at least two teeth (PTF-E1 and PTF-E4) originate from distinct archaeological horizons, it is unlikely that this signal comes from a single individual with a unique life history. The remnant of a weaning signal is also improbable, as three samples are M3s, which mineralize after weaning (Hoppe et al. 2004). Another possibility is a difference in diet, metabolism, and/or microbiome between younger and older juveniles; however, in

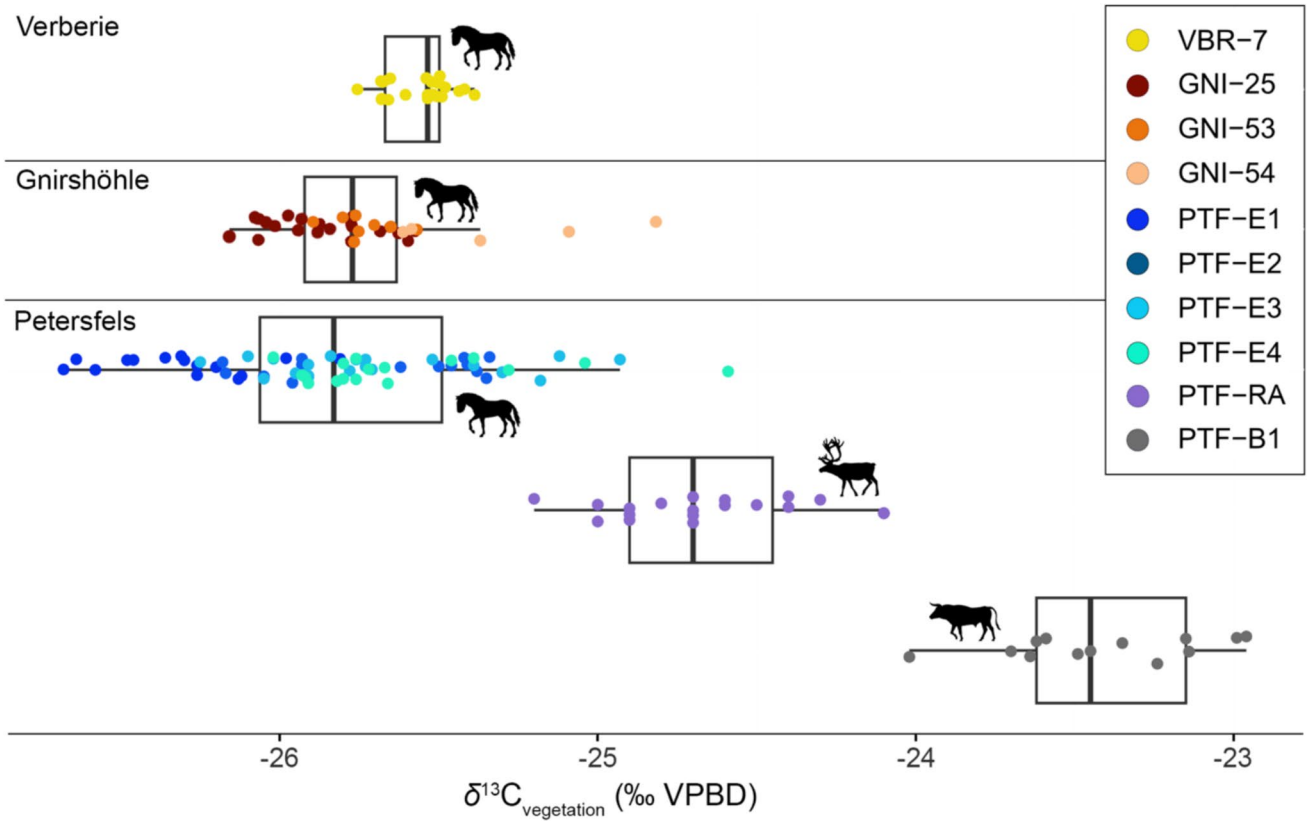

Fig. 6 Carbon ($\delta^{13}C$) values from the studied horses and bovine as well as previously published data from reindeer (PTF-RA, Drucker et al. 2011). To facilitate comparison, tooth carbonate and bone collagen values were converted to vegetation values by subtracting 14‰ from tooth carbonate values and 5‰ from bone collagen values (Lee-Thorp et al. 1989; Koch 1998; Cerling and Harris 1999)

modern horses, the most significant changes in diet and gut function occur much earlier in life (Saastamoinen and Särkijärvi 2018; Lindenberg et al. 2019; Henry and Saastamoinen 2023). Instead, the most probable explanation relates to the nature of enamel maturation. In some ungulates, the carbonate content closest to the occlusal surface can be significantly lower than the rest of the tooth. This is because carbonate content decreases as the enamel matures, and the lowest carbonate values thus come from the oldest portions of the tooth (Sydney-Zax et al. 1991). This results in the observed signal of higher $\delta^{18}O$ and lower $\delta^{13}C$ in the uppermost few millimeters of the tooth (De Winter et al. 2016). However, it is unclear why this signal only appears in the Petersfels individuals.

The stratigraphic information on the Petersfels samples provides additional, albeit tenuous, information on the climatic conditions associated with PTF-E1 (AH 3/4) and PTF-E4 (AH 2/3). The former exhibits lower $\delta^{18}O$ values than the latter, indicating PTF-E1 lived during a colder period. As AH 3/4 underlies AH 2/3, this colder period occurred first and was followed by a warmer period. The range of $\delta^{18}O$ values from PTF-E1 also matches that of GNI- 25 and GNI- 53 (Sup. Figure 3–4), perhaps indicating similar or the same climatic conditions. However, due to the low sample number, this assumption is preliminary, and it is possible that our individuals capture only a small portion of the total variation in each chronological period. Additional research is required to refine the chronology at the sites and determine the likelihood that occupations took place coevally.

Comparing the horses and the bovine, dietary niche partitioning best explains the observed difference in $\delta^{13}C$ between species. As previously mentioned, Pleistocene horses in this region were likely specialized graminoid grazers but could broaden their diets to include other forage, such as leaves and forbs. Similarly, aurochs and steppe bison consumed a diet of primarily graminoids, although steppe bison were particularly flexible and able to consume a wider range of resources than both aurochs and extant bison (Julien et al. 2012; Saarinen et al. 2016; Kelly et al. 2021; Drucker 2022). The elevated $\delta^{13}C$ values of the Petersfels bovine suggests that it consumed a more diverse diet including vegetation with higher $\delta^{13}C$ values, like the C3 plants from a more open or arid environment (Kohn 2010). Consequently, it is suggested that the bovine likely consumed a broader range of plant resources than the horses. The difference between the species is best explained by dietary niche partitioning; the bovine occupies a niche that allows a more diverse diet compared to the likely more consistent, grass-based diet of the horses. More significant variation occurs in $\delta^{18}O$ between horses and the bovine. Oxygen values vary due to a variety of factors including the water source, habitat preference, and physiology, which makes inter-species comparison difficult. However, as prior research suggests, some horses and bovines were minimally migratory during this period (Pellegrini et al. 2008; Julien et al. 2012), and we assume individuals obtained water from similar sources. Instead, the most parsimonious explanation for both inter- and intra-species variation is differences in climate between chronological periods. For example, the elevated $\delta^{18}O$ of PTF-E1 would indicate a warmer period, while the lower $\delta^{18}O$ values of PTF-E3 and PTF-E4 represent colder periods.

Similarly, bovine $\delta^{18}O$ values are lower than any of the horses, likely representing the coldest period. This is further supported by the radiocarbon dates, which span both warm and cold periods (Fig. 2). However, it is challenging to fully evaluate this signal, as baseline variability may be obscured by species-specific differences in oxygen intake and fractionation (Cerling and Harris 1999; Kohn 2010). Additionally, sample size limits our interpretations, as our individuals may be outliers within the larger climatic scheme (e.g., a few especially cold years within a warm period).

The isotopic results from Verberie provide an additional perspective on Late Glacial ungulate diet and environment. Compared to the Hegau Jura, the Verberie horse presents similar, albeit lower amplitude, $\delta^{13}C$ values (Fig. 4) and strongly elevated $\delta^{18}O$ values (Fig. 5). The carbon results suggest the Verberie horse experienced less pronounced seasonal variation in diet and perhaps consumed a narrower range of resources. Similarly, differences in oxygen can be explained by the environmental conditions, namely temperature, with Verberie exhibiting more temperate conditions than the northern Alpine foreland. This is consistent with other evidence from northern France, which suggests this region was more hospitable during the LGM and Late Glacial, serving as a "cryptic" refugium for human and animal groups (Bignon-Lau et al. 2021). Other evidence from southern Germany attests to cold conditions during the LGM and Late Glacial. Schürch et al. (2024) and Wong et al. (2020) suggest the first post-LGM inhabitants arrived between 19.5–16.5 ka cal BP and initially experienced tundra-like conditions that gradually became more temperate, resulting in greater ecological diversity. However, the earliest date from Vogelherd (Schürch et al. 2024) is unique compared to the majority of Magdalenian data in the region (Kind 2003; Taller et al. 2014; Pasda 2019b; Kind and Beutelspacher 2020). Further east in the Altmühl Valley, climatic barriers to recolonization appear stronger, as hunter-gatherers only consistently occupied the area after 15 ka with the appearance of wetter conditions (Barbieri et al. 2022).

It is also possible to discuss the larger ungulate isospace at Petersfels. Figure 6 presents the range of carbon values between the main ungulates at the site: horses (this study), bovines (this study), and reindeer (Drucker et al. 2011). Surprisingly, reindeer plot between the other two taxa, suggesting an intermediate diet. It is well established that Late Glacial reindeer altered their diets to include more browse

as their preferred forage of high $\delta^{13}C$ lichen grew scarce (Drucker et al. 2011, 2012; Rivals et al. 2020). However, this decrease in high $\delta^{13}C$ vegetation should have impacted all ungulates in the same manner; instead, the bovine exhibits elevated $\delta^{13}C$ relative to reindeer. Although musk oxen are known to consume lichen, ZooMS excluded this possibility (Sup. Text 1); aurochs are not known to consume lichen, while steppe bison were more flexible and may have accessed this resource (Bocherens et al. 2015; Saarinen et al. 2016). If the Petersfels bovine is indeed a lichen-consuming steppe bison, it is still unclear why reindeer did not access this niche. The most likely explanation is that the bovine and the reindeer originate from different climatic periods, which is consistent with the radiocarbon dates (Fig. 2). Likely, the bovine is associated with an earlier, colder period. This is also supported by the broader bovine record, which shows a large-scale decrease in their population between the Last Glacial-Interglacial transition and the Bølling/Allerød, coeval with rising temperatures and $\delta^{18}O$ (Markova et al. 2015).

Unfortunately, comparative horse and bovine tooth carbonate data from the Magdalenian of the studied regions is scarce. However, some tentative inferences can be drawn from contemporaneous bone collagen data, despite representing a later and more averaged period of life (Bocherens and Drucker 2007; Bocherens 2015). First, concerning horses, Stevens and Hedges (2004) sampled bone collagen from various Late Glacial sites. When converted to equivalent vegetation values, our horse results fit well within their reported range of $\delta^{13}C$ (approximate $\delta^{13}C_{vegetation} = -27.0‰$ to $-25.0‰$) for the period between ~22–12 cal ka BP (calibrated with OxCal v4.4, IntCal20) (Reimer et al. 2020). This is just prior to a larger drop in carbon values, signaling the major climatic changes associated with the transition to the Holocene. Stevens and Hedges (2004) argue that this post- 12 cal ka BP decrease in $\delta^{13}C$ is associated with a global change in CO_2 and/or increased forestation and the canopy effect. Our results also match well with horses from Langmahdhalde (approximate $\delta^{13}C_{vegetation} = -26.0‰$ to $-25.5‰$) (Wong et al. 2020) and two sites in northern Switzerland, Kastelhöhle-Nord (approximate $\delta^{13}C_{vegetation} = -26.5‰$ to $-25.0‰$) and Monruz (approximate $\delta^{13}C_{vegetation} = -26.5‰$ to $-25.0‰$) (Reade et al. 2020), for which a relationship to Petersfels is already attested by proximity, shared raw material sources, and similar personal ornamentation (Álvarez-Fernández 2006, 2009; Maier 2015). Conversely, most of our results fall beneath the $\delta^{13}C$ values presented by Stevens et al. (2009) from Gönnersdorf (~ 18.0–14.0 ka cal BP) and Andernach-Martinsberg (~ 16.5–13.0 ka cal BP) (approximate $\delta^{13}C_{vegetation} = -24.0‰$ to $-25.5‰$). The average $\delta^{13}C$ from Verberie is, however, closer and perhaps represents ecological similarities between the northern latitude sites relative to the Hegau Jura.

Collagen results presented by Richards and Hedges (2003) from Late Glacial *Bos/Bison* sp. individuals are close but do not overlap with the Petersfels bovine (approximate $\delta^{13}C_{vegetation} = -25.5‰$ to $-24.0‰$); however, this dataset lacks samples from ~27–15 cal ka BP (calibrated with OxCal v4.4, IntCal20) (Reimer et al. 2020), which spans the much of the chronological overlap with Petersfels (Richards and Hedges 2003). Bovine values from Kastelhöhle-Nord, dated to ~16.0–16.5 ka cal BP, are also separate (approximate $\delta^{13}C_{vegetation} = -25.1‰$ to $-24.7‰$) (Reade et al. 2020), suggesting the Petersfels bovine consumed a different diet, perhaps related to spatial differences in environment and/or temporal differences in climate. Another comparison can be made with the steppe bison kill site of Amvrosievka in Ukraine (~ 20.5 cal ka BP) (Julien et al. 2012) and bovines from Bobyliok Cave in Russia (17.6 and 14.5 cal ka BP) (Velivetskaya et al. 2016) (both calibrated with OxCal v4.4, IntCal20) (Reimer et al. 2020). Although chronologically and geographically asynchronous with our samples, these studies utilize enamel and a comparable technique. Results from the Petersfels bovine fit well within the higher range of third molar $\delta^{13}C$ values from Amvrosievka ($\delta^{13}C_{enamel} = \sim -11‰$ to $-9‰$), the lower range of third molar $\delta^{13}C$ values from Bobyliok Cave ($\delta^{13}C_{enamel} = \sim -10‰$ to $-6‰$), and within the range of third molar $\delta^{18}O$ values from both sites ($\delta^{18}O_{enamel} = \sim +16‰$ to $+21‰$). Strontium results from the Amvrosievka individuals also suggest steppe bison were non-migratory (Julien et al. 2012).

In summary, our isotopic results from equids in the Hegau Jura and northern France fit well within the broader isotopic scheme of the Late Glacial and expectations for the taxon. Our bovine matches well with individuals from further east but is elevated relative to another *Bos/Bison* sp. specimen from the northern Alpine foreland at Kastelhöhle-Nord. Observed differences in both horses and bovines likely relate to regional ecological conditions (e.g., northern vs. southern sites). However, we approach these interpretations with caution, as the datasets are not directly comparable. Future studies will add greater clarity to this picture.

Significance for Magdalenian subsistence

Evidence from the Hegau Jura and Verberie suggests Magdalenian hunter-gatherers occupied diverse environments in a range of climatic conditions, attesting to the varied and mosaic nature of Late Glacial landscapes (Guthrie 1982, 1989; Maier 2015; Schürch et al. 2024). During this period, humans and animals experienced significant ecological turnover as warming reduced the habitable ranges of cold-adapted ungulates and the carnivores who relied upon them. By the Holocene, the once expansive Mammoth-Steppe disappeared from Western and Central Europe and was replaced by a new ecosystem characterized by

warm-adapted taxa (von Koenigswald 2003; Sommer et al. 2014; Niedziałkowska et al. 2021; Drucker 2022). The Magdalenian sites presented here reflect the earlier phase of this transition, when cold-adapted fauna were still abundant on the landscape, but ecological shifts had already begun (e.g., reindeer encroachment on the horse dietary niche) (Drucker et al. 2011, 2012; Rivals et al. 2020).

In the Hegau Jura, hunter-gatherers occupied Gnirshöhle and Petersfels during different climatic periods, and at least two distinct phases are represented in our data. Radiocarbon dates and $\delta^{18}O$ values suggest that Gnirshöhle was occupied earlier, during a cooler period with greater seasonal variability, while Petersfels was occupied during both warm and cold episodes. Other archaeological evidence suggests Gnirshöhle was frequented for shorter stays, likely by a smaller number of people, while Petersfels evidences a large-scale aggregation (Albrecht et al. 1977, 1983; Weniger 1989; Albrecht and Hahn 1991; McCartin et al. 2023). However, smaller occupations at Petersfels are likely concealed by the depositional palimpsest, as demonstrated at Felsställe (Kind et al. 1987; Weniger 1989).

Whether occupation size, duration, and/or intensity are linked to the prevailing climatic conditions remains unclear. One possible scenario is that warm and stable periods facilitated the large-scale aggregations at Petersfels, while cooler, less stable conditions might be associated with the small-scale habitations at both sites. However, new dates may reveal earlier occupations, and the idea that aggregations also took place during colder periods remains untested.

Other factors also contributed to the nature of occupations at each site. For example, Gnirshöhle's elevated position above the valley floor made the site less accessible than Petersfels. Similarly, Gnirshöhle's chambers are smaller, which is less ideal for large groups and is perhaps one reason only Petersfels shows evidence of large-scale aggregations. The south-facing orientation of Gnirshöhle and the north-facing orientation of Petersfels also means the sites received different sun exposure, perhaps a limiting factor during colder periods, influencing hunter-gatherers' choice of camp (Kvamme and Jochim 1989). Together, these factors, the archaeological evidence, and the isotopic data paint a picture of human behavior influenced by the prevailing environmental conditions. Their ability to adapt to diverse conditions was likely a defining characteristic of Magdalenian people, facilitating their recolonization of and wide dispersal across Central Europe at hundreds of sites in varied environments, including the three sites presented here.

Scope of this study and future work

Our study is one of few to reconstruct paleoecology during the Magdalenian of Central Europe using stable isotopes analyses on serially sampled hypsodont dentition. Despite promising results, our study is limited by the chronological and archaeological resolution as well as sample size and appropriate comparative material. Although radiocarbon dates constrain the occupation period of each site to a few thousand years, the lack of direct dates from each tooth limits our ability to assess smaller-scale climatic changes (e.g., between the Bølling and the Older Dryas). Sample size is another limitation, as bovines are only represented by a single individual, which likely underestimates the full range of bovine variability. Although we sampled greater numbers of horses, prior studies have shown that even larger samples (i.e., 25–40 individuals) are better for capturing a taxon's full isotopic range (DeNiro and Epstein 1978; Vaudo and Heithaus 2011), and sample sizes between sites and species should be comparable (Jackson et al. 2011). It is thus possible that our individuals are not reflective of larger climatic trends and may capture, for example, a handful of cold winters within a larger warm period.

Regarding the oxygen ($\delta^{18}O$) results, it is possible that the values also reflect variation in the source of precipitation (moisture provenance) (Lewis et al. 2010; Jasechko et al. 2015). Nowadays, northern France and southwestern Germany are influenced by Atlantic-sourced moisture. However, it is not clear if this was the case during the period under study or the ways in which the regional pattern may have differed. Additionally, since Verberie is represented by a single individual, it is also possible that this animal accessed a particular water source with stronger evaporative enrichment, resulting in the observed signal (Jasechko et al. 2015).

Lastly, the contextualization of our results within the broader Magdalenian technocomplex is limited by the number of comparable samples. Although multiple studies present isotopic information from bone collagen (Stephan 1999; Drucker et al. 2011; Baumann et al. 2021), few collect data by serially sampling tooth carbonate and thus provides an important comparative dataset. The only other comparative material at our disposal was the horse tooth from Verberie. Our study thus provides a first foray into isotopic investigations of Late Glacial paleoecology using serially sampled tooth carbonate. Future studies should focus on gathering additional, well-dated samples from a wider set of sites and species.

Conclusion

Our isotopic study of horses and a bovine from the Magdalenian sites of Petersfels, Gnirshöhle, and Verberie offers new insights into the paleoenvironmental conditions and dietary behaviors of Late Glacial fauna. In serially sampling tooth enamel carbonate for carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) stable isotopes, we provide a unique reconstruction of Late Glacial paleoenvironment in the northern Alpine foreland. Contrary

to prior studies on bone collagen, results from serially sampled enamel add a new, higher-resolution perspective on animal diet and environment in the region.

In the Hegau Jura, horse oxygen results exhibit sinusoidal trends, revealing variation over time due to seasonal climatic oscillations and dietary shifts. Amplitude varies between the Petersfels and Gnirshöhle individuals, suggesting the latter experienced more extreme seasonal fluctuations. In comparison, Verberie presents elevated oxygen values, indicating that northern France was more temperate than the Hegau Jura. Carbon isotope values are more homogenous between samples, which is consistent with the specialized grazing habits of Pleistocene horses, albeit with minor dietary variations due to individual variation and seasonal changes in vegetation.

Compared to the horses, the bovine clearly occupied a different niche exhibiting elevated carbon values and decreased oxygen values. The latter suggests the bovine inhabited a colder environment, while the former points towards dietary niche partitioning between ungulates. By including previously published carbon data from reindeer bone collagen (Drucker et al. 2011), it appears that each of the three ungulate taxa at Petersfels occupied a separate dietary niche. Relative to reindeer, the bovine's elevated carbon indicates it was able to access high $\delta^{13}C$ resources, such as lichen, a niche that formerly belonged to reindeer before the Late Glacial. Together, our results suggest the bovine individual lived during an earlier, colder period when lichen was still available, while the reindeer, as well as some horses, inhabited a later, warmer period when lichen grew scarce, forcing reindeer in particular to broaden their diets to include more browse (Drucker et al. 2011). The varied isotopic signals thus highlight the dynamic and mosaic nature of Late Glacial landscapes. Overall, our findings contribute to the broader understanding of Magdalenian paleoecology, illustrating how climatic shifts influenced faunal diet and availability on the landscape for Magdalenian hunter-gatherers.

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Author contribution Theoni Panagiotopoulou (TP) and Madison J. McCartin (MJM) contributed equally and should be considered co-first authors. TP, MJM and Chris Baumann (CB) contributed to the study conception and design. Material preparation, data collection and analysis were performed by TP, MJM, Samantha Brown (SB), Susanne C. Münzel (SCM), and Britt M. Starkovich (BMS). Visualization was done by TP, MJM, CB, Yvonne Tafelmaier (YT) and SB. Funding acquisition and resources were provided by YT and Dorothée G. Drucker (DGD). Supervision was done by CB, SB, BMS, and DGD. Project administration was done by CB. The first draft of the manuscript was written by TP, MJM and all authors commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

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References

Albrecht G (1979) Magdalénien-Inventare vom Petersfels Siedlungsarchäologische Ergebnisse der Ausgrabungen 1974–1976. Verlag Archaeologica Venatoria, Tübingen

Albrecht G, Berke H (1980) Neue "Venus"-Gravierungen auf einem Knochenfragment aus dem Magdalénien vom Petersfels. Archäologisches Korrespondenzblatt 10:111–115

Albrecht G, Drautz D, Kind J (1977) Eine Station des Magdalénien in der Gnirshöhle bei Engen-Bittelbrunn im Hegau. Archäologisches Korrespondenzblatt 7:161–179

Albrecht G, Berke H, Burkert W et al (1994) Die Funde vom Petersfels in der Städtischen Sammlung Engen im Hegau. Fundberichte aus Baden-Württemberg 19:1–62

Albrecht G (2010) Gnirshöhle. Kleiner Führer. Stadt Engen, 2. Auflage

Albrecht G, Engelhardt H (1988) Eiszeitliche Funde aus dem Brudertal bei Engen. Archaeologica Venatoria, Tübingen

Albrecht G, Hahn A (1991) Rentierjäger im Brudertal. Die jungpaläolithischen Fundstellen um den Petersfels und das Städtische Museum Engen im Hegau. Führer zu archäologischen Denkmälern in Baden-Württemburg 15:1–102 Konrad Theiss Verlag, Stuttgart

Albrecht G, Berke H, Poplin F (1983) Naturwissenschaftliche Untersuchungen an Magdalénien-Inventaren vom Petersfels, Grabungen 1974–1976. Verlag Archaeologica Venatoria, Tübingen

Albrecht G, Wong GL, Münzel SC (2019) Das Drexlerloch im Brudertal bei Engen im Hegau. Neue Daten zu der ungestörten Fundstelle aus dem Magdalénien. In: Baales M, Pasda C, Merthen C (eds) "All der holden Hügel ist keiner mir fremd ..." Festschrift zum 65. Geburtstag von Claus-Joachim Kind. Dr. Rudolf Habelt, Bonn, pp 301–310

Álvarez-Fernández E (2006) Los objetos de adorno-colgantes del paleolítico superior y del mesolítico en la cornisa cantábrica y en el valle del Ebro: una visión europea. PhD Thesis, Universidad de Salamanca

Álvarez-Fernández E (2009) Magdalenian personal ornaments on the move: a review of the current evidence in Central Europe. Zephyrus LXIII:45–59

Apple Maps (2023) Baden-Wuerttemberg. https://satellites.pro/Germany_map#47.861477,8.805327,15. Accessed 3 Apr 2023

Audouze F, Cahen D, Keeley LH, Schmider B (1981) Le site Magdalénien du Buisson Campin à Verberie (Oise). Gallia Préhistoire 24:99–143

Audouze F, Enloe JG (2017) High resolution archaeology at Verberie: limits and interpretations. In: High Definition Archaeology: Threads Through the Past. Routledge, pp 195–207

Balasse M (2002) Reconstructing dietary and environmental history from enamel isotopic analysis: time resolution of intra-tooth sequential sampling. Int J Osteoarchaeol 12:155–165. https://doi.org/10.1002/oa.601

Balasse M, Bocherens H, Mariotti A (1999) Intra-bone variability of collagen and apatite isotopic composition used as evidence of a change of diet. J Archaeol Sci 26:593–598. https://doi.org/10.1006/jasc.1998.0376

Barbieri A, Maier A, Lauer T et al (2022) Post-LGM environments and foragers on the move: New data from the lower Altmühl Valley (Franconian Jura, SE Germany). J Hum Evol 173:103267. https://doi.org/10.1016/j.jhevol.2022.103267

Baumann C, Bocherens H, Drucker DG, Conard NJ (2020a) Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems. PLoS ONE 15:e0235692. https://doi.org/10.1371/JOURNAL.PONE.0235692

Baumann C, Starkovich BM, Drucker DG et al (2020b) Dietary niche partitioning among Magdalenian canids in southwestern Germany and Switzerland. Quatern Sci Rev 227:106032

Baumann C (2023) The paleo-synanthropic niche: a first attempt to define animal's adaptation to a human-made micro-environment in the Late Pleistocene. Archaeol Anthropol Sci 15. https://doi.org/10.1007/s12520-023-01764-x

Baumann C, Pfrengle S, Münzel SC, et al (2021) A refined proposal for the origin of dogs: the case study of Gnirshöhle, a Magdalenian cave site. Sci Rep 11. https://doi.org/10.1038/s41598-021-83719-7

Berke H (1987) Archäozoologische Detailuntersuchungen an Knochen aus südwestdeutschen Magdalénien-Inventaren. Verlag Archaeologica Venatoria, Tübingen

Bignon O, Baylac M, Vigne J-D, Eisenmann V (2005) Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. J Archaeol Sci 32:375–391. https://doi.org/10.1016/j.jas.2004.02.016

Bignon O, Eisenmann V (2000) Western European Late Glacial horse diversity and its ecological implications. In: Equids in time and space: papers in honour of Véra Eisenmann

Bignon-Lau O, Catz N, Bemilli C et al (2021) The Last Glacial Maximum and the Late Glacial in northern France - Palaeoecological implications of animal community structuration and feeding behaviours based on dental microwear texture analysis. Bull De La Société Préhistorique Française 118:195–219

Bliss LC, Richards JH (1982) Present-day arctic vegetation and ecosystems as a predictive tool for the arctic-steppe mammoth biome. In: Hopkins DM, Matthews JV, Schweger CE, Young SB (eds) Paleoecology of Beringia. Academic Press, pp 241–257

Blockley SPE, Donahue RE, Pollard AM (2000) Rapid human response to Late Glacial climate change: a reply to Housley et al (2000). Antiquity 74:427–428. https://doi.org/10.1017/S0003598X00059524

Blumenthal SA, Cerling TE, Smiley TM et al (2019) Isotopic records of climate seasonality in equid teeth. Geochim Cosmochim Acta 260:329–348. https://doi.org/10.1016/j.gca.2019.06.037

Bocherens H (2003) Isotopic biogeochemistry and the palaeoecology of the mammoth steppe fauna. Deinsea 9:57–76

Bocherens H (2015) Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quatern Sci Rev 117:42–71. https://doi.org/10.1016/j.quascirev.2015.03.018

Bocherens H, Koch PL, Mariotti A et al (1996) Isotopic biogeochemistry (13C, 18O) of mammalian enamel from African Pleistocene hominid sites. Palaios 11:306–318. https://doi.org/10.2307/3515241

Bocherens H, Billiou D, Patou-Mathis M et al (1997) Paleobiological Implications of the Isotopic Signatures (13C,15N) of Fossil Mammal Collagen in Scladina Cave (Sclayn, Belgium). Quatern Res 48:370–380. https://doi.org/10.1006/qres.1997.1927

Bocherens H, Hofman-Kamińska E, Drucker DG et al (2015) European bison as a refugee species? Evidence from isotopic data on Early Holocene bison and other large herbivores in northern Europe. PLoS ONE 10:e0115090

Bocherens H, Drucker DG (2007) Carbonate Stable Isotopes: Terrestrial Teeth and Bones. In: Elias SA (ed) Encyclopedia of Quaternary Science. Elsevier, Oxford

Bombin M, Muehlenbachs K (1985) $^{13}C^{12}C$ ratios of pleistocene mummified remains from beringia. Quatern Res 23:123–129. https://doi.org/10.1016/0033-5894(85)90076-6

Britton K, Jimenez E-L, Le Corre M et al (2023) Multi-isotope zooarchaeological investigations at Abri du Maras: The paleoecological and paleoenvironmental context of Neanderthal subsistence strategies in the Rhône Valley during MIS 3. J Hum Evol 174:103292. https://doi.org/10.1016/j.jhevol.2022.103292

Bronk Ramsey C (2009) Bayesian analysis of radiocarbon dates. Radiocarbon 51:337–360

Bronk Ramsey C (2021) OxCal v4.4.4

Brown WB, Christofferson PV, Massler M, Weiss MB (1960) Postnatal tooth development in cattle. Am J Vet Res 21:7–34

Bryant JD, Froelich PN, Showers WJ, Genna BJ (1996) Biologic and climatic signals in the oxygen isotopic composition of Eocene-Oligocene equid enamel phosphate. Palaeogeogr Palaeoclimatol Palaeoecol 126:75–89. https://doi.org/10.1016/S0031-0182(96)00071-5

Cattin M-I (2018) Moving with the Magdalenians: Examples from the camp sites of Monruz and Champréveyres (Switzerland). Quatern Int 498:4–11. https://doi.org/10.1016/j.quaint.2017.06.056

Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120:347–363. https://doi.org/10.1007/s004420050868

Cerling TE, Hart JA, Hart TB (2004) Stable isotope ecology in the Ituri Forest. Oecologia 138:5–12. https://doi.org/10.1007/s00442-003-1375-4

Clark PU, Dyke AS, Shakun JD et al (2009) The Last Glacial Maximum. Science 325:710–714. https://doi.org/10.1126/science.1172873

Conkey MW, Beltrán A, Clark GA et al (1980) The Identification of Prehistoric Hunter-Gatherer Aggregation Sites: The Case of Altamira. Curr Anthropol 21:609–630

Coplen TB, Kendall C, Hopple J (1983) Comparison of stable isotope reference samples. Nature 302:236–238. https://doi.org/10.1038/302236a0

Czernielewski M (2023) New data on the Sciuridae (Rodentia) from the Villafranchian site of Węże 2 in southern Poland. Geol Q 67:44–https://doi.org/10.7306/gq.1714

Dansgaard W (1964) Stable isotopes in precipitation. Tellus 16:436–468. https://doi.org/10.3402/tellusa.v16i4.8993

De Winter NJ, Snoeck C, Claeys P (2016) Seasonal cyclicity in trace elements and stable isotopes of modern horse enamel. PLoS ONE 11:e0166678. https://doi.org/10.1371/journal.pone.0166678

Debout G, Olive M, Bignon O et al (2012) The Magdalenian in the Paris Basin: New results. Quatern Int 272–273:176–190. https://doi.org/10.1016/j.quaint.2012.05.016

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506. https://doi.org/10.1016/0016-7037(78)90199-0

Diefendorf AF, Mueller KE, Wing Scott L et al (2010) Global patterns in leaf 13C discrimination and implications for studies of past and future climate. Proc Natl Acad Sci 107:5738–5743. https://doi.org/10.1073/pnas.0910513107

Drucker DG (2022) The isotopic ecology of the Mammoth Steppe. Annu Rev Earth Planet Sci 50:395–418. https://doi.org/10.1146/annurev-earth-100821-081832

Drucker DG, Bridault A, Hobson KA et al (2008) Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. Palaeogeogr Palaeoclimatol Palaeoecol 266:69–82. https://doi.org/10.1016/j.palaeo.2008.03.020

Drucker DG, Kind CJ, Stephan E (2011) Chronological and ecological information on Late-glacial and early Holocene reindeer from northwest Europe using radiocarbon (14C) and stable isotope (13C, 15N) analysis of bone collagen: Case study in southwestern Germany. Quatern Int 245:218–224. https://doi.org/10.1016/j.quaint.2011.05.007

Drucker DG, Bridault A, Cupillard C (2012) Environmental context of the Magdalenian settlement in the Jura Mountains using stable isotope tracking (13C, 15N, 34S) of bone collagen from reindeer (Rangifer tarandus). Quatern Int 272–273:322–332. https://doi.org/10.1016/j.quaint.2012.05.040

Drucker DG, Audouze F, Enloe JG et al (2015) Résultats des analyses isotopiques 13C, 18O) sur une dent de cheval de la couche II-2 de Verberie. In: Valentin B, Griselin S, Mevel L (eds) Paléolithique final et Mésolithique dans le Bassin parisien et ses marges. Habitats, sociétés et environnements, Rapport de Projet collectif de recherche, pp 143–149

Enloe JG, Audouze F (2010) The Magdalenian site of Verberie (Le Buisson Campin). the magdalenian household: Unraveling Domesticity 15

Eriksen BV (1991) Change and continuity in a prehistoric hunter-gatherer society: a study of cultural adaptation in late glacial-early postglacial southwestern Germany. Archaeologica Venatoria, Institut für Urgeschichte der Universität Tübingen

Gifford-Gonzalez D (2018) An Introduction to Zooarchaeology. Springer International Publishing, Cham

Graves MW, Addison DJ (1996) Models and methods for inferring the prehistoric colonization of Hawai'i. Bull Indo-Pacific Prehistory Assoc 15:3–8

Green DR, Green GM, Colman AS et al (2017) Synchrotron imaging and Markov Chain Monte Carlo reveal tooth mineralization patterns. PLoS ONE 12:e0186391. https://doi.org/10.1371/journal.pone.0186391

Guthrie RD (1982) Mammals of the Mammoth Steppe as paleoenvironmental indicators. In: Hopkins DM, Matthews JV, Schweger CE, Young SB (eds) Paleoecology of Beringia. Academic Press, pp 307–326

Guthrie RD (1989) Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe. University of Chicago Press, Chicago, IL

Hahn J (1978) New Aspects of the Magdalenian in Central Europe. Reviews in Anthropology 313–331

Henry S, Saastamoinen M (2023) Nutrition and Management at and after Weaning. In: Saastamoinen M (ed) Feeding and Management of Foals and Growing Horses. Springer International Publishing, Cham, pp 39–65

Higgins P, MacFadden BJ (2009) Seasonal and geographic climate variabilities during the Last Glacial Maximum in North America: Applying isotopic analysis and macrophysical climate models. Palaeogeogr Palaeoclimatol Palaeoecol 283:15–27. https://doi.org/10.1016/j.palaeo.2009.08.015

Hoppe KA, Stover SM, Pascoe JR, Amundson R (2004) Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. Palaeogeogr Palaeoclimatol Palaeoecol 206:355–365

Ivy-Ochs S, Kerschner H, Reuther A et al (2008) Chronology of the last glacial cycle in the European Alps. J Quat Sci 23:559–573. https://doi.org/10.1002/jqs.1202

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jackson A, Parnell A (2023) SIBER: Stable Isotope Bayesian Ellipses in R

Jackson A, Parnell A, Jackson MA (2019) Package 'SIBER'

Jaguttis-Emden M (1983) Die Radiokarbondatierungen der Ausgrabung Petersfels. Naturwissenschaftliche Untersuchungen an Magdalénien-Inventaren Vom Petersfels, Grabungen 1974–1976:47–58

Jasechko S, Lechler A, Pausata FSR et al (2015) Late-glacial to late-Holocene shifts in global precipitation δ18O. Climate of the past 11:1375–1393. https://doi.org/10.5194/cp-11-1375-2015

Jochim M, Herhahn C, Starr H (1999) The Magdalenian Colonization of Southern Germany. Am Anthropol 101:129–142

Julien M-A, Bocherens H, Burke A et al (2012) Were European steppe bison migratory? 18O, 13C and Sr intra-tooth isotopic variations applied to a palaeoethological reconstruction. Quatern Int 271:106–119

Kassambara A (2023) ggpubr: "ggplot2" Based Publication Ready Plots

Kelly A, Miller JH, Wooller MJ et al (2021) Dietary paleoecology of bison and horses on the mammoth steppe of eastern Beringia based on dental microwear and mesowear analyses. Palaeogeogr Palaeoclimatol Palaeoecol 572:110394

Kind C-J (2003) Die absolute Datierung des Magdaléniens und des Mesolithikums in Süddeutschland. In: JM Burdukiewicz/L Fiedler/ W-D Heinrich/A Justus/E Brühl (ed) Erkenntnisjäger – Kultur und Umwelt des frühen Menschen. Festschrift für Dietrich Mania. Veröffentlichungen des Landesamtes für Archäologie Sachsen-Anhalt 57 (Halle/Saale 2003) 303–320

Kind CJ, Beutelspacher T (2020) Das Kohlhau-Abri: Eine neue Felsdachfundstelle in Nachbarschaft zum Lonetal. Fundberichte aus Baden-Württemberg 40:15–36

Kind C-J, Berke H, Torke W et al (1987) Das Felsställe. Eine jungpaläolithisch-frühmesolithische Abri-Station bei Ehingen-Mühlen, Alb-Donau-Kreis. Die Grabungen 1975–1980. Forschungen und Berichte zur Vor- und Frühgeschichte in Baden-Württemberg 23. Konrad Theiss Verlag, Stuttgart

Koch PL (1998) Isotopic reconstruction of past continental environments. Annu Rev Earth Planet Sci 26:573–613. https://doi.org/10.1146/annurev.earth.26.1.573

Kohn MJ (2010) Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proc Natl Acad Sci 107:19691–19695. https://doi.org/10.1073/pnas.1004933107

Kohn MJ, Cerling TE (2002) Stable isotope compositions of biological apatite. Rev Min Geochem 48:455–488. https://doi.org/10.2138/rmg.2002.48.12

Kraft G (1939) Nachträge zum Petersfels. Badische Fundberichte 15:58–60

Krajcarz MT, Krajcarz M (2014) The 200,000 year long record of stable isotopes (δ18O, δ13C) of cave bear (*Ursus spelaeus*) teeth from Biśnik Cave, Poland. Quatern Int 339–340:119–130. https://doi.org/10.1016/j.quaint.2013.07.022

Krajcarz MT, Krajcarz M, Bocherens H (2018) Collagen-to-collagen prey-predator isotopic enrichment (Δ13C, Δ15N) in terrestrial mammals - a case study of a subfossil red fox den. Palaeogeogr Palaeoclimatol Palaeoecol 490:563–570. https://doi.org/10.1016/j.palaeo.2017.11.044

Kretschmer I (2015) Demographische Untersuchungen zu Bevölkerungsdichten, Mobilität und Landnutzungsmustern im späten Jungpaläolithikum. Kölnder Studien zur Prähistorischen Archäologie 6. Verlag Marie Leidorf, Rahden/Westf

Krönneck P (2009) Vögel - Bonusmaterial in der Archäozoologie. Jungpleistozäne Inventare als Auswertungsbeispiele. In: Knochen pflastern ihren Weg. Festschrift für Margarethe und Hans-Peter Uerpmann. Verlag Marie Leidorf GmbH, Rahden/Westf., pp 133–141

Kvamme KL, Jochim MA (1989) The environmental basis of Mesolithic settlement. In: The Mesolithic in Europe: Papers Presented at the Third International Symposium, John Donald Publishers, Edinburgh, pp 1–12

Laville H (1983) Die Magdalénien-Station Petersfels: Eigenschaften, klimatische Bedeutung und Chronologie der Schichten. In: Naturwissenschaftliche Untersuchungen an Magdalénien-Inventaren vom Petersfels, Grabungen 1974–1976, pp 21–46

Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of tropic structure? Ecology 88:42–48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Leesch D, Müller W, Nielsen E, Bullinger J (2012) The Magdalenian in Switzerland: Re-colonization of a newly accessible landscape. Quatern Int 272–273:191–208. https://doi.org/10.1016/j.quaint.2012.04.010

Leesch D, Bullinger J, Müller W (2019) Vivre en Suisse il y a 15 000 ans. Le Magdalénien. Archéologie suisse (Préhistoire de la Suisse), Bâle

Lee-Thorp JA, Sealy JC, van der Merwe NJ (1989) Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. J Archaeol Sci 16:585–599. https://doi.org/10.1016/0305-4403(89)90024-1

Lee-Thorp JA (1989) Stable Carbon Isotopes in Deep Time: The Diets of Fossil Fauna and Hominids. PhD Dissertation, University of Cape Town

Lewis SC, LeGrande AN, Kelley M, Schmidt GA (2010) Water vapour source impacts on oxygen isotope variability in tropical precipitation during Heinrich events. Climate Past 6:325–343. https://doi.org/10.5194/cp-6-325-2010

Lindenberg F, Krych L, Kot W et al (2019) Development of the equine gut microbiota. Sci Rep 9:14427. https://doi.org/10.1038/s41598-019-50563-9

Maier A (2015) The Central European Magdalenian. Regional Diversity and Internal Variability. Springer Dordrecht, Dordrecht

Markova AK, Puzachenko AY, Van Kolfschoten T et al (2015) Changes in the Eurasian distribution of the musk ox (Ovibos moschatus) and the extinct bison (Bison priscus) during the last 50 ka BP. Quatern Int 378:99–110

Mauser PF (1970) Die jungpaläolithische Höhlenstation Petersfels im Hegau (Gemarkung Bittelbrunn, Ldkrs. Konstanz). Badische Fundberichte Sonderheft 13. Otto Kehrer, Freiburg

McCartin MJ, Starkovich BM, Conard NJ (2023) New insights into Magdalenian subsistence at Petersfels (Hegau Jura, southwestern Germany). Quatern Sci Rev 322:108417. https://doi.org/10.1016/j.quascirev.2023.108417

Mourer-Chauvire C (1983) Die Vogelknochen aus dem Magdalénienzeitlichen Fundplatz Petersfels, Grabungen 1974-1976. In: Naturwissenschaftliche Untersuchungen an Magdalénien-Inventaren vom Petersfels, Grabungen 1974-1976, pp 129–132

Niedziałkowska M, Doan K, Górny M et al (2021) Winter temperature and forest cover have shaped red deer distribution in Europe and the Ural Mountains since the Late Pleistocene. J Biogeogr 48:147–159. https://doi.org/10.1111/jbi.13989

Parnell AC, Phillips DL, Bearhop S et al (2013) Bayesian stable isotope mixing models. Environmetrics 24:387–399. https://doi.org/10.1002/env.2221

Pasda C (1998) Wildbeuter im archäologischen Kontext: das Paläolithikum in Südbaden. Folio-Verlag Wesselkamp, Bad Bellingen

Pasda C (2019a) Das Magdalénien an Hoch- und Oberrhein in Baden und der Pfalz. In: Floss H (ed) Das Magdalénien im Südwesten Deutschlands, im Elsass und in der Schweiz. Kerns Verlag, Tübingen, pp 131–158

Pasda C (2019b) Versuch einer zeitlichen Gliederung des Magdalén iens in Südwestdeutschland. In: Baales P, und Pasda C (ed) All der holden Hügel ist keiner mir fremd…"– Festschrift zum 65. Geburtstag von Claus-Joachim Kind. Dr. Rudolf Habelt GmbH, Bonn 2019, pp 259–278

Passey BH, Robinson TF, Ayliffe LK et al (2005) Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals. J Archaeol Sci 32:1459–1470. https://doi.org/10.1016/j.jas.2005.03.015

Pedersen TL (2024) patchwork: The Composer of Plots

Pederzani S, Britton K (2019) Oxygen isotopes in bioarchaeology: Principles and applications, challenges and opportunities. Earth Sci Rev 188:77–107. https://doi.org/10.1016/j.earscirev.2018.11.005

Pellegrini M, Donahue RE, Chenery C et al (2008) Faunal migration in late-glacial central Italy: implications for human resource exploitation. Rapid Commun Mass Spectrom 22:1714–1726. https://doi.org/10.1002/rcm.3521

Peters E (1930a) Die altsteinzeitliche Kulturstätte Petersfels. Dr. Benno Filser Verlag GmbH, Augsburg

Peters E (1930b) Urgeschichtliche Untersuchungen Im Hegau. Badische Fundberichte 2:121–128

Peters E, Toepfer V (1932) Der Abschluß der Grabungen am Petersfels bei Engen im badischen Hegau. Prähistorische Zeitschrift 23:155–199

Peters E (1936) Eine neue Wildpferdgravierung vom Petersfels im badischen Hegau. Prähistorische Zeitschrift XXVII

Peters E (1946) Meine Tätigkeit im Dienst der Vorgeschichte Südwestdeutschlands. Veringenstadt

Pfeifer SJ (2014) Von Grönland zum Petersfels - Taphonomische Untersuchungen an Rezenten Rentiergeweihen und ihre Relevanz für die Archäologie. Archäologisches Korespondenzblatt 44:11–28

Pfeifer SJ (2016) Die Geweihfunde der Magdalénzeitlichen Station Petersfels. Ein archäologisch-taphonomische Studie. Forschungen und Berichte zur Archäologie in Baden-Württemberg 3. Dr. Ludwig Reichert Verlag, Bonn

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/. Accessed 29 Apr 2025

Rasmussen SO, Bigler M, Blockley SP et al (2014) A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quatern Sci Rev 106:14–28. https://doi.org/10.1016/j.quascirev.2014.09.007

Reade H, Tripp JA, Charlton S et al (2020) Deglacial landscapes and the Late Upper Palaeolithic of Switzerland 1 2. Quatern Sci Rev 239:106372

Reimer PJ, Austin WEN, Bard E et al (2020) The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). Radiocarbon 62:725–757. https://doi.org/10.1017/RDC.2020.41

Reinhard E, de Torres T, O'Neil J (1996) 18O16O ratios of cave bear tooth enamel: a record of climate variability during the Pleistocene. Palaeogeogr Palaeoclimatol Palaeoecol 126:45–59. https://doi.org/10.1016/S0031-0182(96)00069-7

Revelle W (2024) psych: Procedures for Psychological, Psychometric, and Personality Research

Richards MP, Hedges REM (2003) Variations in bone collagen δ13C and δ15N values of fauna from Northwest Europe over the last 40 000 years. Palaeogeogr Palaeoclimatol Palaeoecol 193:261–267. https://doi.org/10.1016/S0031-0182(03)00229-3

Rivals F, Julien M-A, Kuitems M et al (2015) Investigation of equid paleodiet from Schöningen 13 II-4 through dental wear and isotopic analyses: Archaeological implications. J Hum Evol 89:129–137. https://doi.org/10.1016/j.jhevol.2014.04.002

Rivals F, Drucker DG, Weber M-J et al (2020) Dietary traits and habitats of the reindeer (Rangifer tarandus) during the Late Glacial of Northern Europe. Archaeol Anthropol Sci 12:98. https://doi.org/10.1007/s12520-020-01052-y

Robinson JR (2021) Investigating Isotopic Niche Space: Using rKIN for stable isotope studies in archaeology. J Archaeol Method Theory 29:831–861. https://doi.org/10.1007/s10816-021-09541-7

RStudio Team (2024) RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA http://www.rstudio.com/. Accessed 29 Apr 2025

Rudis B (2024) hrbrthemes: Additional Themes, Theme Components and Utilities for "ggplot2"

Saarinen J, Eronen J, Fortelius M et al (2016) Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation. Palaeontologica Electronica 19.3.32A:1–58

Saastamoinen MT, Särkijärvi S (2018) Digestibility of a forage-based diet in weanling horses during development and maturation. Livest Sci 215:49–53. https://doi.org/10.1016/j.livsci.2017.05.018

Schürch B, Wong GL, Luzi E, Conard NJ (2024) Evidence for an earlier Magdalenian presence in the Lone Valley of southwest Germany. J Archaeol Sci Rep 57:104632. https://doi.org/10.1016/j.jasrep.2024.104632

Sharp ZD, Cerling TE (1998) Fossil isotope records of seasonal climate and ecology: Straight from the horse's mouth. Geol 26:219. https://doi.org/10.1130/0091-7613(1998)026<0219:FIROSC>2.3.CO;2

Sommer RS, Nadachowski A (2006) Glacial refugia of mammals in Europe: evidence from fossil records. Mammal Rev 36:251–265. https://doi.org/10.1111/j.1365-2907.2006.00093.x

Sommer RS, Zachos FE (2009) Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. J Biogeogr 36:2013–2020. https://doi.org/10.1111/j.1365-2699.2009.02187.x

Sommer RS, Kalbe J, Ekström J et al (2014) Range dynamics of the reindeer in Europe during the last 25,000 years. J Biogeogr 41:298–306. https://doi.org/10.1111/jbi.12193

Stephan E (1999) Sauerstoffisotopenverhältnisse im Knochengewebe großer terrestrischer Säugetiere Klimaproxies für das Quartär in Mittel- und Westeuropa. PhD Thesis

Stevens RE, Hedges REM (2004) Carbon and nitrogen stable isotope analysis of northwest European horse bone and tooth collagen, 40,000 BP–present: Palaeoclimatic interpretations. Quatern Sci Rev 23:977–991. https://doi.org/10.1016/j.quascirev.2003.06.024

Stevens RE, O'Connell TC, Hedges REM, Street M (2009) Radiocarbon and stable isotope investigations at the Central Rhineland sites of Gönnersdorf and Andernach-Martinsberg, Germany. J Hum Evol 57:131–148. https://doi.org/10.1016/j.jhevol.2009.01.011

Storch G (1983) Die Kleinsäugerreste der Grabung Petersfels 1974–1976. In: Naturwissenschaftliche Untersuchungen an Magdalénien-Inventaren vom Petersfels, Grabungen 1974–1976, pp 128

Street M, Terberger T (1999) The last Pleniglacial and the human settlement of Central Europe: new information from the Rhineland site of Wiesbaden-Igstadt. Antiquity 73:259–272. https://doi.org/10.1017/S0003598X00088232

Sydney-Zax M, Mayer I, Deutsch D (1991) Carbonate content in developing human and bovine enamel. J Dent Res 70:913–916. https://doi.org/10.1177/00220345910700051001

Tafelmaier Y, Beutelspacher T, Toniato G, Vogt R (2022) Wiederentdeckt: die Drexlerhöhle im Brudertal, Arch Ausgr. Baden-Württemberg 2021:89–92

Tafelmaier Y, Bubenzer O, Beutelspacher T, Engel M, Hecht S, Toniato G (2024) Vor verschlossener Tür – Eingang zu Drexlerhöhle und Drexlerloch entdeckt! Arch. Ausgrabungen Baden-Württemberg 2023:75–80

Taller A (2014) Das Magdalénien des Hohle Fels: chronologische Stellung, lithische Technologie und Funktion der Rückenmesser. Kerns Verlag, Tübingen

Taller A, Bolus M, Conard NJ (2014) The Magdalenian of Hohle Fels Cave and the Resettlement of the Swabian Jura after the LGM. In: Otte M, Lebrun-Ricalens F (ed) Modes de contacts et de déplacements au Paléolithique Eurasiatique - Modes of contact and displacements during the Eurasian Palaeolithic, Actes du Colloque international de la commission 8 (Paléolithique supérieur) de l´UISPP, Université de Liège, 28–31 mai 2012, pp 383–402

Tieszen LL (1991) Natural variations in the carbon isotope values of plants: Implications for archaeology, ecology, and paleoecology. J Archaeol Sci 18:227–248. https://doi.org/10.1016/0305-4403(91)90063-U

Trayler RB, Kohn MJ (2017) Tooth enamel maturation reequilibrates oxygen isotope compositions and supports simple sampling methods. Geochim Cosmochim Acta 198:32–47. https://doi.org/10.1016/j.gca.2016.10.023

Vaudo JJ, Heithaus MR (2011) Dietary niche overlap in a nearshore elasmobranch mesopredator community. Mar Ecol Prog Ser 425:247–260. https://doi.org/10.3354/meps08988

Velivetskaya TA, Smirnov NG, Kiyashko SI et al (2016) Resolution-enhanced stable isotope profiles within the complete tooth rows of Late Pleistocene bisons (Middle Urals, Russia) as a record of their individual development and environmental changes. Quatern Int 400:212–226. https://doi.org/10.1016/j.quaint.2014.12.011

von Koenigswald W (2003) Mode and causes for the Pleistocene turnovers in the mammalian fauna of Central Europe. Deinsea 10:305–312

Walter R (2000) Knochennadeln: Archäologischer Befund, Experiment und Museumspräsentation. Magdalénienzeitliche Knochennadeln aus Baden-Württemberg, Experimente zu möglichen Bruchursachen sowie die Präsentation dieser Fundgattung im Rahmen einer Aktion am Urgeschichtlichen Museum Blaubeuren. Magister Thesis, Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters, Tübingen

Wang L, D'Odorico P, Ries L, Macko SA (2010) Patterns and implications of Plant-soil δ13 C and δ15 N values in African savanna ecosystems. Quat Res 73:77–83. https://doi.org/10.1016/j.yqres.2008.11.004

Weinstock J (2000) Late Pleistocene reindeer populations in Western and Middle Europe: An osteometrical study of Rangifer tarandus. BioArchaeologica 3:1–307

Weniger G-C (1982) Wildbeuter und ihre Umwelt: Ein Beitrag zum Magdalénien Südwestdeutschlands aus ökologischer und ethno-archäologischer Sicht. Archaeologica Venatoria, Tübingen

Weniger G-C (1987) Magdalenian Settlement Pattern and Subsistence in Central Europe. In: The Pleistocene Old World. Regional Perspectives, pp 201–215

Weniger G-C (1989) The Magdalenian in Western Central Europe: Settlement Pattern and Regionality. J World Prehist 3(3):323–372

Weninger B, Jöris O (2008) A 14C age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in Western Eurasia. J Hum Evol 55:772–781. https://doi.org/10.1016/j.jhevol.2008.08.017

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York

Wickham H (2023) plyr: Tools for Splitting, Applying and Combining Data

Wiedemann FB (2000) Experimental data on enamel deposition in sheep: Implications for sampling strategies for stable isotope analyses. J Hum Evol 38:A34

Wild M (2020) Coping with risk through seasonal behavioural strategies. Untersuchungen und Materialien zur Steinzeit in Schleswig-Holstein und im Ostseeraum 12:105–180

Wille W (1978) Pollenanalytische Untersuchungen in jungpaläolithischen Höhlensedimenten des Geißenklösterles (Südwest-Deutschland). Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 157:261–265

Wong GL, Drucker DG, Starkovich BM, Conard NJ (2020) Latest Pleistocene paleoenvironmental reconstructions from the Swabian Jura, southwestern Germany: Evidence from stable isotope analysis and micromammal remains. Palaeogeogr Palaeoclimatol Palaeoecol 540:109527. https://doi.org/10.1016/j.palaeo.2019.109527