Crazy like a fox?

How the study of archaeological fox remains can help to understand human behavior in the Late Pleistocene of the Swabian Jura (Germany)

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Abbreviations

General abbreviations

A	Aurignacian	LGM	Last glacial maximum
AH	Archaeological horizon	M	Magdalenian
AMH	Anatomically modern human	MIS	Marine isotope stage
cal BP	Before Present (calibrated)	MNI	Minimum number of Individuals
G	Gravettian	MP	Middle Palaeolithic
G/A	Gravettian/Aurignacian transition	n	Number
GH	Geological horizon	NISP	Number of identified specimens
kyr	Kilo years = 1000 years	Pre-LGM	ime before the last glacial maximum

Archaeological Sites

BH	Brillenhöhle (Ach Valley)	HF	Hohle Fels (Ach Valley)
BS	Bockstein (Lone Valley)	HS	Hohlenstein-Stadel (Lone Valley)
FH	Fetzershaldenhöhle (Lone Valley)	KS	Kogelstein (Ach Valley)
GG	Große Grotte (Ach Valley)	Ksl	Kesslerloch (Hegau Jura)
GK	Geißenklösterle (Ach Valley)	LM	Langmahdhalde (Lone Valley)
Gn	Gnirshöhle (Hegau Jura)	Si	Sirgenstein (Ach Valley)
HA	Helga Abri (Ach Valley)	VH	Vogelherd (Lone Valley)

Indices for fox quantity and Bayesian Statistics

CI	Credibility interval	LH	Large herbivores
fox/LH	Ratio of foxes to large herbivores	lm	Normal linear model
%Fox of Carnivora	Ratio of foxes within the carnivore sub-assemblages	NCT	Niche construction theory
		OFT	Optimal foraging theory
hare/LH	Ratio of hares to large herbivores	r^2	Correlation variable for linear models
HBE	Human behavioral ecology		

Indices for isotopic analysis

$\delta^{13}C$	Stable isotope of carbon	CE Mag	Central European Magdalenian isospace
$\delta^{15}N$	Stable isotope of nitrogen	SJ pre-LGM	Swabian Jura pre-LGM isospace

Zusammenfassung

In vielen Ländern werden seit langer Zeit dem Fuchs Eigenschaften, wie „clever“ und „klug“ sowie in Fabeln ein menschliches Verhalten zugeschrieben. Aber ist es auch clever und klug Füchse zu nutzen, um menschliches Verhalten vor langer Zeit nachzuweisen?

Überreste von Eis- und Rotfüchsen (*Vulpes lagopus* und *Vulpes vulpes*) sind aus fast jeder archäologischen Fundstelle des Spätpleistozäns (ca. 100 000 bis 13 000 Jahre vor heute) in Europa bekannt. Besondere Bedeutung erlangten ihre Eckzähne, welche in den Höhlen der Schwäbischen Alb (Baden-Württemberg, Deutschland) gefunden wurden und aus dem Aurignacien (ca. 42 000 bis 34 000 Jahre vor heute) und dem Gravettien (ca. 34 000 bis 30 000 Jahre vor heute) stammen. Sie wurden von frühen modernen Menschen durchlocht und sehr wahrscheinlich als Anhänger oder Verzierung an der Kleidung getragen. Schnittspuren auf Fuchsknochen zeigen, dass Fell und Fleisch der Tiere ebenfalls verwendet wurden. Mit meiner Doktorarbeit möchte ich hinter die offensichtlichen Spuren schauen und folgenden drei Fragen nachgehen: Wie jagten und nutzten Neandertaler im Mittelpaläolithikum (ca. 100 000 bis 42 000 Jahre vor heute) und moderne Menschen im Jungpaläolithikum (ca. 42 000 bis 14 000 Jahre vor heute) Füchse? Welche Ernährungsstrategien zeigten spätpleistozäne Füchse und wurden jene durch Neandertaler oder moderner Mensch beeinflusst, z.B. durch deren Jagdverhalten? Sind Füchse ein Indikator für die Intensität paläolithischer Besiedlungen und den Einfluss des Menschen auf die spätpleistozäne Umwelt?

Für die Beantwortung dieser Fragen fokussierte ich mich auf die Höhlenfundplätze der zentrale Schwäbische Alb (Ach- und Lonetal) sowie der Hegau Alb, welche am südwestlichen Ende der Schwäbischen Alb liegt. Um meine erste Frage zu erörtern, nutzte ich 26 publizierte, archäozoologischen Auswertungen von zwölf Fundstellen des Ach- und Lonetals und untersuchte die Abundanz der Füchse im Laufe der Zeit mittels Bayesischer Statistik neu. Hierbei fand ich heraus, dass Füchse ab dem Aurignacien stärker im Fundmaterial auftraten und dies auf die Jagd durch modernen Menschen zurückzuführen ist. Für die Jagd wurden sehr wahrscheinlich Fallen genutzt, welche teilweise mit Nahrungsresten beködert, an Wildwechseln in der Umgebung der besiedelten Höhlen platziert wurden. Im Gegensatz dazu sind Füchse aus den mittelpaläolithischen Schichten auf natürliche Weise in die Höhlen gelangt. Die zweite Frage erschloss ich mittels der Analyse stabiler Kohlenstoff- und Stickstoffisotope aus dem Kollagen der archäologischen Fuchsknochen und rekonstruierte sowohl deren Nahrung, als auch die trophischen Nischen. Hierbei konnte ich drei grundlegende Ernährungsstrategien nachweisen, wobei eine durch den Menschen beeinflusst war und die anderen beiden natürliches Verhalten wiederspiegelten. Einige Füchse aus dem Jungpaläolithikum zeigten synanthropes Verhalten, also eine Anpassung an den Menschen und dessen Nahrungsressourcen, und das schon ungefähr 30 000 Jahre vor dem Neolithikum. Zur Bearbeitung meiner letzten Fragestellung, nutzte ich die gewonnenen Erkenntnisse der beiden vorherigen Fragen. Ich konnte dadurch eine positive Korrelation zwischen der Fuchsabundanz und der menschlichen Besiedlungsintensität, sowie dem Auftreten der synanthropen Füchse in Verbindung mit der Populationsdichte der Menschen und dem Jagddruck auf die Megafauna in der Region feststellen. Füchse können somit als Proxy für menschliche Aktivitäten und Besiedlungsdichte genutzt werden. Die opportunistischen Füchse reagierten schon im Jungpaläolithikum auf die, durch menschliches Verhalten beeinflusste Umwelt mit Anpassung ihrer Ernährungsstrategien.

Summary

In many countries and fables, characteristics such as "smart" and "sly" as well as other human-like behavior have been attributed to foxes for a long time. However, is it also smart and sly to invoke foxes to prove human behavior from a long time ago?

Remains of arctic and red foxes (*Vulpes lagopus* and *Vulpes vulpes*) are known from almost every European Late Pleistocene archaeological site (about 100 to 13 kyr ago). Of particular interest in archaeological studies are their canines, found in the cave sites of the Swabian Jura (Baden-Württemberg, Germany), originating from Aurignacian (about 42 to 34 kyr ago) and Gravettian (about 34 to 30 kyr ago). The canines were perforated by early modern humans and most likely worn as pendants or ornaments on clothes. Cut marks on fox bones show that fur and meat were important as well. With my PhD thesis, I would like to explore beyond the obvious evidences the following three questions: How did Neanderthals in the Middle Palaeolithic (about 100 to 42 kyr ago) and modern humans in the Late Palaeolithic (about 42 to 14 kyr ago), hunt and use foxes? Which feeding habits did Late Pleistocene foxes follow and were they influenced by Neanderthals or modern humans, for example by human hunting behavior? Could foxes be used as an indicator of Palaeolithic occupation intensity and human impact on the Late Pleistocene environment?

To answer these questions, I focused on the cave sites of the central Swabian Jura (Ach- and Lonetal) and the Hegau Jura, located at the southwestern edge of the Swabian Jura. To discuss my first question, I used 26 published zooarchaeological reports from twelve sites in the Ach- and Lonetal and re-examined the abundance of foxes over time using Bayesian statistics. I found out that foxes were more abundant in the archaeological record from the Aurignacian period onwards and that this was due to hunting activities by modern humans. Traps were likely used for hunting foxes, some of them baited with food leftovers and set at game passes in the vicinity of the inhabited caves. In contrast, foxes from the Middle Palaeolithic layers entered the caves naturally. To answer my second question, I used the analysis of stable carbon and nitrogen isotopes from the collagen of archaeological fox bones and reconstructed both the diet and the trophic niches. Thereby I could prove three basic feeding behaviors, one of them was influenced by humans. Some foxes from the Upper Palaeolithic showed synanthropic behavior, i.e. an adaptation to humans and their food resources, and this already about 30,000 years before the Neolithic. To address my last question, I used the knowledge gained from the previous two questions. This allowed me to establish a positive correlation between the abundance of foxes and the intensity of human settlement, as well as the occurrence of synanthropic foxes with the human population density and the hunting pressure on the megafauna in that region. Foxes can thus be used as a proxy for human activities and population density. The opportunistic foxes reacted to the environment influenced by human behavior by adapting their feeding strategies already in the early Palaeolithic periods.

Danksagung

Eine Dissertation anzufertigen und dies auch noch in angebrachter Zeit zu beenden, hängt nicht nur vom Doktoranden selbst ab. Es sind viele Menschen nötig, die ihn unterstützen, an ihn glauben und letztendlich auch dafür sorgen, dass er mal Abstand zur Promotion gewinnt, um sich nicht in Details zu verrennen und das große Ganze aus den Augen zu verlieren. Genau bei diesen Menschen möchte ich mich hiermit bedanken!

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Ceterum censeo meum cattum esse confitendum.

List of Publications

Publication 1: **Baumann, C.**, Wong, G.L., Starkovich, B.M., Münzel, S.C. & Conard, N.J.(**2020**): The role of foxes in the Upper Palaeolithic economies of the Swabian Jura (Germany). Archaeological and Anthropological Sciences 12 (208). DOI: 10.1007/s12520-020-01173-4.

Publication 2: **Baumann, C.**, Bocherens, H., Drucker, D.G. & Conard, N.J. (**2020**): Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems. PLoS ONE 15(7):,e0235692. DOI: 10.1371/journal.pone.0235692.

Publication 3: **Baumann, C.,** Starkovich, B.M., Drucker, D.G., Münzel, S.C., Conard, N.J. & Bocherens, H. (**2020**): Dietary niche partitioning among Magdalenian canids in southwestern Germany and Switzerland. Quaternary Science Reviews 227, 106032. DOI: 10.1016/j.quascirev.2019.106032.

Personal Contribution

Publication 1: I was the first and corresponding author, as well as the main person responsible for conceiving the study design, conducting the reported research, and lead author of writing the manuscript. The coauthors helped to analyze faunal data from Langmahdhalde (Gillian L. Wong) and Helge Abri (Susanne C. Münzel). Furthermore, they helped in writing the manuscript and gave editorial input (Gillian L. Wong, Britt M. Starkovich, Susanne C. Münzel, Nicholas J. Conard), and oversaw the study as supervisor (Nicholas J. Conard).

Publication 2: I was the first and corresponding author, as well as the main person responsible for conceiving the study design, conducting the reported research and lab work, and lead author of writing the manuscript. The coauthors helped in writing the manuscript and gave editorial input (Hervé Bocherens, Dorotée G. Drucker, Nicholas J. Conard), and oversaw the study as supervisor (Hervé Bocherens, Nicholas J. Conard).

Publication 3: I was the first and corresponding author, as well as the main person responsible for conceiving the study design, conducting the reported research and lab work, and lead author of writing the manuscript. The coauthors helped with interpreting isotopic (Hervé Bocherens, Dorothée G. Drucker) and zooarchaeological results (Britt M. Starkovich, Susanne C. Münzel), with writing the manuscript and gave editorial input (Hervé Bocherens, Dorotée G. Drucker, Britt M. Starkovich, Susanne C. Münzel, Nicholas J. Conard), and oversaw the study as supervisor (Hervé Bocherens, Nicholas J. Conard).

1. Introduction

1.1. The European Late Pleistocene ecosystem

The Late Pleistocene is the glacial period following the Eemian interglacial (Dahl-Jensen et al., 2013) and ends after the Younger Dryas (Walker et al., 2018). Concerning marine isotope stages, it is dated between MIS 5 and MIS 1, approximately 110 kyr to 11.7 kyr before today (Lisiecki and Raymo, 2005).

The global cooling at the end of the Eemian Interglacial (MIS 5e) had substantial effects on Europe. In the beginning, there were cool summers and mild winters with high precipitation, which favored a steady growth of the Alpine and Scandinavian glaciers, as they did not melt in summer (Ahn and Brook, 2008; Clement and Peterson, 2008). This process triggered a chain reaction, as the surface of the white glaciers reflected the sunlight and thus led to a faster cooling, which in turn caused the glaciers to grow into kilometer-thick masses of ice. At their maximum extension, the Last Glacial Maximum (LGM), dated between 26 to 20 kyr ago (based on sea-levels; Clark et al., 2009), the Alpine glaciers reached as far as the Danube and, together with the Scandinavian glaciers, bound enough water to lower the sea level by up to 120 m (Lisiecki and Raymo, 2005). Due to the lack of heat radiation from sunlight, and the lower evaporation on the global water surface, the precipitation in continental areas decreased drastically (Ahn and Brook, 2008). The low temperature caused the ground to freeze and permafrost soils to form, which only thawed superficially in summer. However, the climate was not consistently cold and dry; instead, there were climate fluctuations during the millennia, the so-called stadials and interstadials, which were recorded by ice cores and deep-sea core samples (Ahn and Brook, 2008; Clark et al., 2009). Stadials are colder phases in which glacial advances occurred, and inter-stadials are short-term warmer phases during which glaciers retreated. Furthermore, the local temperature and environmental conditions could also vary to some extent from the general continental pattern, as I will show for the Swabian Jura in chapter 1.2.1.

However, the climatic factors have created a unique, though not wholly uniform, continental biome in the northern hemisphere, which extended from Spain to Canada and from the Arctic islands to China (Adams et al., 1990; Guthrie, 1990; Guthrie, 2001; Schwartz-Narbonne et al., 2019; Zimov et al., 2012): the mammoth steppe.

1.1.1. The mammoth steppe biome

The Pleistocene mammoth steppe formed about 460 kyr ago during MIS 12 (Kahlke, 2014; Kahlke and Lacombat, 2008) and represented the largest continuous continental ecosystem on earth. This ecosystem is named after the mammoth (*Mammuthus trogontherii*, the steppe mammoth in the Middle Pleistocene and *Mammuthus primigenius*, the wooly mammoth in the Late Pleistocene) representing the continental megafauna which characterized this biome.

In general, the Late Pleistocene landscape is considered a mixture of cold steppe and tundra elements, without an equivalent comparison today (Bocherens, 2003; Guthrie, 1990; Guthrie, 2001). The climate was continental and, since a high amount of water was bound in the glaciers, hardly any clouds could form, resulting in sunny, comfortably warm daytime temperatures, but also ice-cold, star-blue nights (Guthrie, 2001). However, this environment was not as harsh as it sounds at first.

Although the faunal biodiversity of this biome was not as high as in interglacial ecosystems (Guthrie, 1990; Guthrie, 1982; Kahlke, 2014; Zimov et al., 2012), the productivity of the plants and animals in the mammoth steppe was very high (Bocherens, 2003; Schwartz-Narbonne et al., 2019; Zimov et al., 2012), demonstrated by generally higher nitrogen (δ^{15}N) isotope values compared to other ecosystems. Zimov et al. (2012) even assume similar high productivity of mammoth steppe organisms as in modern African savannas. One reason for this may be the behavior of the megafauna, which promoted rapid plant growth by trampling and grazing and fertilizing with feces and urine (Guthrie, 1982; Willerslev et al., 2014; Zimov et al., 2012).

While most pollen studies assume a low floral diversity for the mammoth steppe (Anderson et al., 2003; Murray, 1995), DNA data from permafrost show more diversity (Willerslev et al., 2014). The flora of the mammoth steppe biome, called herb-steppe-tundra flora (Bocherens, 2003; Guthrie, 1982, 2001; Schwartz-Narbonne et al., 2019), was a mosaic of dry steppe species and tundra elements adapted to dry habitats, saline soils, moist and rocky habitats with plant communities dominated by grasses, sedges, forbs and herbaceous species (Willerslev et al., 2014). Small forests dominated by willows and shrubs were partially present as well. As with the climate, regional differences during the Late Pleistocene are evident, and the Swabian Jura's local variations are explained in chapter 1.2.1. Only after the end of the LGM did the biome change and plants of the dry steppe became rarer, while plants of the humid tundra increased (Willerslev et al., 2014).

As with plants, the fauna of the mammoth steppe, the so-called *Mammuthus-Coelodonta* faunal complex (Kahlke, 2014), consisted of two groups; on the one hand, animals were originating from the Central Asian steppes and, on the other hand, from the Arctic tundra. Kahlke (2014) describes that in the glacial period of MIS 12, about 460 kyr ago, both species complexes joined for the first time and formed the earliest *Mammuthus-Coelodonta* faunal complex. During the Holstein (MIS 11) and Eemian (MIS 5e) interglacials, the mammoth steppe biome collapsed and the fauna was forced back to *refugia* in the continental steppes of Asia and the Arctic region (Kahlke, 2014; Kahlke and Lacombat, 2008). Finally, in the Late Pleistocene, a new and more developed *Mammuthus-Coelodonta* faunal complex appeared.

Typical herbivores from the Asian continental steppes were saiga antelope (*Saiga tatarica*), steppe bison (*Bison priscus*), and woolly rhinoceros (*Coelodonta antiquitatis*) (Boeskorov et al., 2014; Kahlke, 2014; Markova et al., 2015). According to Kahlke (2014), muskox (*Ovibos moschatus*), reindeer (*Rangifer tarandus*), and woolly mammoth (*Mammuthus primigenius*) originated from the Arctic region. Horses (*Equus ferus*) originally came from the continental regions of North America and migrated via Beringia to Asia and Europe (Boulbes and van Asperen, 2020), integrating into the mammoth steppe fauna. Other animals, such as woolly mammoth, reindeer, bison, and muskox, also migrated via Beringia and reached North America (Guthrie, 1968, 2001; Kahlke, 2014, 2015; Mann et al., 2013; Zimov et al., 2012). However, this did not lead to an equality of the mammoth steppe fauna between North America, Europe, and Asia. Individual species, such as the American mastodon (*Mammut americanum*) never reached Asia or Europe (Guthrie, 2001), while animals such as the woolly rhinoceros and the cave bears (*Ursus spelaeus* and *Ursus ingressus*) were restricted to Europe (Gretzinger et al., 2019; Guthrie, 2001; Kahlke, 2014; Knapp, 2019).

The most prominent representatives of the Late Pleistocene mammoth steppe carnivore guild are cave lion (*Panthera leo spelaea*), cave hyena (*Crocuta crocuta spelaea*) and brown bear (*Ursus arctos*), which originated in the continental steppes of Asia (McLellan and Reiner, 1994; Rohland et al., 2005; Stuart and Lister, 2011), while wolf (*Canis lupus*) and wolverine (*Gulo gulo*) came from the Arctic tundra of Beringia (Tedford et al., 2009; Tomasik and Cook, 2005). The Arctic fox (*Vulpes lagopus*) seems to come from continental steppes too (Wang et al., 2014), although it is still under debate (Kahlke, 2014). Red fox (*Vulpes vulpes*) originated in Europe and is so adaptable that it found its niche in both, glacial and interglacial periods. More information about foxes in chapter 1.3 and chapter 3.2.3.

1.1.2. When Neanderthals and modern humans met

Besides the Late Pleistocene predators of the order Carnivora, two other hunters of the order Primates emerged in the mammoth steppe biome: Neanderthal, *Homo neanderthalensis*, and anatomically modern human (AMH), *Homo sapiens*.

Neanderthals developed in the Middle Pleistocene from European *Homo heidelbergensis* populations (Hublin, 1988, 2009; Meyer et al., 2016) and were named after the valley where the first of its kind had been found and described in 1856: the Neandertal near Düsseldorf in Germany (Schaaffhausen, 1858). Most of Neanderthal remains have been recorded from the Eemian period onwards (Klein, 1983). This leads to a lively discussion about how and where Neanderthals developed. Churchill (2014) assumes an anagenetic origin, which potentially took place in Israel (Churchill, 2014; Grün and Stringer, 2000; Trinkaus, 1988) while maintaining a gene flow with European groups. The hypotheses of Hublin (1988, 2009) and Serangeli and Bolus (2008) are in contrast to this, suggesting the evolution of the Neanderthal phenotype in Europe. The distribution of Neanderthals extended from Western, Central, and Eastern Europe to the Mediterranean and from Southwestern, Central, and Northern Asia to the Altai Mountains (Klein, 1983; Serangeli and Bolus, 2008). For further information on Neanderthal's occupation of the Swabian Jura, see chapter 1.2.2.

Neanderthals probably lived in sparsely distributed groups with an average size of 10 to 30 individuals (Bocquet-Appel and Degioanni, 2013; Duveau et al., 2019; Hayden, 2012; Rosas et al., 2013). The most reliable evidence for group size and structure was found in Sidrón Cave in Spain, where a group consisting of seven adults, three adolescents, two children, and one infant were identified by teeth (Rosas et al., 2013). Furthermore, the footprints of Le Rozel from France show a group of 10 to 13 members, which consisted primarily of adolescents (Duveau et al., 2019).

The picture, created at the beginning of the last century about the Neanderthal as a barbarian ape, is long outdated (Papagianni and Morse, 2015). More and more archaeological finds are testifying to the social and cultural features of our Pleistocene relatives. The lithic technology of Neanderthals, the Levallois core reduction technology (Delagnes et al., 2007), is considered to be quite developed (Hoffecker, 2018; Lycett and von Cramon-Taubadel, 2013). It includes the Middle Palaeolithic toolsets of Micoquian, Mousterian, and Châtelperronian (Bordes and Teyssandier, 2011; Kozłowski, 2014; Richter, 2012; Rosendahl, 2011; Ruebens, 2007). Furthermore, Neanderthals used fire (Brittingham et al., 2019; Sorensen et al., 2018) and built cave hearths (Kedar and Barkai, 2019) to roast and smoke food (Hardy et al., 2012; Krief et al., 2015).

They could make simple clothes (Collard et al., 2016; Hardy et al., 2013a; Wales, 2012) and birch pitch (Schmidt et al., 2019), extract medicine from plants (Bergmann, 2018; Hardy et al., 2012; Hardy et al., 2013b; Weyrich et al., 2017) and heal serious injuries (Kent, 2016; Nakahashi, 2017; Spikins et al., 2018; Spikins et al., 2019). Neanderthals even crossed the Mediterranean Sea (Ferentinos et al., 2012; Strasser et al., 2011), which requires a safe boat or raft and navigation. However, whether they also created art is highly controversial debate, as the Iberian cave paintings (Aubert et al., 2018; Finlayson, 2019; Hoffmann et al., 2018a; Hoffmann et al., 2018b; Slimak et al., 2018; Than, 2012) and the Slovenian Divje Babe flute show (d'Errico et al., 1998; Kunej and Turk, 2000; Morley, 2006; Tuniz et al., 2012; Turk and Košir, 2017; Turk et al., 2018). Nevertheless, the use of red ochre, which could also be used for tanning skin, and manganese dioxide were confirmed (Duarte, 2014; Heyes et al., 2016; Roebroeks et al., 2012). Besides, the use of feathers could be proven in several studies (Finlayson et al., 2012; Garofoli, 2017; Negro et al., 2016; Peresani et al., 2011; Wood, 2019), possible for hunting weapons and ornaments. Furthermore, worked bird bones, such as from raven and eagle, were found in Neanderthal sites and were mentioned as possible ornaments (Majkić et al., 2017; Radovčić et al., 2015).

In the Late Pleistocene mammoth steppe, Neanderthals primarily hunted large herbivores such as woolly rhinoceros, mammoth, reindeer or ibex (Bocherens, 2009; Bocherens et al., 2005b; Bocherens et al., 1991; Churchill, 2014; Dusseldorp, 2013; Jaouen et al., 2019; Niven, 2006; Weyrich et al., 2017; Wißing et al., 2019; Wißing et al., 2016). In some cases, even cave bears and brown bears were identified as prey (Romandini et al., 2018). There is increasing evidence that Neanderthals included plants and mushrooms in their diet (Hardy and Moncel, 2011; Hardy et al., 2012; Henry et al., 2011; Krief et al., 2015; Madella et al., 2002; Shipley and Kindscher, 2016; Weyrich et al., 2017; Wroth et al., 2019), or used aquatic resources. The latter were mainly found in coastal Mediterranean sites (Brown et al., 2011; Cortés-Sánchez et al., 2011; Hardy et al., 2013a; Stringer et al., 2008; Villa et al., 2020; Zilhão et al., 2020) where Neanderthals hunted marine mammals, went fishing or collected mussels and crabs. However, there is evidence of the use of freshwater fish such as eel, salmon, trout, chub or perch in archaeological sites from France, Italy, Portugal and Russia as well (Bocherens et al., 2014; Hardy and Moncel, 2011; Hardy et al., 2013a; Zilhão et al., 2020).

Between 41 and 39 kyr before present, Neanderthal's success story has ended (Agustí and Rubio-Campillo, 2017; Higham, 2011; Higham et al., 2014; Hublin, 2017; Pinhasi et al., 2011; Pleurdeau et al., 2016). By this time, *Homo sapiens* (AMH) reached Europe (Benazzi et al., 2011; Finlayson and Carrion, 2007; Higham et al., 2012; Higham et al., 2011; Wißing et al., 2019) and archaeological findings associated with Neanderthals became increasingly rare. There are many hypotheses about how the Neanderthal finally became extinct. Until the end of the last century, hypotheses of conscious extinction via violent conflict were most common (Boule, 1920; Dart, 1953; Diamond, 1991; Jones, 1962; Langdon, 2016; Zilhão, 2001). However, evidence for these hypotheses is scarce. Only one case so far from Les Rois Cave, (France) is known, where cut marks on a Neanderthal mandible can be linked to Aurignacian AMHs (Rozzi et al., 2009). Other hypotheses suggest that indirect competition for equal dietary resources and habitat increased with AMHs (Adler et al., 2006; Banks et al., 2008; Drucker et al., 2017; El Zaatari et al., 2016; Finlayson and Carrion, 2007; Roebroeks, 2006; Villa and Roebroeks, 2014; Wißing et al., 2019). The domestication of wolves may have led to a better hunting success of AMHs as well (Shipman, 2015).

However, these hypotheses are not without controversy, since e.g., in the Swabian Jura no direct contacts could be proven (Conard et al., 2006) and the AMHs found a Neanderthal-free environment (see chapter 1.2.2). The domestication of wolves was not simultaneous with the disappearance of the Neanderthals, but only thousands of years later (Germonpré et al., 2018; Larson et al., 2012; Ovodov et al., 2011; Thalmann and Perri, 2018; Wayne et al., 2006). A further hypothesis refers to the climate decrease, which occurred about 40 kyr ago (El Zaatari et al., 2016; Staubwasser et al., 2018). Due to poor clothing and lack of insulation, Neanderthals were therefore probably not equipped for these temperatures (Bradtmöller et al., 2012; Collard et al., 2016; Staubwasser et al., 2018). Also, diseases introduced by AMHs are suspected to have made life difficult for Neanderthals (Sullivan et al., 2017; Underdown, 2008). Neanderthals were probably forced into isolated populations and may have succumbed to inbreeding, low genetic diversity, disease, and climate change (Degioanni et al., 2019; Ríos et al., 2019). However, genetic studies also show that Neanderthals and AMHs were able to coexist, interbreed and even produce fertile offspring (Green et al., 2010; Kuhlwilm et al., 2016; Sankararaman et al., 2012).

With the disappearance of the Neanderthals and the appearance of AMHs in Europe, the Upper Palaeolithic began, including the archaeological periods Aurignacian, Gravettian, Solutrean, and Magdalenian in western Europe. Genetic studies suggest that *Homo sapiens* evolved from *Homo erectus* populations in Africa about 500 kyr ago (Neubauer et al., 2018; Scerri et al., 2018). However, the oldest fossil remains of AMH dated to about 300 - 200 kyr ago and were found in Morocco, South Africa, and Ethiopia (Hublin et al., 2017; Scerri et al., 2018; Stringer, 2016). For the question of how the AMH came to Europe, there are also different hypotheses in which the Swabian Jura plays a central role (see chapter 1.2.2).

Population densities and group sizes of AMHs in the Aurignacian depended strongly on the regions they occupied. In more densely populated core regions, such as in Belgium or the Swabian Jura, population densities of 3 persons per 100 km² and group sizes of about 40 to 50 persons could be calculated (Schmidt and Zimmermann, 2019). For the early Gravettian (33,000 to 29,000 calBP), a population density of 1.4 persons per 100 km² on average was calculated in the occupied regions, such as southwestern France, while in the late Gravettian (29,000 to 25,000 calBP) the population density decreases dramatically to an average of 0.8 persons per 100 km² (Maier, 2017; Maier and Zimmermann, 2017). During the following Solutrean, the archaeological period during the LGM, which is only found in the ice-free regions from France, Spain and Portugal (Aura et al., 2012; Davidson, 1974; Smith, 1964), the population density rose again to the early Gravettian value of 1.4 persons per 100 km² on average (Maier, 2017). An even stronger increase in population density is observed in the Magdalenian, where it was calculated to between 1.6 and 3.6 persons per 100 km² in the occupied areas (Kretschmer, 2015; Maier, 2017).

The main prey of AMHs was similar to that of Neanderthals: large herbivores (Bocherens et al., 2015; Discamps et al., 2011; Drucker et al., 2017; Meadows et al., 2019; Münzel et al., 2017; Wilczyński et al., 2015; Wißing et al., 2019; Wojtal and Wilczyński, 2015a; Wojtal and Wilczyński, 2015b). Especially, mammoths played an important role for AMHs, as bones and ivory were used as construction material (Furrer et al., 2007; Münzel et al., 2017; Niven, 2007; Pidoplichko, 1998; Zozlowski et al., 1974), as raw material for tools (Münzel, 2001; Münzel et al., 2017) and for the first figurines (Conard, 2003b, 2009; Hahn, 1970, 1986; Wehrberger, 2007), ornaments (Wolf, 2015; Wolf and Conard, 2015) and music instruments (Conard et al., 2009). Reindeer antlers were used as raw material for tools as well (Tejero, 2014; Tejero and Grimaldi, 2015; Tejero et al., 2016).

From a zooarchaeological point of view, reindeer was a main prey of the Upper Paleolithic hunter-gatherers (Mellars, 2004; Niven, 2006, 2007; Weinstock, 2002), but could not be identified as the main diet by isotope studies until now (Bocherens et al., 2015; Drucker et al., 2017; Wißing et al., 2019). The domestication of wolves, probably started in the Gravettian (Germonpré et al., 2015; Germonpré et al., 2012; Germonpré et al., 2018; Germonpré et al., 2016; Germonpré et al., 2013; Germonpré et al., 2009; Morey, 2014; Morey and Jeger, 2017; Ovodov et al., 2011; Thalmann and Perri, 2018; Thalmann et al., 2013), although the dating is not accepted by all scientists (Crockford and Kuzmin, 2012; Morey, 2014; Perri, 2016), and may have improved the success of big game hunting (Lupo, 2017; Morey and Jeger, 2015, 2017; Ruusila and Pesonen, 2004; Shipman, 2015). As a result of higher population density, larger group sizes and better hunting techniques of AMHs, compared to Neanderthals, hunting pressure on large game such as mammoths increased during the Upper Palaeolithic (Drucker et al., 2015; Stiner, 2009; Stiner et al., 1999; Wißing et al., 2019). In addition, climate degradation in the Aurignacian and Gravettian was added to this and led to massive declines in the populations of the main prey animals (see chapter 1.1.3).

As a consequence, people had to switch to small game and develop techniques to hunt it effectively (Stiner et al., 2000). The transition from Middle to Upper Palaeolithic is often interpreted as a change in human hunting behavior and an expansion of the food spectrum (Romandini et al., 2019; Starkovich, 2012, 2014; Stiner, 2009; Stiner et al., 2000; Stiner et al., 1999). Although recent studies suggest that Neanderthals had a broad diet (Droke et al., 2020; Henry et al., 2011; Weyrich et al., 2017; Wißing et al., 2019; Wißing et al., 2016; Wroth et al., 2019; Yravedra et al., 2019), many sites in Europe and the Middle East have rapid increases in faunal diversity from their Middle to Upper Palaeolithic layers (Conard et al., 2013a; Starkovich, 2012, 2014; Stiner, 2009; Stiner et al., 2000). Stiner et al. (2000) explained this phenomenon with the broad-spectrum revolution hypothesis formulated by Flannery (1969) and influenced by Binford (1968). While during the Middle Palaeolithic, Neanderthals collected and ate easy to access animals such as mussels, turtles or crabs and frequently plants, AMHs had to switch to new food resources due to their higher population density and the low main prey (high-ranked prey) density (Stiner, 2009; Stiner, 2001; Stiner et al., 2000; Stiner et al., 1999). This argumentation is based on optimal foraging theory by Charnov (1976) (more details in chapter 3.2.1). Such new food resources primarily include fast small game, such as hares, rabbits, fish, or ptarmigans, which occur in larger populations and have a high reproductive rate (Stiner et al., 2000; Stiner et al., 1999). In brief, a dietary resource which is regularly self-renewing and constantly available. However, the exploitation of these new resources requires technical innovations, such as trapping (Conard et al., 2013a; Stiner et al., 2000; Stiner et al., 1999). Additionally, Kuhn et al. (2006) pointed out that the exploitation of small game correlates with the gendered division of labor. For further information on small game exploitation in the Swabian Jura, see chapter 1.2.3.

1.1.3. Late Pleistocene ecosystem collapse and the beginning of the Anthropocene

With the increasing global warming, starting with the end of the Magdalenian, not only the Upper Palaeolithic and the Pleistocene ended, but also the mammoth steppe biome disappeared forever (Guthrie, 1982; Kahlke, 2015; Schwartz-Narbonne et al., 2019). Suitable *refugia*, as they were available during the last interglacial, the Eemian, existed even longer, but did not host any megafauna at all. The last mammoths found refuge on Alaskan St. Pauls Island (Crossen et al., 2005; Graham et al., 2016; Guthrie, 2004; Yesner et al., 2005) and Siberian Wrangel Island (Stuart et al., 2004; Vartanyan et al., 1995; Vartanyan et al., 1993), where they became extinct 5,600 years ago and 4,000 years ago respectively due to inbreeding (Nyström et al., 2010; Nyström et al., 2012; Palkopoulou et al., 2015; Rogers and Slatkin, 2017) or a catastrophic environmental event (Arppe et al., 2019). The last mammoth on the Eurasian mainland became extinct about 9,600 years ago on the Siberian Kyttyk Peninsula (Stuart et al., 2004; Stuart et al., 2002), whereas most mammoths disappeared between 14 and 10 kyr before today (Kahlke, 2015). During the same time range, most of the other European megafauna, such as giant deer, woolly rhinoceros, steppe bison or cave lion got extinct as well (Hughes et al., 2006; Immel et al., 2015; Kuzmin, 2010; Stuart and Lister, 2011). Cave bears and cave hyena became extinct before the end of the glacial period (Baca et al., 2016; Pacher and Stuart, 2009; Rohland et al., 2005; Varela et al., 2010). This extinctions happened not only in Europe but worldwide (Barnosky et al., 2004; Barnosky and Lindsey, 2010; Faith and Surovell, 2009; Gill et al., 2009; Krantz, 1970; Louys et al., 2007; Mann et al., 2013; Miller et al., 1999; Roberts et al., 2001), even if not completely simultaneously, leading to two main hypotheses of Late Pleistocene megafauna extinction (Brook and Bowman, 2002).

The first hypothesis justifies the worldwide extinction of the glacial megafauna with the abrupt climate change at the end of the Magdalenian (Barnosky et al., 2004; Barnosky and Lindsey, 2010; Carotenuto et al., 2018; Cooper et al., 2015; Doughty et al., 2010; Řičánková et al., 2018), probably driven by cosmic impact (Firestone et al., 2006; Sokeland, 2017). According to this hypothesis, the megafauna could not adapt well enough to the warming conditions and became extinct. Body size plays an important role since adaptations for better thermoregulation of the Pleistocene megafauna only worked in cold regions (Bergmann, 1847). The study of Smith et al. (2018) showed, in contrast, that an adaptation of body size would have been possible since this has already happened in other surviving mammals. However, the main criticism is that in Holstein and Eemian interglacials, the megafauna of the first mammoth steppe biome, the earliest *Mammuthus-Coelodonta* faunal complex, found refuge and could thus survive in Asian continental steppes and Arctic tundra for thousands of years (Kahlke, 2014). The same refuge habitats existed until the Holocene and partly even until today, and thus a further existence of those cold-adapted animals would have been possible, as it can be seen for example in reindeer, saiga antelopes, and horses.

The second hypothesis, the so-called "overkill“ hypothesis, formulated by Martin and Wright (1967), identifies human hunting activities as the cause of mass extinction (Alroy, 2001; Barnosky and Lindsey, 2010; Bartlett et al., 2016; Brook and Bowman, 2002; Brook and Johnson, 2006; Bulte et al., 2006; Choquenot and Bowman, 1998; Doughty et al., 2010; Grayson, 1977; Krantz, 1970; Louys et al., 2007; Meltzer, 2015; Miller et al., 1999; Mosimann and Martin, 1975; Roberts et al., 2001; Sandom et al., 2014; Surovell et al., 2016; Wroe et al., 2004). The occurrence of humans in North America, South America, Southeast Asia, or Australia correlated each time with the extinction of the megafauna. This hypothesis is criticized primarily for the European megafauna (Barnosky et al., 2004; Carotenuto et al., 2018; Řičánková et al., 2018), as this coexisted with Neanderthal and AMH for thousands of years. Nevertheless, humans, especially the AMH, cannot be taken out of responsibility (Haynes, 2018; Kitagawa et al., 2012; Lorenzen et al., 2011; Münzel and Conard, 2004a; Pacher and Stuart, 2009; Stiller et al., 2010; Stiner, 1999). For example, isotopic studies showed that the mammoth was locally over-hunted during the Aurignacian (Wißing et al., 2019) and the Gravettian (Drucker et al., 2015; Münzel et al., 2017). Climatic stress and human hunting pressure ultimately led to a sustainable decline in megafauna populations (Barnosky et al., 2004; Brook and Bowman, 2002; Haynes, 2018; Řičánková et al., 2018). Due to lower reproduction rates of megafauna compared to other herbivores, the populations thinned out more and more until they finally became extinct. The elimination of large prey animals triggered an ecological chain reaction and decimated the obligatory carnivores, such as cave lions (Stuart and Lister, 2011). Opportunistic predators such as wolves and foxes, however, found new niches and survived the mass extinction (Leonard et al., 2007; Szuma and Germonpré, 2019, 2020).

Doughty et al. (2010) even blame humans for having ultimately driven climate change by overhunting and exterminating the Late Pleistocene megafauna. This statement attributes Upper Palaeolithic humans great power over their environment and leads to the discussion of when the Anthropocene, the age of humans, began. The Anthropocene is the name suggested for the geological epoch, characterized by considerable human influences on geology, ecosystems, and climate (Crutzen, 2002, 2006, 2016; Crutzen and Stoermer, 2000; Ellis and Ellis, 2018; Lewis and Maslin, 2015; Ruddiman, 2013). The term was popularized by Crutzen and Stoermer (2000), who considered the influence of human behavior on earth's atmosphere over the past centuries to be so significant that it represents a new geological epoch. However, he was not the first scientist who talked about the human age. Already Haughton (1865) mentioned the Anthropozoic as the epoch in which we are living and Stoppani (1873) recognized the increasing influence of humans on earth’s geological systems and spoke of an "anthropozoic" age as well. Only about 130 years later the term was picked up again and controversially discussed by many scientists (Baker, 2014; Bird et al., 2016; Crutzen, 2006, 2016; Dirzo et al., 2014; Dürbeck and Hüpkes, 2020; Edgeworth et al., 2019; Ellis and Ellis, 2018; Laurance, 2019; Lewis and Maslin, 2015; Malm and Hornborg, 2014; Ruddiman, 2013; Smith and Zeder, 2013; Waters et al., 2016; Winfried et al., 2004). The most controversial issue was the dating of the beginning.

Initially, the starting point of the Anthropocene was discussed to be set at the middle of the 20th century (Crutzen, 2002, 2006; Crutzen and Stoermer, 2000), since among other things, the use of atomic energy changed the environment and atmosphere of the planet in a lasting way. Other important social, ecological and economic events, such as the industrial revolution, the colonization of America, or the beginning of the final phase of the Holocene, about 2000 years ago, were also discussed as potential starting points (Lewis and Maslin, 2015; Smith and Zeder, 2013). However, the “early Anthropocene” hypothesis by Ruddiman (2003) even dates the start to the beginning of the Neolithic. During this period, humans changed the existing biomes by cultivation and domestication (Bird et al., 2016; Certini and Scalenghe, 2015; Lewis and Maslin, 2015; Ruddiman, 2003, 2013; Smith and Zeder, 2013). With the construction of the first cities, humans created their own micro-ecosystem, influencing other organisms (Hulme-Beaman et al., 2016; O'Connor, 2013), such as commensal rodents (O'Connor, 2013; Tangri and Wyncoll, 1989), which benefited from these new niches. Some researchers even go one step further and consider starting the Anthropocene already during the Late Pleistocene (Doughty et al., 2010; Haynes, 2018). This step is justified by the extensive ecological change at the end of the Pleistocene: the extinction of the megafauna. The sustainable influence of humans on the environment was thus already present before the Neolithic and justifies the predating of the Anthropocene into the late Upper Palaeolithic.

1.2. The occupation of the Swabian Jura

The Swabian Jura (Fig. 1) is an approx. 180 km long German low mountain range, which stretches from Bavaria (Franconian Jura) in the north-east, through Baden-Württemberg to the Swiss canton of Schaffhausen (Hegau Jura) in the south-west (Binder and Jantschke, 2003). The predominant rock is the White Jura (Bloos et al., 2006), a limestone formation consisting of remains of marine life, which was deposited at the end of the Jurassic period, about 150 million years ago, at the bottom of a tropical sea. In the Cretaceous period, about 60 to 70 million years ago, the Swabian Jura rose above the sea surface due to tectonic disturbances. From this time on, the beginning of the karstification of the White Jura is assumed (Conard et al., 2015a). For millions of years, acidic water was able to penetrate through cracks in the limestone and thus create an underground river system. This also created extensive cave systems for which the region is known today (Conard et al., 2015a).

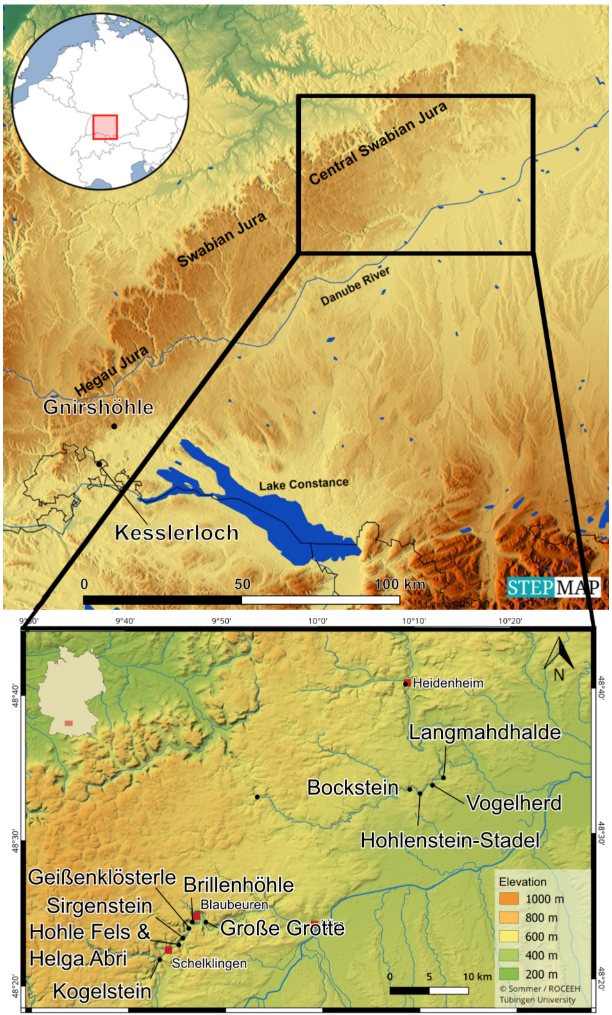

***Fig. 1:** Map of the archaeological sites included in the present thesis. Originally published in Baumann et al. (2020) and https://doi.org/10.5281/zenodo.3460300 (CC BY 4.0 license), modified by C. Baumann.*

The Swabian Jura first became interesting for archaeological studies of the Late Pleistocene (Fig. 2). Especially the cave sites of the Ach and Lone valleys have been the focus of research for decades. Archaeological remains, especially lithic tools and worked faunal remains, indicate a Middle Palaeolithic (MP) settlement of the region by Neanderthals (from early to middle Würm Glacial and older than 42 kyr (Conard and Bolus, 2008; Richards, 2019; Richter et al., 2000)). Subsequent layers, dated from 42 kyr to 34 kyr cal BP, showed the presence of the Aurignacian in both valleys (Conard and Bolus, 2003, 2008; Hahn, 1982; Higham et al., 2012). The Gravettian (34 to 30 kyr cal BP (Conard and Bolus, 2008; Housley et al., 1997; Taller and Conard, 2019)) is primarily recorded in the Ach Valley, although individual layers from the Lone Valley have been dated to this period as well (Conard et al., 2015b; Lykoudi, 2017). Between 30 kyr and 16 kyr cal BP, there is a hiatus in both valleys, a deposit where no human occupation could be proven. It is only in the Magdalenian (16.3 kyr to approx. 14 kyrs cal BP (Gaudzinski and Street, 2003; Hahn, 1995; Housley et al., 1997; Kind, 2003; Taller et al., 2014)) that archaeological evidence has been found in both valleys again. The region southwest of the Swabian Jura, near the Hegau region, was occupied in the Magdalenian as well. Due to the glaciation in the Würmian, a settlement was firstly possible after the glacier receded, starting at about 16.2 kyr cal BP (Geyh and Schreiner, 1984).

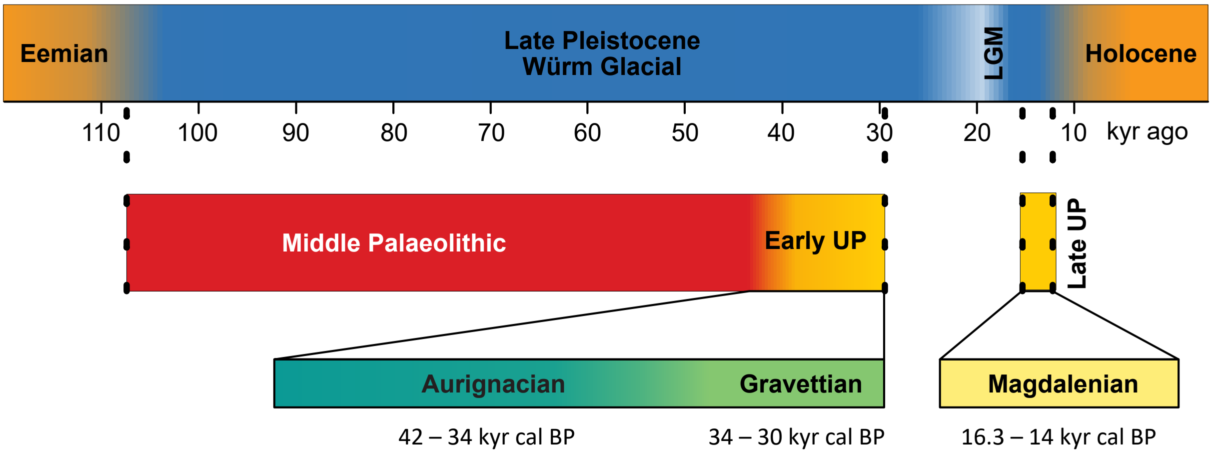

Fig. 2: *Schematic illustration of the geological and archaeological periods in the Late Pleistocene of Europe. The dates are based on the dating of the corresponding archaeological layers from the Swabian Jura (see chapter 1.2.). LGM = Last Glacial Maximum, UP = Upper Palaeolithic.*

1.2.1. Regional climate and environmental reconstructions

Due to the karstified White Jura, caves and underground river systems have existed in the Swabian Jura for millions of years. Caves in general act as sediment traps (Collcutt, 1979; White, 2007), although not only sediments (Barbieri et al., 2018; Goldberg et al., 2003; Miller, 2015a; Miller, 2015b) are preserved in them, but also botanical remains, such as pollen (Riehl et al., 2015), brought in by the wind, or faunal remains introduced by animals, such as microfaunal bones from owl pellets (Andrews and Cook, 1990; Rhodes et al., 2018). Finally, caves also offered shelter to humans, as countless finds in the caves of the Swabian Jura testify. Therefore, caves represent an important archive for the reconstruction of the climate and environment of the Late Pleistocene on a regional scale.

Based on microfaunal (Rhodes et al., 2019; Rhodes et al., 2018; Ziegler, 2019), micromorphological (Miller, 2015a; Miller, 2015b) and sedimentary (Campen, 1990) analyses of Hohle Fels and Geißenklösterle, the climate and environmental conditions of the Middle Palaeolithic in the Ach Valley could be reconstructed. All methods agree that the lowest MP layers, probably indicating the beginning of the Würm Glacial, showing an oscillating temperate environment with a warm and wet climate in summer. These results are based on the evidence of alternating periods of heavy and light solifluction (Campen, 1990; Miller, 2015a) and the presence of moisture and temperate climate adapted species (Rhodes et al., 2019; Ziegler, 2019), such as common vole (*Microtus arvalis*), field vole (*Microtus agrestis*) and Tundra vole (*Microtus oeconomus*). In the subsequent layers, remains of cold-adapted species such as lemmings increase, although species adapted to grassland and forest never completely disappear (Rhodes et al., 2019; Ziegler, 2019).

Bertacchi (2017) studied the stable δ^{18}O isotopic values in horse tooth enamel from Sirgenstein (Ach Valley) and was able to calculate an annual average temperature of 0 to +6.9°C during the Middle Palaeolithic. Summarized, the MP layers show a progressively colder climate with warm and wet summers, but still more temperate than in the following Aurignacian (Bertacchi, 2017; Rhodes et al., 2019; Ziegler, 2019). Since the preservation of botanical remains, such as pollen, in the MP layers of the Swabian Jura sites is relatively poor (Conard et al., 2015a), no exact estimations about the vegetation of this period could be given until now. Nevertheless, it can be assumed that due to the increasing permafrost during the MP, closed forests have disappeared and were replaced by forest-steppe and mammoth steppe environments.

The climate in the early Aurignacian of the Swabian Jura was quite cool and dry, with annual average temperatures of -2.4°C to +3.9°C (Bertacchi, 2017). This result is visible in the micromorphological record of Geißenklösterle and Hohle Fels in the Ach Valley by the presence of ice lensing features and a decrease in the presence of water within the deposits indicated by decreased phosphatization as well (Miller, 2015a). With the beginning of the Aurignacian period, an increase in cold-adapted species such as Arctic lemming (*Dicrostonyx torquatus*) and Norwegian lemming (*Lemmus lemmus*) can be seen in the microfaunal record of Geißenklösterle (Ziegler, 2019). However, we cannot speak of a uniform cooling in this period either. Instead, a pattern of oscillating cold/moderate and dry/wet conditions must be assumed (Campen, 1990; Miller, 2015a; Rhodes et al., 2019; Rhodes et al., 2018; Ziegler, 2019). In a micromorphological study of the Lone Valley, Barbieri et al. (2018) conclude that at the beginning of the Aurignacian there was still shallow permafrost and sparse tree vegetation along the slopes and riverbanks, which was able to drain off the water from the snowmelt in spring/summer. Riehl et al. (2015) describe the vegetation as tundra with boreal elements, such as pines. After the complete adaptation of the vegetation to the increasingly cold climate, the Ach and Lone valleys were covered with grassland and few Arctic willows (Kitagawa, 2014; Krönneck, 2012; Krönneck, 2019; Riehl et al., 2015). As a result, the valley flanks and riverbanks were no longer stabilized and protected by the sparse tree vegetation, which led to heavy flooding during the snowmelt and consequently to massive erosion of the riverbanks (Barbieri et al., 2018).

Riehl et al. (2015) were able to reconstruct the transition from Aurignacian to Gravettian as interglacial tundra vegetation with a mosaic of cold steppe elements and some forest patches by using the archaeobotanical record of Hohle Fels. In addition, the avian faunal analysis of Krönneck (2019) showed increasing evidence for coniferous vegetation near Geißenklösterle throughout the Gravettian. The oldest layers of the Gravettian record a short sequence dominated by boreal rodents in Hohle Fels (Riehl et al., 2015) and Geißenklösterle (Ziegler, 2019), which may reflect interstadial conditions. Towards the end of the Gravettian, rodents, and botanical remains indicate cooling with increasing tundra components (Riehl et al., 2015; Ziegler, 2019).

The most significant climate degradation in the Swabian Jura was identified during the LGM. At that time none of the caves were inhabited by humans for a long time (Conard and Bolus, 2003; Conard and Moreau, 2004; Taller et al., 2014), although some of them, such as Geißenklösterle, must still have been accessible since animal bones of large mammals (Münzel, 2019) and microfauna (Ziegler, 2019) can be found in the layers.

Ziegler (2019) reported that cold steppe species in the LGM layers account for 50 to 70% of the microfaunal record. He, therefore, reconstructs an open, all-season cold and dry habitat for this period. The biodiversity of small mammals decreased drastically, leaving only four species verifiable. Similar results were obtained by analyzing the high glacial layers of Brillenhöhle, where cold steppe species account for over 97% of the microfaunal record (Boessneck et al., 1973).

The environmental conditions in the Magdalenian of the Swabian Jura are characterized by the decay of the LGM. Weniger (1982) described the climate as continental, which resulted in strong contrast in temperatures between summer and winter months. The differences between day and night temperatures were stronger as well, as the sky was unclouded. However, this allowed more sunlight to reach the earth during the day, which led to partly higher temperatures than today (Bosinski, 1987), hypothesized that due to the high pressure weather conditions there were more sunny days in the Magdalenian of the Swabian Jura compared to present day (Albrecht, 1983) with average temperatures of +8°C to +10°C in summer and -20°C in winter (Weniger, 1982). In contrast to the assumptions of Weniger (1982), who suggests a pure Tundra-like landscape with predominant grass steppe on the Swabian Jura, new studies on small mammals and stable isotopes from herbivores' bone collagen showed that the landscape was more mosaic-like (Wong et al., 2020). Due to the long summer vegetation periods and the partial thawing of the permafrost soils, it was possible for tree formations to form. At the southwestern edge of the Swabian Jura, near the Swiss-German border, similar reconstructions have been made for the Magdalenian based on pollen analyses (Lechterbeck, 2001). Here, small accumulations of pine, willow, and birch trees are assumed, which structured the steppe landscape with small forests. Furthermore, juniper and sea buckthorn bushes are common in the Magdalenian landscape (Lechterbeck, 2001; Napierala, 2008; Weniger, 1982).

1.2.2. Human occupation from the Middle to the Upper Palaeolithic

We assume that Neanderthals and AMHs have spent most of their lives outside of the caves (Çep and Waiblinger, 2001; Münzel, 1997; Niven, 2007), although archaeological evidence from the Swabian Jura is mainly documented from cave sites. In contrast, open-air sites of this region are very rare (Barbieri et al., 2018; Bolus et al., 1998; Çep and Waiblinger, 2001; Floss et al., 2012) and often have bad organic preservation (Conard et al., 2012). On the one hand, the reason for the small number of open-air sites is due to the archaeological research history that focused on caves sites for several decades (Conard and Bolus, 2006) and, on the other hand, due to the geological and Pleistocene environmental conditions, such as glacier formation and movement.

Human remains are very rare in the archaeological record of the Swabian Jura. Only one femur of Neanderthal exists from Hohlenstein-Stadel, which was chewed on both ends by carnivores (Kunter and Wahl, 1992). Since the cave was likely a hyena den during the Middle Palaeolithic (Kitagawa, 2014), the bone may have been introduced by these animals. Even from later layers of the Swabian Jura caves, there are only a few human remains. In the Aurignacian layers of Hohle Fels and Sirgenstein, some human teeth (AMH) have been found (Sala and Conard, 2016), while from the Gravettian no human remains are recorded.

One isolated tooth, a mandible, and some cranial fragments were found from the Magdalenian layers of Brillenhöhle (Riek, 1973), which show traces of skinning, defleshing, and human tooth marks and have been associated with cannibalism (Sala and Conard, 2016). In addition, two femora were found in the Magdalenian layer of Hohle Fels, also showing cut marks (Czarnetzki, 1983; Haas, 1991; Sala and Conard, 2016). Due to the proximity to Brillenhöhle, Sala and Conard (2016) assumed cannibalism in this case as well.

In order to be able to draw valid conclusions about the human occupation of the region, the studies of lithic artifacts and animal bones are of crucial importance. During the Middle Palaeolithic, the Levallois technology was decisive for the production of lithic artifacts (Delagnes et al., 2007). This technology existed in different technocomplexes (Gamble, 1986), which differed in characteristic tool types. Important for the Swabian Jura are the Micoquian (Rosendahl, 2011; Ruebens, 2007) with its bifacial tools, the Keilmesser group (Conard and Fischer, 2000) with bifacial backed knives and the Blattspitzen group (Bolus, 2004; Bosinski, 1967) with the leaf point tools. The raw material for the tools originated primarily from local sources (Jurassic grey chert and Bohnerz brown chert), or was collected near the Danube (radiolarite) (Burkert and Floss, 2005; Çep et al., 2011). The discovery of remains of a straight-tusked elephant (*Palaeoloxodon antiquus*) from an MP layer of Vogelherd Cave (Hahn et al., 1985; Niven, 2006) suggests that Neanderthals were already present in the Swabian Jura during the Eemian.

In most sites, such as Sirgenstein (Schmidt et al., 1912), Hohle Fels (Blumentritt and Hahn, 1978), and Geißenklösterle (Hahn, 1988), there is an occupation hiatus in the layers following the MP. Taphonomic studies on faunal remains (Bertacchi, 2017; Conard et al., 2012; Conard et al., 2013a; Kitagawa et al., 2012; Münzel, 2019) in these layers, as well as micromorphological studies (Barbieri, 2019; Barbieri et al., 2018; Miller, 2015a), have shown that no human activity can be detected during this time. A simultaneous occupation of Neanderthals and AMHs in the Swabian Jura is therefore unlikely (Conard, 2011; Conard et al., 2015a; Conard et al., 2006; Conard et al., 2012).

The earliest evidence of a re-occupation by AMHs in this region dates to approx. 47 to 43 kyr cal BP in Sirgenstein (Bertacchi, 2017) and to approx. 42 kyr cal BP in Geißenklösterle (Higham et al., 2012). Aurignacian is indicated by new lithic artifacts made from local Jurassic chert, such as scrapers, burins, and blades, all produced by unidirectional knapping techniques (Bolus, 2003; Conard et al., 2006), burnt bones (Conard et al., 2013a; Münzel, 2019), and wood (Riehl et al., 2015), organic artifacts of ivory, antler or bone (Barth et al., 2009; Conard et al., 2006; Münzel, 2001; Münzel and Conard, 2004b; Münzel et al., 2017) and numerous personal ornaments (Conard, 2003a; Hahn, 1992; Langguth and Malina, 2003; Wolf, 2015; Wolf and Conard, 2015), first mobile arts (Conard, 2003b, 2009; Conard et al., 2010; Floss, 2018; Hahn, 1970, 1986), and first musical instruments (Conard et al., 2009; Hahn and Münzel, 1995).

Three hypotheses have been proposed to explain the sudden appearance of the Aurignacian in the Swabian Jura: first, there is the "Population Vacuum" hypothesis (Conard et al., 2006), which assumes that there were few or no Neanderthals left in the region when AMHs first occupied the Swabian Jura. The second hypothesis, the "Danube Corridor" hypothesis (Conard and Bolus, 2003, 2008; Conard et al., 2006), assumes that AMHs followed the Danube upstream, reached the upper Danube (Urdonau) valley, and thus also the Swabian Jura, and from there populated the rest of Central Europe. The third hypothesis is the "Kulturpumpe" hypothesis (Conard and Bolus, 2003), which describes that the Aurignacian and Gravettian in the Swabian Jura either originated from the competition between Neanderthals and AMHs or from the successful adaptation of the AMHs to the prevailing environmental conditions. Estimates by Conard et al. (2012), based on lithic artifact density, indicate a roughly ten to fifteen times higher occupation intensity and population density of AMHs in the Aurignacian then that of Neanderthals during the MP. Schmidt and Zimmermann (2019) calculated that 98 to 197 people (on average 140 people) lived in two to five groups during the Aurignacian period in the Swabian Jura. This corresponds to a population density of 2.1 to 4.2 people per 100 km^2, making this region an Aurignacian hotspot in Europe (Schmidt and Zimmermann, 2019).

In the sites of the Ach Valley, the Aurignacian is closely followed by the Gravettian. To be more precise, there is even overlap between the most recent Aurignacian layers and the oldest Gravettian layers between about 35 and 34 kyr cal BP (Taller and Conard, 2019). In the Lone Valley, the Gravettian is only found in Bockstein-Törle and Vogelherd (Conard and Bolus, 2003). In the Fetzershaldenhöhle a Gravettian/Aurignacian transition horizon was recorded as well (Lykoudi, 2017). Due to the compositions of the lithic assemblages between the sites Brillenhöhle, Geißenklösterle and Hohle Fels, it is assumed that there were coherent groups of hunter-gatherers occupying the region (Taller and Conard, 2019; Taller et al., 2019). Radiocarbon dating by Taller and Conard (2019) showed that an early Gravettian was present in Hohle Fels, although this does not prove the origin of Gravettian in this region. Rather, it is assumed that Gravettian people were well connected and exchanged lithic techniques in addition to goods such as shell ornaments or teardrop-shaped pendants, thus spreading Gravettian (Taller and Conard, 2019). New lithic techniques were standardized, straight and regular blades, burins, end scrapers, splintered pieces, fléchettes, gravette points and micro-gravette points (Conard and Moreau, 2004; Floss and Kieselbach, 2004; Moreau, 2009; Taller and Conard, 2016; Taller et al., 2019). The raw material used was radiolarite and, in smaller quantities than in the Aurignacian, local Jurassic chert (Floss and Kieselbach, 2004; Taller and Conard, 2016; Taller et al., 2019). There were also changes in the organic raw materials: Ivory artifacts were less frequent and replaced by artifacts from mammoth ribs (Barth et al., 2009; Münzel, 2019; Münzel et al., 2017). As ornaments, perforated teeth and shells became more common and ivory beads were replaced by the teardrop-shaped pendants mentioned above (Conard, 2003a; Hahn, 1992; Langguth and Malina, 2003; Wolf, 2015; Wolf and Conard, 2015).

Between 30 and 16 kyr cal BP there was no occupation of the Swabian Jura, which was primarily due to the environmental conditions of the LGM (Jochim et al., 1999; Taller et al., 2014; Taller and Conard, 2016; Weniger, 1987a; Weniger, 1987b). However, some caves may have been visited for short periods of time, as few cut marks on animal bones indicate from this period (Conard and Bolus, 2003; Conard and Moreau, 2004; Lykoudi, 2017). However, most of the caves show no human activity during the LGM.

It was after the LGM and the slow rise of temperatures in the region when new re-population took place (Jochim et al., 1999; Kind, 2003; Taller et al., 2014; Weniger, 1982; Weniger, 1987a; Weniger, 1987b). The people who brought the Magdalenian probably came from France, where the Magdalenian developed from the Solutrean/Badegoulian (Jochim et al., 1999). Similar to the Gravettian, it can be assumed that the people were well connected, since certain, though rarely existing, raw materials have been found, e.g. tabular chert and Jasper coming from Lower Bavaria and the Upper Rhine respectively (Taller, 2014; Taller et al., 2014), both over 200 km far from the Swabian Jura. Most of the typical Magdalenian lithic inventory (Taller, 2014), such as backed pieces, burins, perforators, conical bladelet cores, cheddar points with a double-angled back, shouldered points, tanged points and backed pieces with oblique end retouch, was made from local (present within a radius of 20-40 km) radiolarite, Bohnerz brown chert, Keuper and tertiary chert. Bone needles and antler harpoons with bilateral barbs were typical tools as well. The Magdalenian colonization of the Swabian Jura probably took place quite quickly, although only short, irregular visits to the cave sites over a period of about 1000 years can be proven (Taller, 2014; Taller et al., 2014). As fast as it appeared, the Magdalenian disappeared about 12.7 kyr ago (Gaudzinski and Street, 2003; Hahn, 1995; Housley et al., 1997; Kind, 2003; Taller et al., 2014), which may be related to the adaptation of Magdalenian people to a dry grassland steppe environment (Taller, 2014; Taller et al., 2014). With the continued climatic improvement, the landscape, vegetation, and fauna changed too much, causing the people of the Magdalenian to leave the Swabian Jura. In Kesslerloch, on the south-western edge of the Swabian Jura, people stayed longer, as numerous finds prove, and the site is assumed to have been a base camp of hunter-gatherers (Leesch and Müller, 2012; Napierala, 2008). Mobile art is showing the fauna of the mammoth steppe biome, such as musk oxen (Leesch and Müller, 2012), indicate that these animals were known and present during the occupation period. Radiocarbon dating on mammoth bones (Huber and Reinhard, 2016; Napierala, 2008) also proves that megafauna, although rare, still existed in the Magdalenian of this region. Could it be possible that exactly these regions, where people settled for a long time and where the last megafauna was present, were small inter-European *refugia* of the decaying mammoth steppe biome in the Magdalenian?

1.2.3. Small game exploitation in the Swabian Jura

As described above (chapter 1.1.2), changes in the faunal record, regarding the hunting of prey by humans, can indicate resource stress driven by changing population densities or overhunting of the main prey (Stiner et al., 1999), but also a change in the socio-economic strategies such as the emergence of the gender division of labor (Kuhn et al., 2006). In the zooarchaeological assemblages of the Swabian Jura sites, these changes are visible, especially in the transition between MP and Aurignacian (Bertacchi, 2017; Conard et al., 2013a). The main prey of Neanderthals and AMHs in the Swabian Jura was basically the same (Conard et al., 2006; Münzel and Conard, 2004b) and consisted of mammoth, reindeer and horse (Boger et al., 2014; Conard et al., 2013a; Kitagawa, 2014; Krönneck, 2012; Münzel, 2019; Münzel and Conard, 2004b; Niven, 2006, 2007). Although the environmental conditions in the Middle Palaeolithic were even more comfortable than in the Aurignacian, where cooling occurred, this had no decisive influence on the primary prey.

An important point in this topic is the difference in the preservation of small bones compared to large bones. Taphonomic processes can affect the preservation of faunal remains and thus falsify studies of the relationship between large and small prey (Lyman, 1994). At least for the cave sites Geißenklösterle and Hohle Fels, Conard et al. (2013a) assumed that taphonomic processes have hardly affected the faunal remains since fragile microfauna is present from all layers of the caves (Rhodes et al., 2019; Rhodes et al., 2018; Ziegler, 2019) and the good state of collagen preservation in bones has been proven by many studies across all layers (Baumann et al., 2020; Bocherens, 2015; Drucker et al., 2015; Immel et al., 2015; Münzel et al., 2014). In order to get a valid statement about the exploitation of small game, excavation methods that include wet-sieving and sediment selection are of crucial importance. Unfortunately, most of the faunal inventories of the old excavations were only manually collected bones and are therefore not properly comparable with the wet-sieved material. This issue is described in more detail in **publication 1**, since our analysis of the published fox remains could only refer to single finds for reasons of comparability. However, I will focus on the well-studied faunal assemblages of Hohle Fels, Geißenklösterle, Sirgenstein, and Langmahdhalde for an overview of the small game exploitation in the Swabian Jura from the Middle Palaeolithic to the Magdalenian.

Conard et al. (2013a) described the exploitation of small game in Hohle Fels and Geißenklösterle. Data from the MP to Gravettian layers of Hohle Fels are the most recent so far, as analyses of the newly excavated material are still pending (personal communication with Susanne Münzel). Additionally, Napierala et al. (2014) published the faunal remains of the Magdalenian layers. The data from Geißenklösterle have not changed either, as they are identical with the data in the final zooarchaeological study (Münzel, 2019). In addition to these two sites, there is the analysis of Sirgenstein, which was done by Alex Bertacchi as part of his master's thesis (Bertacchi, 2017) and the faunal analysis of the Magdalenian site Langmahdhalde by Gillian Wong (Wong et al., 2017).

In the MP layers, the number of hare/fox-size mammal remains is very low and songbirds, which are not due to human introduction, dominate the avian faunal remains (Bertacchi, 2017; Conard et al., 2013a). However, this situation changes abruptly in the Aurignacian: here we see a sudden increase in the evidence of small mammalian game species (Bertacchi, 2017; Conard et al., 2013a) and a change in the composition of avian fauna. Especially galliforms, such as ptarmigans (*Lagopus* sp.), are increasing (Conard et al., 2013a; Krönneck, 2019). There are also more fish remains in the Aurignacian layers of Geißenklösterle (Böhme, 2019) and Hohle Fels (Conard et al., 2013a). Salmonids, such as trout (*Salmo trutta*), salmon (*Salmo salar*), and grayling (*Thymallus thymallus*), are as common as the burbot (*Lota lota*), which was the dominant species in the MP fish assemblages. The fact that humans were responsible for the introduction of the small game species into the sites is shown by cut marks on hare and bird bones (Conard et al., 2013a; Münzel, 2019). Finally, the use of bird bones as raw material for the production of flutes (Conard et al., 2009; Hahn and Münzel, 1995) and the use of fox teeth as raw material for pendants (Camarós et al., 2016; Conard, 2003a; Hahn, 1992; Langguth and Malina, 2003) show the increased benefit of the small game species for humans as well.

In the Gravettian layers, this benefit seems to have been even greater. For the mammalian small game assemblage, this was particularly true for hare remains, which in Sirgenstein and in Brillenhöhle surpassed the group of high-ranged large herbivores in their NISP (Bertacchi, 2017; Boessneck et al., 1973; **publication 1**). Cut marks on these bones indicated the production of beads from metapodials (Münzel, 2019). The high number of small game remains in many sites of the Swabian Jura can actually only be explained by a trap hunt (Conard et al., 2013a; **publication 1**), even though no archaeological evidence has been found yet. In the case of bird remains, NISP in Hohle Fels decreased, but increased in Geißenklösterle (Conard et al., 2013a; Krönneck, 2019). Here the ratio between the various taxa did not change much. However, in the case of fish ensembles, the burbot was completely replaced by salmonid species, which can be associated with human fishing activities (Conard et al., 2013a).

Since the Magdalenian was only sparsely represented in the Swabian Jura, it is not surprising that there were also few remains of small game. However, high NISPs for hares and foxes are still documented from Hohle Fels (Napierala et al., 2014), and Brillenhöhle (Boessneck et al., 1973), the NISPs of hare remains are still higher than those of large herbivores (**Publication 1**). In Langmahdhalde (Lone Valley), one fox mandible with cut marks was also found, indicating skinning (Wong et al., 2017). Furthermore, ptarmigans and large birds, such as geese, were also present in the sites (Boessneck et al., 1973; Wong et al., 2017), and even show cut marks or were used for needle production (Wong et al., 2017). If we consider the south-western end of the Swabian Jura, we see that also in Kesslerloch, mountain hare ($37\%_{\text{NISP}}$) was as common as reindeer ($36\%_{\text{NISP}}$) and thus played an important role for the Magdalenian hunter-gatherers (Napierala, 2008). For the first time, tools for fishing (e.g., harpoons) were recorded in the archaeological inventory (Taller, 2014).

1.3. Underestimated species: red and Arctic foxes

The archaeological sites investigated in this study are dominated by remains of cave bear and ungulates throughout the Palaeolithic (e.g., Bertacchi (2017); Camarós et al. (2016); Conard et al. (2013a); Kitagawa et al. (2012); Krönneck (2012); Lykoudi (2017); Münzel (2019, in prep.-b); Münzel and Conard (2004a); Münzel and Conard (2004b); Napierala (2008); Napierala et al. (2014); Wong et al. (2017)). However, there are also small numbers of carnivore taxa in almost all of the sites, including red fox (*Vulpes vulpes*) and Arctic fox (*Vulpes lagopus*). Foxes must have played an important role in the lives of Palaeolithic peoples, based on, among other things, the presence of perforated fox teeth in the archaeological record, which were most likely used as pendants (Camarós et al., 2016; Conard, 2003a; Hahn, 1992; Langguth and Malina, 2003; Münzel, 2019). However, the nature of this relationship has not yet been studied in detail. Besides the regular occurrence of fox remains in archaeological sites, another feature makes foxes interesting for palaeoecological and zooarchaeological studies: they are small, opportunistic carnivores (Pulliaines, 1993; Wandeler and Lüps, 1993). This means that they are able to adapt to different types of diet and could probably act as food resource indicators, by using their stable isotopic signature (see chapter 5.3). Since scavenging belongs to their feeding strategies as well and Palaeolithic humans must have produced food waste, it could be possible to detect this human-made resource in the foxes' diet. The more people occupied the same place at the same time, hunted and processed meat, the more food waste is attracted to foxes, which could be consumed. The third reason is the behavior of foxes: as many scavengers, foxes can live commensal to large predators (Bassi et al., 2012; Jędrzejewski and Jędrzejewska, 1992; Kapel, 1999; MacDonnald, 1977; Murdoch et al., 2010; Panek and Budny, 2017; Roth, 2003; Soe et al., 2017; Van Haaften, 1970; Wikenros et al., 2017). Neanderthals and AMHs were among the top predators in the Late Pleistocene of Europe (Benazzi et al., 2011; Bocherens, 2009; Droke et al., 2020; Musil, 2003; Niven, 2006; Wißing et al., 2019; Wißing et al., 2016; Yravedra et al., 2019), hunting for large prey and thus providing sufficient food for scavengers (Bocherens, 2015; Bocherens et al., 2015). Hence the transition to a synanthropic behavior of foxes is predictable. Modern red foxes and Arctic foxes demonstrate this behavior as soon as they are in the periphery of humans, e.g., in cities (Forsyth et al., 2014; Kapel, 1999; MacDonnald, 1977; Macpherson, 1969; Panek and Budny, 2017; Reshamwala et al., 2018; Soe et al., 2017; Van Haaften, 1970). It is therefore likely that Late Pleistocene foxes showed synanthropic behavior to a certain extent as soon as humans occupied the caves and changed their direct vicinity for their own needs. Therefore, foxes could act as an excellent proxy for estimating human population densities, occupation intensity, and determining the impact of humans on the Late Pleistocene ecosystem.

In the Late Pleistocene zooarchaeological assemblages discussed in this study, remains of both Arctic and red fox are present, probably deposited at the same time. In several studies, the distinction between both species was made by the dimensions of the postcranial bones (Baumann, 2016; Boessneck et al., 1973; Germonpré and Sablin, 2004; Münzel, 2019; Weinstock, 1999). In general, Arctic fox bones are smaller than red fox bones (Pulliaines, 1993; Wandeler and Lüps, 1993). The proportions of the tibia's distal part (largest width and largest depth) show a clear distinction between the two fox species (Münzel, 2019), additionally, in humerus, femur, atlas, axis, ulna, radius and pelvis, a metric distinction is possible as well (Baumann, 2016). Strong sexual dimorphism in red foxes may also play a role in this context, as there can be overlaps in the postcranial dimensions between smaller, female red foxes and male Arctic foxes. A further uncertainty can result from time depth since modern red and Arctic foxes have different proportions than their Pleistocene ancestors (Germonpré and Sablin, 2004). However, often only values of the modern representatives are available as references, leading to possible metric inaccuracies. Late Pleistocene red foxes followed Bergmann's rule (Germonpré and Sablin, 2004; Meiri and Dayan, 2003), which predicts larger body sizes for better thermoregulation in colder habitats (Bergmann, 1847). Arctic foxes, in contrast, appeared to have been smaller during the Late Pleistocene than modern foxes (Germonpré and Sablin, 2004). These results originate mainly from Late Pleistocene foxes from Belgium, but can also be found in Late Pleistocene foxes of the Swabian Jura (Baumann, 2016; Münzel, 2019).

Another possibility is to distinguish both fox species according to the size of their teeth (Böttcher et al., 2000; Münzel, 2019; Poplin, 1976). In this case, molars are often used, as well as the canines. The dimensions of Arctic foxes are generally smaller than those of red foxes as well (Pulliaines, 1993; Wandeler and Lüps, 1993). Measurements on the crown should be taken with caution because, due to abrasion, measuring points are often missing and can only be estimated, which increases the overlapping range of both species (Münzel, 2019). Similar to the bones, the proportions in Late Pleistocene fox teeth are not equal to those of modern foxes. Late Pleistocene red and Arctic foxes have relatively larger carnassials compared to modern foxes, suggesting a more extensive carnivorous diet (Szuma and Germonpré, 2019, 2020). The fact that both fox species consumed a similar diet, and, therefore, share similar trophic niches, was proven in studies with stable isotopes as well (Baumann, 2016; Baumann et al., 2020).

I will treat in the following both fox species together as "fox".

2. Objectives and expected output of research

In the present thesis, I will discuss three research questions that fundamentally deal with human behavior and the interaction of humans, namely Neanderthals and AMH, with the Late Pleistocene environment of the Alpine foreland. For this purpose, I will focus on cave sites and rock shelters of the central Swabian Jura (Ach and Lone valley) and Hegau Jura, located at the southwestern edge of the Swabian Jura (Germany).

First, I will analyze how both human species exploited foxes during the Middle and Upper Palaeolithic. In this context, I consider the Central Swabian Jura and use published zooarchaeological data of the archaeological sites located there. A new evaluation of these assemblages and a focus on fox remains will help to gain new insights into the economy of Middle Palaeolithic, Aurignacian, Gravettian, and Magdalenian people. Discussing this question will also provide a new understanding of the hunting methods of small game developed by Palaeolithic hunter-gatherers from the Aurignacian onwards. In particular, the question of hunting behavior is explored with different scenarios based on optimal foraging theory. I expect a clear differentiation in hunting and exploitation of foxes between Neanderthals and AMHs and an increase in the importance of foxes from the Aurignacian onwards.

Second, I will study the trophic behavior of Late Pleistocene foxes and investigate whether humans have created new trophic niches for scavenging foxes through their hunting behavior for big game, or through food waste. For this purpose, I investigate the stable isotopes (δ^{13}C and δ^{15}N) in the preserved collagen of red and Arctic fox bones from the same archaeological sites of the Swabian Jura and additionally from archaeological sites of the Hegau Jura. As foxes are opportunists, they may have adapted to different trophic niches. This behavior can be observed in modern foxes and I assume that it was similar in the Late Pleistocene. With increasing human occupation in the region during the Upper Palaeolithic, it may be possible that humans acted as food providers, creating new niches for scavenging foxes. I expect, therefore, a significant shift in the niches between the Middle Palaeolithic, which was only sparsely populated in the Swabian Jura, and the more populated Upper Palaeolithic periods.

Finally, I will pursue the question of whether it is possible, with the knowledge gained previously, to trace regional human population densities, the intensity of their activities and thus ultimately the influence of humans on the Late Pleistocene environment, namely the mammoth steppe biome. In this context, I assume that human interventions, such as big game hunting, not only created seasonally limited trophic niches for foxes but that these niches had existed for a long time, at least as long as humans were active in the region. An adaptation of foxes to anthropogenic niches would have resulted in synanthropic behavior, which has caused an increased abundance of foxes in the direct vicinity of humans and, therefore, a higher probability to encounter their remains as hunted prey at the sites. In addition, the fox remains in the archaeological layers would have to correlate with other proxies used to determine human population density, such as lithic artifact density. Such a clear influence of humans on the behavior of wild animals would provide a further argument for predating the Anthropocene, the age of humans. I expect correlations between fox remain densities and artifact densities will be possible from the Aurignacian onwards and a correlation of the occurrence of human-influenced trophic fox niches to the intensity of human activity.

3. Archaeological and theoretical background

3.1. Archaeological and zooarchaeological context

In my dissertation, faunal data from a total of 14 sites from the central Swabian Jura and the Hegau Jura, were included (Fig. 1). These sites are briefly presented in this paragraph. Special attention is given to the zooarchaeological data.

3.1.1. Sites of the Ach Valley

The Ach valley is situated on the southern border of the central Swabian Jura and was part of the Urdonau valley during the Pleistocene (until the Würm Glacial). Today only the small stream Ach flows through the valley and gave it its name (Binder and Jantschke, 2003). Table 1 shows the sites of the Ach Valley and the corresponding archaeological horizons (AH) with the corresponding periods of interest for this study.

Table 1: *Sites of the Ach Valley and the corresponding archaeological horizons (AH) and periods of interest for this study. A = Aurignacian, G = Gravettian, G/A = Gravettian/Aurignacian transition, M = Magdalenian, MP = Middle Palaeolithic.*

Site	Coordinates		Elevation	AH	Period
Brillenhöhle	48°24'19" N	9°46'40" E	600 m	IV	M
				V-VII	G
				XIV	A
Geißenklösterle	48°23’54” N	9°46’20” E	585 m	Io	M
				I	G
				II-III	A
				IV-VIII	MP
Große Grotte	48°24'22" N	9°48'05" E	580 m	II-XI	MP
Helga Abri	48°22'45" N	9°45'14" E	545 m	II F7-IIId	M
Hohle Fels	48°22’45” N	9°45’14” E	534 m	0-IIa (light)	M
				IIb-cf	G
				IId-e	G/A
				IIIa-Vb	A
				VI-IX	MP
Kogelstein	48°21'45" N	9°43'17" E	550 m		MP
Sirgenstein	48°23’13” N	9°45’40” E	565 m	I-III	G
				IV-VII	A

The cave site **Brillenhöhle** was completely excavated by Gustav Riek between 1956 and 1963 and published together with Joachim Boessnek and Angela von den Driesch (Boessneck et al., 1973). This is the only source for the zooarchaeological data as well. In the pre-LGM layers, cave bear dominates (A: NISP = 134, G: NISP = 940), followed by reindeer in the Aurignacian (NISP = 12) and mountain hare in the Gravettian (NISP = 738). In the Magdalenian there are primarily remains of mountain hare (NISP = 183), horse (NISP = 46) and reindeer (NISP = 45).

Geißenklösterle Cave is part of a limestone massif located 60 m above the floor of the Ach Valley. It was first excavated in 1973 by Eberhard Wagner (Hahn, 1988) and final excavations at the site were undertaken from 2001 to 2002 by Nicholas Conard (Conard and Malina, 2003). The site became particularly famous due to the discovery of the first musical instruments, flutes made of swan bone and ivory, which were first composed in 1995 (Hahn and Münzel, 1995). Since 2017 this cave has been a UNESCO World Heritage Site. The most complete and recent faunal analysis is from Münzel (2019). In the Middle Palaeolithic layers cave bear (NISP = 586) is dominant, followed by reindeer (NISP = 53). All other animal species occur in very small numbers. In the Aurignacian layers, mammoth (NISP = 5061, including ivory) and cave bear (NISP = 2972) are the dominant species, followed by reindeer (NISP = 493) and horse (NISP = 483). In the Gravettian, cave bear (NISP = 1417) also dominates, however, the second most common species is hare (NISP = 240), followed by mammoth (NISP = 204). The Magdalenian was sparsely populated in Geißenklösterle and the layer has only a few animal bones. The fox (NISP = 28) is most common in this layer.

Große Grotte Cave is located above Blaubeuren and was excavated by Gustav Riek between 1960 and 1964. The archaeological layers were dated to the Middle Palaeolithic and contained about 2000 lithic artifacts (Wagner, 1983) as well as a large number of animal bones, which were studied by Jaco Weinstock (Weinstock, 1999). More than 70% of the bones are from cave bear (NISP = 857), followed by ibex remains (NISP = 114) and bones of reindeer (NISP = 50).

Helga-Abri is a rock shelter located on the southern flank of Hohle Fels (see below). The first excavations were conducted by Gustav Riek and Gertrud Matschek between 1958 and 1960 (Hahn and Scheer, 1983). The goal of the excavation was to find a second entrance to the Hohle Fels. From 1976 to 1984 further excavations were initiated by Joachim Hahn (Hahn and Scheer, 1983; Hahn and Scheer, 1985). Zooarchaeological analysis of the site has not yet been performed but is being processed by Susanne Münzel (Münzel, in prep.-a). The most recent data is given in **publication 1**.

Hohle Fels Cave is one of the largest caves in southwestern Germany. Theodor Hartmann and Oscar Fraas conducted the first excavations at the site between 1870 and 1871. This site has a long history of excavation that includes work by Robert Rudolf Schmidt, Gustav Riek, and Joachim Hahn. Since 1997, Nicholas J. Conard has been leading the annual excavations at Hohle Fels (Conard and Uerpmann, 1998; Conard et al., 1999; Conard and Malina, 2015; Conard and Wolf, 2014). The Aurignacian layers of Hohle Fels are of particular importance because of their ivory ornaments, such as the "Venus" (Conard, 2009) or the "Waterfowl" (Conard, 2003b). Fragments of flutes were also found in these layers (Conard et al., 2009). Since 2017 this cave has been a UNESCO World Heritage Site. A final zooarchaeological evaluation has not yet been conducted for the site, as it is still excavated annually. The most recent published data are from Conard et al. (2013a) with a focus on the Middle to Upper Palaeolithic transition and the exploitation of small game, such as hare, fish and birds, and from Napierala et al. (2014) with focus on the Magdalenian. Cave bear accounted for the majority of the fauna in all pre-LGM periods (MP: NISP = 534, A: NISP = 1021, G/A: NISP = 946, G: NISP = 2273). In addition, cervids (NISP = 237) and horses (NISP = 126) are very numerous in the Aurignacian layers. In the Gravettian layers, hare remains (NISP = 474) and also cervids and horses (NISP = 315 and NISP = 336 respectively) are very abundant. In the Magdalenian layers, the most abundant species are horse (NISP = 351), reindeer (NISP = 287), and hare (NISP = 122).

Kogelstein Cave is located at the crossroads between the Urdonau (original Danube) Valley and the Schmiech Valley. The first exploratory excavations were conducted by Claus-Joachim Kind in 1987, who finally also excavated in 1996 (Kind, 1997). The archaeological record includes only 450 Middle Palaeolithic lithic artifacts, but over 20,000 faunal remains. Böttcher et al. (2000) performed the faunal analysis. In the site, the most common animal species, measured by the number of identified specimens ,were fox (NISP of *Vulpes* sp. = 298 and NISP of red fox = 118), horse (NISP = 143) and cave hyena (NISP = 127). Due to the bite marks on many of the bones, Böttcher et al. (2000) assumed that the site was a hyena den, regularly occupied by Neanderthals, but only for short periods.

Sirgenstein Cave is also an important site in this region. There was only one excavation in 1906 by Robert R. Schmidt. The stratigraphy reaches from the Middle Palaeolithic to the Middle Ages and was published already in 1912 (Schmidt et al., 1912). Since 2017 this cave has been a UNESCO World Heritage Site. The most recent zooarchaeological evaluations are by Alex Bertacchi, who studied the fauna as part of his master's thesis in 2017 (Bertacchi, 2017), but has not yet published it. Most of the bones from the Aurignacian came from cave bears (NISP = 144), followed by reindeer (NISP = 134) and ptarmigan (NISP = 89). In the Gravettian layers, more than 50% of the bones found came from ptarmigan (NISP = 985), followed by cave bear (NISP = 149) and reindeer (NISP = 82).

3.1.2. Sites of the Lone Valley

During the Late Pleistocene, the Lone Valley, located on the eastern part of the Swabian Jura, was a wide riverbed, which, only had a small stream, the Lone (Binder and Jantschke, 2003; Wagner, 1960). This circumstance and the proximity to the original Danube in the Ach Valley made the Lone Valley an ideal place for human settlement, as the partly densely occupied caves prove. Table 2 shows the sites of the Lone Valley and the corresponding archaeological horizons (AH) with the corresponding periods of interest for this study.

Table 2: *Sites of the Lone Valley and the corresponding archaeological horizons (AH) and periods of interest for this study. A = Aurignacian, G = Gravettian, G/A = Gravettian/Aurignacian transition, M = Magdalenian, MP = Middle Palaeolithic.*

Site	Coordinates		Elevation	AH	Period
Bockstein	48°33’15“ N	10°09’18“ E	496 m	BT IV-VI	G
				BT VII	A
				GH 3 & BS I-V	MP
Fetzershaldenhöhle	48°33’17“ N	10°09’49“ E	505 m	GH III	G/A
Hohlenstein-Stadel	48°32’58“ N	10°10’23“ E	487 m	A	A
				MP R & MP U	MP
Langmahdhalde	48°56'69'' N	10°21'33'' E	462 m	IV-VI	M
Vogelherd	48°33’31“ N	10°11’38“ E	478m	III	M
				IV/V & HL/KS	A

Bockstein complex consists not only of one site, but of more than six. Largest sites are Bocksteinhöhle, Westloch, Bockstein-Törle, Bockstein-Loch, Bockstein-Schmiede and Bockstein-Grotte (Conard et al., 2015a; Krönneck, 2012). First excavations took place in 1883/84 by Ludwig Bürger and Friedrich Losch. In 1908, Robert R. Schmidt conducted a re-excavation and from 1953 to 1956, further excavations were undertaken by Robert Wetzel with the aim to excavate the original entrance of the cave complex, the Bockstein-Törle (Wetzel, 1958). Bockstein is one of the most important Middle Palaeolithic sites of the Swabian Jura, although it also has many remains from the Upper Palaeolithic, and was added to the UNESCO World Heritage List in 2017. A detailed correlation of the different archaeological layers in the different areas of the Bockstein was done by Petra Krönneck in the context of her doctoral thesis (Krönneck, 2012). Her publication is also the most extensive and recent zooarchaeological report. The Middle Palaeolithic layers, which were also included in the present study, came from Bocksteingrotte and Bocksteinloch/Bocksteinschmiede. Remains of horse (NISP = 639), reindeer (NISP = 124) and bison (NISP = 87) were most abundant. The Aurignacian is represented primarily in Bockstein-Törle and horse (NISP = 72), reindeer (NISP = 32) and cave bear (NISP = 28) are the most common bone remains of this layer. The richest Gravettian layers are also found in Bockstein-Törle, with mammoth (NISP = 218), reindeer (NISP = 62) and horse (NISP = 51) being the most abundant species.

The cave site **Fetzershaldenhöhle** was first discovered through a systematic field survey by Hermann Glatzle (Glatzle, 2012) and then excavated in 2013-2014 under the direction of Nicholas J. Conard (Conard et al., 2015b). A zooarchaeological evaluation of the faunal assemblages has been done by Maria Lykoudi as part of her master’s thesis (Lykoudi, 2017), but has not yet been published. Due to the frequent bite marks on the animal bones, it is assumed that the cave was a hyena den. Cave bear (NISP = 572) and horse (NISP = 464) make up the majority of the faunal remains identified to species, followed by fox (NISP = 146) and reindeer (NISP = 110).

Hohlenstein-Stadel Cave is located in a site complex called Hohlenstein Complex. This also includes the sites Bärenhöhle, Kleine Scheuer and Stadel-Vorplatz (Conard et al., 2015a). However, the most prominent site is Hohlenstein-Stadel, as the approx. 31 cm tall ivory-made lion man was found here (Wehrberger, 2007). The first planned excavations were conducted from 1937 to 1939 under the direction of Robert Wetzel and Otto Völzing (Hahn, 1970; Völzing, 1938). On the last day of the excavation, the around 300 ivory fragments of the Lion Man were found as well, but it was not until 1969 that Joachim Hahn put them together (Hahn, 1970; Wehrberger, 2007). Further excavations followed irregularly from 1954 to 1983 by Robert Wetzel and Eberhard Wagner. From 2008 to 2013 the last excavation campaigns under the direction of Claus-Joachim Kind were conducted (Beutelspacher et al., 2011; Beutelspacher and Kind, 2012; Kind et al., 2014; Kind and Beutelspacher, 2010). Since 2017, the Hohlenstein Complex has also been a UNESCO World Heritage Site. Most recent faunal analysis was published by Keiko Kitagawa (Kitagawa, 2014). The most abundant species in all layers is the cave bear (MP NISP = 913, A NISP = 642). In the two Middle Palaeolithic layers, the horse is also common (NISP = 249), while in the Aurignacian it is only represented with an NISP of 37. More abundant than the horse in this layer is the wolf (NISP = 42).

Langmahdhalde is a rock shelter with intact Magdalenian layers, approximately 2 km far from Vogelherd cave. For several decades it is the first archaeological site from this time period and since 2016 annually excavated under the direction of Nicholas J. Conard (Wong et al., 2017). The zooarchaeological analysis was conducted by Gillian Wong and is published in Wong et al. (2017). However, the most recent data (up to the excavation year 2018) can be found in **publication 1**. The most common animal remains are of hare (NISP = 23), reindeer (NISP = 19) and horse (NISP = 15).

Vogelherd Cave was discovered and completely excavated by Gustav Riek in 1931 over the course of three months (Riek, 1932, 1934). From 2005 to 2012 Nicholas Conard supervised a re-excavation of the backfill (Conard et al., 2008; Conard et al., 2010; Conard and Zeidi, 2011, 2012; Conard et al., 2013b). This site was of particular importance because of the large number of mobile art objects from the Aurignacian layers. These include not only the well-known animal figurines (Hahn, 1986), such as a horse, mammoths and felids, but also more than 400 double-perforated ivory beads, which were mainly found during the re-excavations (Wolf, 2015). Since 2017, Vogelherd has been included in the UNESCO World Heritage List. The two most recent zooarchaeological studies are from Laura Niven and Ulf Boger. Niven (2006) was mainly focused on the intact layers of Riek's excavation, while Boger et al. (2014) analyzed the fauna of the re-excavations. In the Middle Palaeolithic layers mainly horse bones (NISP = 329) were found. As no foxes were detected, these Middle Palaeolithic layers were not considered further in the present study. In the undisturbed Aurignacian layers bone remains of mammoth (NISP = 3540), horse (NISP = 1423) and reindeer (NISP = 1633) were predominant. A similar result is obtained for the layers of the re-excavation associated with the Aurignacian (mammoth NISP = 686, horse NISP = 229, reindeer NISP = 123). In the Magdalenian layer horse (NISP = 60) and reindeer (NISP = 27) are the dominant species.

3.1.3. Sites of the Hegau Jura

Following the Danube upstream, the last two sites of this study are found at the southwestern end of the Swabian Jura, which merges into the Hegau Jura. Both sites have Magdalenian layers and were isotopically sampled for the present study. Table 3 shows the sites of the Hegau Jura and the corresponding archaeological horizons (AH) with the corresponding periods of interest for this study.

Table 3: *Sites of the Hegau Jura and the corresponding archaeological horizons (AH) and periods of interest for this study. M = Magdalenian.*

Site	Coordinates		Elevation	AH	Period
Gnirshöhle	47°52' N	8°48' E	540 m		M
Kesslerloch	47°74' N	8°69' E	447 m	Schicht I-III	M

Gnirshöhle Cave is located in the Hegau region of southern Germany. From 1977 to 1979 Gerd Albrecht led excavations at the site (Albrecht, 2002; Albrecht et al., 1977). Apparently the Bruder Valley region was a Magdalenian hotspot. Just across the valley, the Magdalenian cave site Petersfels is situated, which is famous for its large Magdalenian inventory including venus and other mobile art objects (Albrecht, 1979; Nübling, 1999). A zooarchaeological analysis is currently being conducted by Susanne Münzel (Münzel, in prep.-b). Dominant species in the Magdalenian layers are horse and reindeer, although no exact NISP values are yet available.

Kesslerloch Cave is located in Switzerland (Kanton Schaffhausen), near the German border, just 30 km far away from Gnirshöhle, and was excavated by Konrad Merk between 1873 and 1903 (Heierli, 1907; Merk, 1875; Nüesch, 1904). This site has gained great importance because at least one Magdalenian dog was found here (Napierala and Uerpmann, 2012; Rütimeyer, 1875). The most recent faunal analysis was published by Hannes Napierala (Napierala, 2008). Most animal bones belong to reindeer (NISP = 9245) and mountain hare (NISP = 8174), followed by horse (NISP =1044) and ptarmigan (NISP = 466).

3.2. Theoretical framework

> *"[…] the environment 'poses the problem'; the organisms 'posit solutions,' of which the best is finally 'chosen'"*
>
> Lewontin (1983): Gene, organism and environment, p. 276

In my thesis, I used three different theoretical concepts. First, to discuss the question how Neanderthals and AMHs hunted and exploited foxes, I used the optimal foraging theory (OFT) and in particular the prey choice model (PCM). To answer my second research question, to what extent humans have affected the behavior of foxes and changed their ecological niches, I used both the niche construction theory (NCT) that deals with the influence of humans on ecosystems and the basic principles of modern fox ecology.

3.2.1. Optimal foraging theory and prey choice model

Optimal foraging theory (OFT) is one aspect of human behavioral ecology (HBE) that applies the principles of Darwin's evolutionary theory and optimization to human behavioral studies. HBE has the most extensive application in ethnographic and ethnoarchaeological studies (Hames and Vickers, 1982; Hawkes et al., 1982; O'Connell and Hawkes, 1984; O'Connell et al., 1988; Smith, 1979, 1991, 1992a, b, 2017; Smith and Winterhalder, 1981), but it has also been used for zooarchaeological studies for several decades (Bayham, 1979; Broughton et al., 2011; Nagaoka, 2019).

The origin of OFT is in behavioral biology and traces back to Eric Charnov, who studied the hunting strategies of mantids (Charnov, 1976). In his study, he defined the basic assumptions of this theory, which were also adopted for ethnographic and zooarchaeological studies. In general, any predator must spend time and energy searching for and handling its prey. In diet, therefore, the net (energy) returns must be weighed against the time and energy used to search and handle the food. To estimate the hunting behavior of predators, different models are used. In HBE these models are prey choice, patch use, and central place foraging (Nagaoka, 2019). However, the prey choice model (PCM) is the most common in zooarchaeological studies (Byers and Ugan, 2005; Dusseldorp, 2012; Jones, 2004; Starkovich, 2014; Stiner, 2009) and addresses the question of which prey should be exploited (Charnov, 1976). Two key aspects that can be investigated in PCM are diet breadth and foraging efficiency. Diet breadth reflects the number of taxa that are included in the diet and could be determined by calculating the net returns of each prey taxon. In this case, the search time is not taken into account because it is assumed that human foragers are searching for all prey taxa included in their diet breadth simultaneously (Nagaoka, 2019). If the net returns are ordered, the rank of the prey is the result. The diet breadth should now expand downward in the ranking of prey taxa until a point is reached where the next lower prey taxon has a lower net return than the average net returns of all prey taxa (Nagaoka, 2019). The availability of the highest ranked prey has a strong effect on diet breadth. If this prey is abundant, the diet breadth is narrow, but conversely, it is broader if the top prey is not available (Pyke et al., 1977). For instance, the diet breadth aspect of PCM can be used to determine whether a predator's hunting strategy is generalized or specialized (Álvarez, 2014). In zooarchaeological studies, it is used to determine whether the over-hunting or over-exploitation of resources has occurred in a particular region. The most prominent example is certainly the hypothesis of over-hunting of Late Pleistocene megafauna in North America (Martin, 1973).

This model was also frequently used in studies on the transition from the Middle Palaeolithic to Upper Palaeolithic in Europe, e.g. to investigate the subsistence strategies of Neanderthals and AMHs (Dusseldorp, 2012; Starkovich, 2012; Stiner, 2009).

Since this study is primarily concerned with specific animal species, i.e. foxes, which have been used by humans in the past, the entire diet breadth is of only limited interest. Rather, the second aspect of PCM is relevant in this study: foraging efficiency. Foraging efficiency is expressed by net returns per unit time and describes how effectively a predator searches for food (Nagaoka, 2019; Smith, 1979, 1991). The basic idea is that predators have a higher foraging efficiency when they obtain higher net returns in a shorter time. The availability of prey in the environment also plays an important role. Similar to diet breadth, the availability of high-ranked prey has a very high influence on foraging efficiency. If high-ranked prey is common, the foraging efficiency is high. Charnov (1976) reports that a decrease in foraging efficiency is often associated with resource depression or a decrease in prey encounter rates as a result of predator's foraging behavior. Other explanations exist, however, that go beyond predator-prey interactions and may explain a shift in the ratio of high-ranked to low-ranked prey. One example is more efficient hunting technology (Grayson and Cannon, 1999; Jones, 2006; Madsen and Schmitt, 1998), which reduces the cost of handling prey and can, therefore, increase the net returns on that prey. Thus, what looks like a shift away from high-ranked prey may in fact be an increase in the net returns and rank of lower-ranked prey (Nagaoka, 2019). Besides technological advances, environmental changes can also affect foraging efficiency by creating more or less favorable habitats, which also affects population density and encounter rates of the prey (Ugan, 2005; Wolverton, 2005). In the case of the fox hunt of prehistoric humans, this point may be decisive, since it can also be linked to the niche construction theory (chapter 3.2.2).

As mentioned above, the OFT is often used in ethnographic or behavioral studies. Here the net returns can be documented directly as calories. In zooarchaeological studies, however, we reach our limits because we only have animal remains available. Fortunately, studies have shown that the body size of prey animals correlates with their calorie count (Bayham, 1979; Broughton et al., 2011; Jones, 2004), allowing PCM to be supplemented with zooarchaeological material. However, even this does not solve all problems. Since taphonomic processes, bone preservation and excavation techniques can strongly affect the relationship between large and small prey in archaeological sites. Another point is the time depth of many archaeological layers. While ethnographic studies have an investigation period of hours to days, archaeological layers often show periods of centuries to millennia, especially in the Middle and Upper Palaeolithic.

3.2.2. Niche construction theory

In ecological studies, niches are complex systems with multiple variables that define a species' role in the ecological system (Araujo et al., 2011; Pocheville, 2015). Niche construction theory (NCT) provides an explanatory approach to the extent that organisms can influence the environment by creating favorable living conditions, thus providing new living conditions (niches) for them and other species (Laland and O'Brien, 2010). This theory originates from evolutionary biology and was first published in the early 1980s by Richard Lewontin (Lewontin, 1982, 1983). In the 1990s, a similar theory was published from the field of ecology called "ecosystem engineering" (Jones et al., 1994, 1997). However, the statements of both theories are the same: ecosystem engineers can regulate energy flows, mass flows and trophic patterns in ecosystems, creating a mosaic of connectivity (Jones et al., 1994, 1997; Wilby, 2002), as is common in ecological niches and as predicted by the NCT (Laland and O'Brien, 2010; Odling-Smee et al., 1996). One of the most widely used examples of a niche constructor in ecology and evolutionary biology is the beaver, which dams up streams by building its shelter (Bartel et al., 2010; Laland and Boogert, 2010; Nummi and Hahtola, 2008; Odling-Smee et al., 1996; Wright et al., 2002). Subconsciously, it creates floodplains that provide habitat and therefore new niches for many different plant and animal species (Hood and Larson, 2014; Nummi and Hahtola, 2008; Nummi and Holopainen, 2014; Nummi and Kuuluvaine, 2013; Wright et al., 2002). Large carnivores are also important ecological engineers in terrestrial ecosystems (Barry et al., 2019; Ceballos et al., 1999; Jones et al., 1994; Wikenros et al., 2017; Wilby, 2002), as they open up new trophic niches for scavengers. Commensal behavior, as it is common in opportunistic scavengers, probably developed this way.

Archaeological studies focus on humans as niche constructors (Laland and Boogert, 2010; Laland and O'Brien, 2010; Smith, 2007a, 2011, 2013, 2016; Stiner and Kuhn, 2016; Zeder, 2016), who still today have the strongest influence on almost all ecosystems worldwide (Smith, 2007b). Moreover, if humans were not able to influence the environment as niche constructors and modify it according to their needs (e.g. by building houses, villages, and towns or by deforesting to create agricultural land for food production), the massive population growth of the past 10,000 years would be impossible (Laland and O'Brien, 2010). Some studies also assume the development of human culture as a consequence of niche construction (Fuentes, 2015; Hardesty, 1972; Kendal et al., 2011; O'Brien et al., 2012). A result of the human construction of niches, visible in the archaeological record, is assumed by many scientists only starting with sedentism, i.e. in the early Neolithic (MacHugh et al., 2017; Smith, 2007a, 2011, 2016; Vigne, 2015; Zeder, 2012a, b, 2015, 2016). Only in this period were the first livestock and crop plants domesticated (Vigne, 2015; Zeder, 2012a, b, 2015), thus directly affecting the niches of these taxa. At this time, the first houses were built, which provided a constant living climate, and the first storage rooms were constructed, which enabled the storage of grains (Bogaard et al., 2009; Bogaard et al., 2010; Fairbairn et al., 2007; Twiss et al., 2009). Only from this time on house mouse (*Mus musculus*) and the African wild cat (*Felis silvestris lybica*) could develop synanthropic behavior and spread worldwide with humans (Cucchi et al., 2011; Cucchi et al., 2005; Cucchi et al., 2002; Driscoll et al., 2009; Driscoll et al., 2007; Faure and Kitchener, 2009; Krajcarz et al., 2016; Tangri and Wyncoll, 1989).

This is true if we consider the niche constructed by humans in its entirety, as defined in ecological terms (Araujo et al., 2011; Pocheville, 2015). However, if we pick just one particular aspect, in case of the present study, the available diet in a niche (= trophic niche, then humans can be identified as niche constructors even earlier (Baumann et al., 2020). The identification and description of trophic niches have been used in several ecological and paleoecological studies (Araujo et al., 2011; Bassi et al., 2012; Hulme-Beaman et al., 2016; Kidawa and Kowalczyk, 2011; Morey and Jeger, 2017; Soe et al., 2017; Wikenros et al., 2017). In particular, studies that focus on dietary reconstructions using stable isotopes make use of trophic niches (Baumann et al., 2020; Bearhop et al., 2004; Bocherens, 2015; Bocherens et al., 1997; Bocherens and Drucker, 2003; Bocherens et al., 2011; Bocherens et al., 2015; Bocherens et al., 1994; Germonpré et al., 2009; Immel et al., 2015; Krajcarz et al., 2018; Wißing et al., 2016) and define the niches of species or even individuals by their position in the food web (Araujo et al., 2011; Bearhop et al., 2004; Higashi et al., 1992; Pocheville, 2015). If the analysis of stable carbon and nitrogen isotopes is used, a so-called isospace, a two-dimensional space, based on the δ^{13}C and δ^{15}N values of consumers and sources, can be determined, which makes the trophic niches visible (more details in chapter 4.2).

In the following, I will use the term “niche” for a trophic niche.

3.2.3. Ecology of modern foxes

The present is the key to the past, is the simplified statement of uniformitarianism, which is a fundamental assumption for interpretation in geological, archaeological, palaeontological and therefore also palaeoecological studies (Baker, 2014; Bottjer et al., 1995; Cameron, 1993; Erwin, 2011; Scott, 1963; Simpson, 1970). Uniformitarianism assumes that fundamental geological and physical processes have not changed over time. To a certain extent, this is also assumed by (behavioral) biological and ecological processes (Erwin, 2011; Scott, 1963). On the one hand, this assumption allows reconstructions of extinct life, biotopes and food webs (Erwin, 2011; Scott, 1963; Simpson, 1970), and on the other hand, it is a proven way to recognize differences between the past and the present (Baker, 2014; Erwin, 2011). Without the assumption of uniformitarianism, unexpected results would not be unexpected because the comparison is missing, and thus would hardly stimulate research. For this reason, I present the key points of ecology and behavioral biology of modern foxes, which I can assume for Late Pleistocene foxes as well.

Red fox (*Vulpes vulpes*) is one of the most common carnivores in Central Europe. The earliest palaeontological evidence in Europe dates back to the Holstein Interglacial (MIS 11) (Larivière and Pasitschniak-Arts, 1996; Wandeler and Lüps, 1993). During this period the red fox evolved from *Canis* (*Vulpes*) *alopecoides* (Haltenorth and Roth, 1968). The weight and size between male and female modern red foxes varies, depending on geographical distribution and seasonality. The average weight in Germany is between 5.5 to 7.5 kg (males) and 5.0 to 6.5 kg (females) and the average size is between 650 to 570 mm in males and 620 to 680 mm in females (Wandeler and Lüps, 1993). The color of their fur is mainly red, but can also vary greatly, especially in winter. Red foxes from Canada and Siberia can also show a silver coloration and are then called silver foxes (Monchot and Gendron, 2011). These silver foxes have become particularly important because they were the focus of the Russian Farm fox experiments by Dmitri K. Beljajew, which demonstrate the influence of tameness on domestication (Belyaev et al., 1985; Dugatkin, 2018; Lord et al., 2019; Trut et al., 2009; Trut, 1999; Trut et al., 2004).

Modern red foxes populate the entire area of the northern hemisphere from the Arctic to the northern border of the Sahara. Red foxes are found in whole Europe, the northern parts of India, and on the Arabian Peninsula. Only some islands, such as Iceland, are not occupied so far (Larivière and Pasitschniak-Arts, 1996; Wandeler and Lüps, 1993). This wide geographical distribution shows that the habitat of the red fox can be very variable and depends only on the food supply and structure of the environment (Kidawa and Kowalczyk, 2011; Larivière and Pasitschniak-Arts, 1996; Soe et al., 2017; Wandeler and Lüps, 1993). Habitats such as highly structured areas with many small meadows and forests are preferred.

Arctic fox (*Vulpes lagopus*), as its name suggests, is a mammal from the Arctic regions and evolved from an alopecoid fox (Kurtén, 1968; Pulliaines, 1993), whose origin probably lies in the Himalayan region (Wang et al., 2014). The earliest European evidence came from the Eemian Interglacial (MIS 5e), although the species had its largest distribution during the Late Pleistocene (Audet et al., 2002; Kurtén, 1968; Pulliaines, 1993). The total length of modern European Arctic foxes is between 450 mm and 650 mm and their weight between 1.2 kg and 6.8 kg (Audet et al., 2002; Pulliaines, 1993). Although a sexual dimorphism can be seen, it is not as pronounced as in the red fox. There are only two fur varieties of Arctic fox: a white morph and a blue morph (Pulliaines, 1993). Unlike red foxes, Arctic foxes have a more distinct change between summer and winter fur. The white morph is most common and has a clear white winter coat and a black-grey summer coat with a white belly. The blue morph is rarer, often found isolated on islands, with a blue winter coat and a darker blue summer coat. In general, the fur of Arctic foxes is denser than that of red foxes and the ears are rounder and hidden in the fur, indicating a morphological adaptation to cold regions (Audet et al., 2002; Pulliaines, 1993). Modern Arctic foxes colonize the Arctic region of Europe, including Iceland, Asia, and North America (Audet et al., 2002; Pulliaines, 1993). In general, the smaller Arctic fox is geographically displaced by the stronger and more opportunistic red fox (Hersteinsson and Macdonald, 1992; Tannerfeldt et al., 2002). In Finland, however, there are some northern regions where both foxes occur together (Pulliaines, 1993). Since they live in the Arctic region, Arctic foxes have to follow their prey. During the breeding season, they occupy the tundra of the mainland, Arctic islands and the alpine, and subalpine coniferous forests. During other seasons, Arctic foxes also occupy the solid ice of the Arctic Ocean, river valleys, swamps, and also urban areas such as villages and dumps (Audet et al., 2002; Macpherson, 1969; Pulliaines, 1993). Modern Arctic foxes can undertake migrations of up to 2,000 km (Pulliaines, 1993).

The number of red or Arctic foxes living in an area and their reproductive rate is mainly determined by the food supply (Pulliaines, 1993; Wandeler and Lüps, 1993). Studies of the average population density of modern foxes find 4 to 18 red foxes and 0.03 to 2.5 Arctic foxes per 10 km² (Pulliaines, 1993; Wandeler and Lüps, 1993). Within modern red fox populations, randomly taken samples have shown that 49 to 77% of the animals were younger than one year old (Bögel et al., 1974; Jensen and Nielsen, 1968; Lloyd et al., 1976; Van Haaften, 1970; Wandeler and Lüps, 1993). Modern red and Arctic foxes in the wild reach a maximum age of 10 years (Pulliaines, 1993; Wandeler and Lüps, 1993).

The main part of modern red foxes' diet comes from small mammals such as voles and hares, however, they feed on birds, carcasses, and fruits as well (Dell'Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Sidorovich et al., 2006). As red foxes are opportunists, they adapt quickly to a given food situation. Several studies have shown that more birds and rodents were consumed in spring and summer, while scavenging was more common in winter (Jędrzejewski and Jędrzejewska, 1992; Larivière and Pasitschniak-Arts, 1996; Lutz, 1978; Sidorovich et al., 2006; Wandeler and Lüps, 1993). Amphibians, fish, and reptiles are only a very small part of the diet. More common in their diet are insects, particularly large beetles such as ground beetles (Carabidae) and dung beetles (Geotrupidae) (Lutz, 1978; MacDonnald, 1977; Murdoch et al., 2010; Russell and Storch, 2004; Wandeler and Lüps, 1993). However, it is not only meat that red foxes consume, but fruits are also an essential part of their omnivorous diet. Therefore, red foxes' stomachs often contain stones of plums and cherries, seeds of apples and pears and acorns (Amores, 1975; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; Lutz, 1978; MacDonnald, 1977; Sidorovich et al., 2006; Wandeler and Lüps, 1993). In contrast to red foxes, modern Arctic foxes do not have such a wide range of food, although this should be due to their geographical distribution. Its primary dietary source is lemming (Audet et al., 2002; Kapel, 1999; Macpherson, 1969; Pulliaines, 1993). Since the lemming population density fluctuates from year to year, Arctic foxes need to forage other food resources as well. Therefore, scavenging is a common behavior, on the mainland mainly on reindeer or other large ungulate carcasses, and on the Arctic coast on marine mammals, such as whales and seals (Audet et al., 2002; Kapel, 1999; Pulliaines, 1993; Roth, 2003). During the summer, Arctic foxes also stay close to coastal bird colonies and hunt there (Kapel, 1999; Roth, 2003).

Both fox species show clear similarities in their protein diet, which is why they are competitors in areas where both occur (Hersteinsson and Macdonald, 1992). In most cases, the larger red fox is the winner. Additionally, both fox species have developed the same trophic behavior to get access to carcasses regularly: They are (at least temporarily) commensal to large carnivores such as polar bears (Kapel, 1999; Pulliaines, 1993) and wolves (Bassi et al., 2012; Wikenros et al., 2017). Commensal behavior is, by definition, a symbiotic behavior between two species, which benefits one species and does not affect the other (Hulme-Beaman et al., 2016; Yeshurun et al., 2009). Both fox species have discovered the benefits of human settlements as well and extended their commensal behavior to humans, by scavenging their food waste (Forsyth et al., 2014; Panek and Budny, 2017; Reshamwala et al., 2018). Animals that benefit from human proximity, meaning occupying the niches created by humans, are known as synanthropes (Hulme-Beaman et al., 2016; O'Connor, 2013). Synanthropic behavior is a kind of commensalism, but to humans and not to large carnivores. Recent research has indicated that this phenomenon is not restricted to modern foxes, but also likely occurred during the Magdalenian (Baumann et al., 2020).

4. Material and methodology

4.1. Investigating Palaeolithic fox exploitation

The studied material for investigating the exploitation of foxes (**Publication 1**) consists of 26 assemblages from twelve different cave and rock shelter sites from the Swabian Jura, dating to the Middle Palaeolithic, Aurignacian, Gravettian/Aurignacian transition, Gravettian and Magdalenian (Table 4). The data presented are based on published single finds (piece-plotted and individual finds), even if many excavation sites were wet-sieved, the majority of these wet-sieved remains have not yet been published. All of the analyses for the quantity of foxes were based on NISP values (Number of identified specimens, Grayson (2014); Lyman (2008)). The reason for using NISP is that these values were published for each of the included assemblages, in contrast to e.g., MNI (Minimum number of individuals, Grayson (2014); Lyman (2008)). Using NISP values had increased the number of comparable sites for further analyses.

Table 4: *NISP data and the %fox of Carnivora, fox/LH and hare/LH indices of the different assemblages. A = Aurignacian, G/A = Gravettian/Aurignacían transition, G = Gravettian, M = Magdalenian, LH = Large herbivores.*

Period / Site	Publication (Zooarch. data)	NISP of fox	NISP of hare	NISP of other carnivores	NISP of LH
M Brillenhöhle	Boessneck et al. (1973)	63	183	20	108
M Geißenklösterle	Münzel (2019)	28	13	26	39
M Helga Abri	Münzel (in prep.-a)	4	15	0	51
M Hohle Fels	Napierala et al. (2014)	41	122	12	313
M Langmahdhalde	**Publication 1**; Wong et al. (2017)	10	14	5	109
M Vogelherd	Niven (2006)	2	0	1	97
Magdalenian (n = 6)		**148**	**347**	**64**	**717**
G Bockstein	Krönneck (2012)	8	11	16	356
G Brillenhöhle	Boessneck et al. (1973)	181	738	36	357
G Geißenklösterle	Münzel (2019)	109	240	19	782
G Hohle Fels	Conard et al. (2013a)	74	497	52	1389
G Sirgenstein	Bertacchi (2017)	56	324	38	186
Gravettian (n = 5)		**428**	**1810**	**161**	**3070**
G/A Fetzershaldenhöhle	Lykoudi (2017)	140	161	72	644
G/A Hohle Fels	Conard et al. (2013a)	14	22	14	212
G/A Transition (n = 2)		**154**	**183**	**86**	**856**
A Bockstein	Krönneck (2012)	6	8	12	125
A Brillenhöhle	Boessneck et al. (1973)	3	6	4	24
A Geißenklösterle	Münzel (2019)	159	209	111	6700
A Hohle Fels	Conard et al. (2013a)	29	37	40	876
A Hohlenstein-Stadel	Kitagawa (2014)	36	31	72	107
A Sirgenstein	Bertacchi (2017)	24	73	37	255
A Vogelherd	Boger et al. (2014); Niven (2006)	122	133	212	9802
Aurignacian (n = 7)		**379**	**497**	**488**	**17889**
MP Bockstein	Krönneck (2012)	36	10	115	993
MP Geißenklösterle	Münzel (2019)	26	8	32	211
MP Große Grotte	Weinstock (1999)	16	35	7	241
MP Hohle Fels	Conard et al. (2013a)	2	0	4	37
MP Hohlenstein-Stadel	Kitagawa (2014)	50	22	223	739
Middle Palaeolithic (n = 5)		**130**	**75**	**381**	**2221**
MP Kogelstein	Böttcher et al. (2000)	418	65	179	397
Middle Palaeolithic (n = 6)		**548**	**140**	**560**	**2618**

4.1.1. Indices of fox quantity

In general, fox remains are not well-represented at archaeological sites compared to other mammalian taxa. To calculate the fox abundance in the assemblages, the ratio of the NISP of foxes to the NISP of large herbivores (**fox/LH index**) were used, following Tchernov (1994) and Yeshurun et al. (2009). Similarly, the ratio of the **hare/LH index** (NISP of hares to the NISP of large herbivores) was calculated. Another method to calculate the relative abundance of foxes is the ratio of foxes within the carnivore sub-assemblage (NISP of foxes to the NISP of all carnivores, including foxes), or **%Fox of Carnivora**. Table 5 shows the taxa that were included to the different categories, used in the analyses of fox quantity, namely “Large herbivores”, “Carnivores”, “Fox”, and “Hare”.

Table 5: *Included taxa for the different categories.*

Large Herbivores (LH)		Carnivore		Fox		Hare	
"mammoth/rhino" size class		*Canis lupus*	Wolf	*Vulpes* sp.	Fox	*Lepus* sp.	Hare
"reindeer" size class		*Crocuta crocuta spelaea*	Cave hyaena	*Vulpes lagopus*	Arctic fox	*Lepus europaeus*	European hare
“horse” size class		*Felis silvestris*	Wild cat	*Vulpes vulpes*	Red fox	*Lepus timidus*	Mountain hare
Bison sp.	Bison	*Gulo gulo*	Wolverine				
Bos primigenius	Aurochs	*Lutra lutra*	Otter				
Capra ibex	Ibex	*Lynx lynx*	Lynx				
Cervus elaphus	Red deer	*Martes* sp.	Marten				
Coelodonta antiquitatis	Wooly Rhinoceros	*Mustela* sp.	Weasel				
Equus ferus	Horse	*Panthera leo spelaea*	Cave lion				
Mammuthus primigenius	Mammoth	*Vulpes* sp.	Fox				
Megaloceros giganteus	Giant deer	*Vulpes lagopus*	Arctic fox				
Rangifer tarandus	Reindeer	*Vulpes vulpes*	Red fox				
Rupicapra rupicapra	Chamois						

To get an impression of whether the number of foxes could be related to the human occupation density, **fox density** (NISP of foxes per m³ excavated sediment) and lithic artifact density (n of lithic artifacts > 2cm per m³ excavated sediment, from Conard et al. (2012)) were used (Table 6). The lithic artifact density can be seen as a simple proxy of human occurrence and activity (Conard et al., 2012), although it must be taken into account that the artifact density is biased by the artifact preparation techniques, the raw material, the proximity to the raw material source, and the excavation techniques. Furthermore, it must be mentioned that not all sites, such as Vogelherd and Hohle Fels, have been completely evaluated or are still being excavated.

Table 6: *Volume of excavated sediments and lithic artifact density, used from Conard et al. (2012). A = Aurignacian, G/A = Gravettian/Aurignacian transition layer, MP = Middle Palaeolithic.*

Site	Periode	Sediment (m³)	Lithic artifact density (n/m³)	Foxes (NISP)	Fox density (NISP/m³)
Geißenklösterle	A	25.45	760	26	1.02
Hohle Fels	A	19.95	1558	29	1.45
Sirgenstein	A	71	27	24	0.34
Vogelherd	A	202.5	27	122	0.60
Hohlenstein-Stadel	A	100	3	36	0.36
Hohle Fels	G/A	12.75	280	14	1.10
Große Grotte	MP	274	7	16	0.06
Geißenklösterle	MP	9.45	70	26	2.75
Hohle Fels	MP	9.7	89	2	0.21
Hohlenstein-Stadel	MP	390	3	50	0.13
Bockstein	MP	12.5	223	36	2.88

4.1.2. Bayesian statistical methods

Since the sample size within the studied archaeological assemblages is small, Bayesian statistics were applied to measure fox and hare abundance. Bayesian statistics have the advantage that they provide usable probability and likelihood information even with small sample sizes (n > 5, Gelman et al. (2014)). Meanwhile, Bayesian statistics are increasingly used in archaeological studies (Borradaile, 2003; Gearey et al., 2009; Halekoh and Vach, 1999; Halekoh and Vach, 2004; Otárola-Castillo and Torquato, 2018). One way to evaluate the reliability of the statistical analysis is by using the credibility interval (CI; 95% by default) of the regression line. The narrower the CI, the more certain is the given regression trend.

For the correlation between fox/LH and hare/LH indices, %fox of Carnivora between periods, and the analysis of the relationship between fox density and lithic artifact density, a normal linear model (lm) analysis in a Bayesian framework (R package arm; Gelman and Hill (2006)) was applied, following the protocol of Korner-Nievergelt et al. (2015). The lm analysis gives an adjusted r^2 value (adj. r^2) between 0 and 1, which can be used for the interpretation of the regression line (Korner-Nievergelt et al., 2015): positive values indicate a positive correlation and negative values indicate a negative correlation. The closer the value is to 0, the less likely the values are to correlate. Using Bayesian statistics eliminates the need for the p-value (probability value in frequency analyses), as this is generally too strongly biased by the sample size (Gelman et al., 2014; Halekoh and Vach, 1999; Halekoh and Vach, 2004; Korner-Nievergelt et al., 2015; Otárola-Castillo and Torquato, 2018). All Bayesian analyses were done with R Version 3.6.1.

4.2. Calculating trophic behavior of Late Pleistocene foxes

To investigate the trophic behavior of Late Pleistocene foxes (**Publication 2 and 3**), the analysis of stable carbon and nitrogen isotopes (δ^{13}C and δ^{15}N isotopic values) from bone collagen of these animals was used. For a better understanding of the trophic relationships between the members of a fossil community, it is necessary to use reliable tracers of predator-prey relationships and not to rely exclusively on modern analogs. During the past three decades, carbon and nitrogen isotopic abundances measured in fossil bone collagen of different species from Late Pleistocene sites have provided such information (e.g. Bocherens (2015); Bocherens et al. (1997); Bocherens et al. (2005a); Bocherens et al. (2005b); Bocherens et al. (2011); Bocherens et al. (2015); Bocherens et al. (1991); Fox-Dobbs et al. (2008)). In general, the collagen carbon and nitrogen isotopic values are reflecting the protein part of the diet for omnivores (Bocherens, 2009), and since meat is much higher in protein than plants, the impact of plant food will be negligible. Thus foxes could be treated in isotopic studies as predators, even if they are known to possibly include plant food in their diet (Pulliaines, 1993; Wandeler and Lüps, 1993). Especially, the δ^{15}N values in collagen are linked to the trophic level and indicate which prey were consumed in which proportions for carnivorous species (Bocherens, 2015; Bocherens and Drucker, 2003; Krajcarz et al., 2018).

Taken together, bone collagen from 127 specimens (foxes, canids, other carnivores, and small mammals) from Middle Palaeolithic, Aurignacian, Gravettian, and Magdalenian layers was extracted, carbon and nitrogen stable isotopes analyzed and finally published (Table 7).

***Table 7:** Used samples for isotopic analysis. A = Aurignacian, G = Gravettian, MP = Middle Palaeolithic.*

Period / Site	Sampled fox bones	Sampled other canid bones	Sampled other carnivore bones	Sampled small mammal bones	Publication
M Geißenklösterle	1			1	**Publication 3**
M Hohle Fels	1	4			**Publication 3**
M Vogelherd	1				**Publication 3**
M Gnirshöhle	1				**Publication 3**
M Kesslerloch		3			**Publication 3**
Magdalenian (n = 4)	**4**	**7**		**1**	
G Bockstein	1				**Publication 2**
G Geißenklösterle	2		2	2	**Publication 2**
G Hohle Fels		4		4	**Publication 2**
G Sirgenstein	6		1		**Publication 2**
Gravettian (n = 4)	**9**	**4**	**3**	**6**	
A Bockstein	1	1			**Publication 2**
A Geißenklösterle	1		1		**Publication 2**
A Hohle Fels	1	3		10	**Publication 2**
A Hohlenstein-Stadel	5	6	1		**Publication 2**
A Sirgenstein	4		2		**Publication 2**
A Vogelherd	9	6			**Publication 2**
Aurignacian (n = 6)	**21**	**16**	**4**	**10**	
MP Bockstein	5	1			**Publication 2**
MP Hohle Fels	1			28	**Publication 2**
MP Hohlenstein-Stadel	2	3			**Publication 2**
MP Vogelherd		2			**Publication 2**
Middle Palaeolithic (n = 4)	**8**	**6**		**28**	
Total	**42**	**33**	**7**	**45**	**127**

Stable isotopic data from further 45 specimens, including possible Magdalenian dogs from Gnirshöhle, mustelids, wild cats, songbirds, and more small mammals, as well as a few foxes from layers/sites with very little/no human influence, are still unpublished but will be included in later publications.

The taxonomic determination of carnivore specimens was done following published morphological and metrical studies (Bertacchi, 2017; Kitagawa, 2014; Krönneck, 2012; Münzel, 2019; Niven, 2006), as well as by comparing the bones with the zooarchaeological collection of the University of Tübingen. However, subsequently, red fox and Arctic fox will be combined as "fox", since they do not show a clear trophic niche differentiation in the Middle and Upper Palaeolithic (see S1 Text: Statistical test for ithe sotopic variance of both fox species in **Publication 3**). The newly analyzed small mammals were determined by using published determination keys (Erfurt, 2003; Jenrich et al., 2012; Neithammer and Krapp, 1982).

4.2.1. Principals of elemental and isotopic analyses

For the isotopic analysis of the carnivore and hare bones (Lab codes: JK, PLC, VLP, KSL, M), bone samples (0.3 – 0.7 g) were cut using a Saeshin Forte 200 alpha micro-circular saw. After successive cleaning in Millipore water and acetone, the samples were ground to powder manually (grain size less than 0.7 mm). In the case of the rodent samples (Lab code: SJM), the complete mandible without teeth was taken for each specimen and ground manually with a mortar, which resulted in a smaller grain size of the samples, but in a higher yield of bone powder. The collagen content of the bone was only measured for the carnivore and hare samples by performing a CNS elemental analysis following Bocherens et al. (2005a). This analysis was performed for PLC and JK samples at the Hydrogeochemisty working group (University of Tübingen) using a Vario EL elemental analyzer. The VLP, KSL ,and M samples were analyzed in the Laboratory for Soil Science and Geoecology (University of Tübingen) by using a Vario EL III elemental analyzer. Sulfanilic acid from Merck was used as the international standard in both laboratories. The rodent samples (SJM) did not have enough material to perform this preliminary analysis and were run directly for collagen extraction.

Collagen extraction following the protocol of Bocherens et al. (1997) was performed in the Biogeology working group (University of Tübingen). Depending on the percentage of nitrogen in the bone powder (%Nbone) of each sample, as measured by the CNS analysis, we used 120 mg (4.0 – 4.5 $\%N_{bone}$) to 450 mg (0.4 – 1.0 $\%N_{bone}$) of bone powder for the extraction. In the case of the rodent samples, the totality of the available powder was used, and, concerning the smaller grain size, the time in which the sample remains in 1 molar HCl solution was reduced to 15 minutes. The collagen extraction process included a step of soaking the bone powder in 0.125 molar NaOH between the demineralization and gelatinization steps to achieve the elimination of lipids and humic acids. After this process, the samples were freeze-dried.

The elemental analyses (C_{coll}, N_{coll}) and isotopic measurements of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) were performed in three different laboratories (Table 8).

Table 8: *List of involved laboratories for isotope analysis and their technical specifications.*

Isotopic Lab ID	Number of samples	Laboratory	Device	Calibration material	Reproducibility
JK, PLC-1 – PLC-49, SJM-1 – SJM-10	61	Laboratory of Chronology (Finnish Museum of Natural History)	NC 2500 elemental analyzer & Thermo Delta V Plus mass spectrometer	USGS-40, USGS-41	<4%
VLP, KSL, M	13	Geochemical department (University of Tübingen)	NC 2500 elemental analyzer & Thermo Quest Delta+XL mass spectrometer	USGS-24, IAEA-305A	<4%
PLC-55 – PLC-85, SJM-11 – SJM-63	53	Institute of Environmental Science and Technology (Universitat Autònoma de Barcelona)	Thermo Flash 1112 elementar analyzer & Thermo Delta V Advantage mass spectrometer	IAEA 600 (caffeine)	<2%

All commissioned laboratories measure the ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ relative to a standard (V-PDB for carbon and AIR for nitrogen). The isotopic ratios are expressed using the δ (delta) value as follows:

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

$$\delta^{15}N = [(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{reference} - 1] \times 1000\ [‰]$$

Following the recommendations of DeNiro (1985) and Ambrose (1990), I only used collagen samples with a carbon-to-nitrogen-ratio ($C:N_{coll}$) between 2.9 and 3.6 and a percentage of nitrogen higher than 5% for palaeoecological interpretations.

4.2.2. Trophic niche modeling

To generate representative isotopic environments (= isospace), published isotope values from herbivores (prey species) and carnivores have been added from literature (Table 9). Using this data and the newly analyzed samples, it was possible to form two isospaces, one for the pre-LGM (MP, A, G) of the Swabian Jura (= **SJ pre-LGM**) and one for the Magdalenian of Central Europe (= **CE Mag**). As the isospaces for the different pre-LGM periods are quite similar (Bocherens et al., 2011), I used the complete set of herbivores and small mammal species as dietary sources to reconstruct the trophic niches of the carnivores during the MP, Aurignacian, and Gravettian. To render this isospace more region-specific, only isotopic data from the Swabian Jura, in particular the Ach and Lone valley, were used. For the Magdalenian isospace (CE Mag) there were not enough isotope values from the Swabian Jura available so that isotopic data from other Central European sites had to be added. Palaeoecological studies have shown that this is possible since the isotope values in the Central European Magdalenian mammoth steppe did not differ significantly in the individual herbivore species so that the same isospace can be assumed (Bocherens et al., 2011).

Table 9: *Additionally used published taxa for the construction of the two isospaces. The figures in the references correspond to the following studies: 1 = Bocherens et al. (2011), 2 = Immel et al. (2015), 3 = Drucker et al. (2018), 4 = Drucker et al. (2011a), 5 = Drucker et al. (2011b), 6 = Stevens and Hedges (2004), 7 = Drucker et al. (2015), 8 = Münzel et al. (2014).*

Isospace	Taxon	Period	Number of specimens	References
CE Mag	Bison (*Bison* sp.)	Magdalenian	3	1
CE Mag	Elk (*Alces alces*)	Magdalenian	2	1
CE Mag	Giant deer (*Megaloceros giganteus*)	Magdalenian	2	2
CE Mag	Ground squirrel (*Spermophilus major*)	Magdalenian	4	1
CE Mag	Horse (*Equus* sp.)	Magdalenian	9	1
CE Mag	Mammoth (*Mammuthus primigenius*)	Magdalenian	3	1, 3
CE Mag	Mountain hare (*Lepus timidus*)	Magdalenian	16	1
CE Mag	Red deer (*Cervus elaphus*)	Magdalenian	5	1, 4
CE Mag	Red fox (*Vulpes vulpes*)	Magdalenian	1	1
CE Mag	Reindeer (*Rangifer tarandus*)	Magdalenian	44	1, 5, 6
CE Mag	Wolf (*Canis lupus*)	Magdalenian	3	1
CE Mag	Wooly rhinoceros (*Coeolodonta antiquitatis*)	Magdalenian	2	1
SJ pre-LGM	Brown bear (*Ursus arctos*)	Gravettian	2	1
SJ pre-LGM	Cave lion (*Panthera leo spelaea*)	Gravettian	3	1
SJ pre-LGM	Horse (*Equus* sp.)	Gravettian	6	1, 7
SJ pre-LGM	Mammoth (*Mammuthus primigenius*)	Gravettian	6	7, 8
SJ pre-LGM	Reindeer (*Rangifer tarandus*)	Gravettian	4	1, 7
SJ pre-LGM	Brown bear (*Ursus arctos*)	Aurignacian	1	1
SJ pre-LGM	Cave hyena (*Crocuta crocuta spelaea*)	Aurignacian	2	1
SJ pre-LGM	Horse (*Equus* sp.)	Aurignacian	18	1, 7, 8
SJ pre-LGM	Mammoth (*Mammuthus primigenius*)	Aurignacian	6	7, 8
SJ pre-LGM	Reindeer (*Rangifer tarandus*)	Aurignacian	11	1, 8
SJ pre-LGM	Brown bear (*Ursus arctos*)	Middle Paleolithic	1	1

Foxes and wolves are generalist predators/scavengers that occupy broad niches. If only species-related niches were built, all the niches will strongly overlap, because individual food preferences can be very broad. This phenomenon has been recognized in other studies as well (Bocherens, 2015; Bocherens et al., 2011; Bocherens et al., 2015; Wißing et al., 2016). However, individuals in such broad niches can specialize under certain circumstances, and eventually build new, more specific, niches (Araujo et al., 2011; Sheppard et al., 2018; Svanbäck and Persson, 2004). We see something similar in modern carnivores that were influenced by human behavior (Poessel et al., 2017; Prange et al., 2004; Roth, 2003; Warsen et al., 2014; Yirga et al., 2012) or in invasive species (Dammhahn et al., 2017; Jackson and Britton, 2014). If individuals feed of the same sources, they occupy the same trophic niche and are competitors.

For the SJ pre-LGM isospace, I was focusing on the trophic niches of foxes and combined wolves with other carnivores as a group. For the CE Mag isospace, there were not enough fox samples available to form resilient fox niches, so I created the niches together with wolves and dogs. However, the significance is the same with both methods. To reconstruct these trophic niches, I first applied a multivariate cluster analysis to the δ^{13}C and δ^{15}N isotopic values in JMP 14 with respect to the stratigraphic association, namely Middle Palaeolithic, Aurignacian and Gravettian in the SJ pre-LGM isospace and Magdalenian in the CE Mag isospace. As a result, different clusters for each of the periods were obtained. I then used the R package SIBER (Stable Isotope Bayesian Ellipses in R) to calibrate the niches out of the clusters (Jackson et al., 2011). It was possible to reconstruct the complete niches (= convex hull or total area, TA, Layman et al. (2007)) that include all members of the clusters, given by the isotopic values of my samples. Furthermore, I calculated the core niches (= standard ellipse area, SEA, Jackson et al. (2011)) that explain 40% of all potential specimens that will fit into these niches, based on the most likelihood estimation in a Bayesian framework. While the complete niche is quite sensitive to the given sample size, the core niche is more reliable for analyzing small assemblages and is recommend by Jackson et al. (2011).

To examine the trophic niche overlap between foxes and large carnivores in the SJ pre-LGM isospace, I calculated, additionally to SEA and TA, the standard ellipse area corrected for sample size (SEAc). Based on this, the percentage of overlap in the respective core niches could be estimated. For the CE Mag isospace, this method of calculating niche overlap between foxes and other carnivores could not be applied, as it requires a minimum number of five individuals per overlapping niche.

4.2.3. Dietary reconstruction

For dietary reconstructions, it was necessary to combine single prey species into larger groups with clearer isotopic differences (e.g. minimum and maximum values of δ^{13}C and δ^{15}N), by using multivariable cluster analysis of their isotopic values with JMP 14. For further calculations, it is necessary that the groups show a clear separation of the core niches (SEA), which was tested with the R package SIBER. These prey groups were calculated separately for each isospace (Table 10). To reconstruct the proportions of different prey groups in the protein fraction of the carnivore diet, I used the R package MixSIAR (Bayesian Mixing Models in R, Stock and Semmens (2016)).

Table 10: *Included isotopic samples for the reconstruction of the two isospaces, divided by prey groups.*

Isospace	Prey group	Taxa	Number of samples
SJ pre-LGM	Horse	Arctic lemming	8
		Horse	19
		Norway lemming	4
	Mammoth	Horse	2
		Mammoth	12
	Reindeer	Arctic lemming	1
		Hare	2
		Reindeer	15
	Rodents	Arctic lemming	2
		Horse	3
		Norway lemming	15
		Vole	15
CE Mag	Megaherbivores	Mammoth	3
	Ungulates	Elk	2
		Bison	3
		Red deer	5
		Wooly rhinoceros	2
		Horse	10
		Giant deer	2
		Reindeer	44
	Small mammals	Ground squirrel	4
		Hare	17

Initially, such Bayesian mixing models (e.g., MixSIAR, FRUITS, SIAR) were designed for ecologists who work with recent ecosystems and food chains but the model has been subsequently successfully applied to archaeological contexts (Baumann et al., 2020; Bocherens et al., 2015; Drucker et al., 2017; Meadows et al., 2019; Wißing et al., 2019; Wißing et al., 2016).

MixSIAR allows the reconstruction of the most likely diet of the carnivores based on the nitrogen and carbon isotopes from their bone collagen relative to the isotopic values from their prey species. Essential for this calculation is the trophic enrichment factor (TEF) that quantifies the increase of δ^{13}C and δ^{15}N values in collagen from prey to predator. Indeed, the stable isotope composition of a predator differs from the composition of its prey in a predictable manner. The TEF values correspond to the difference between the stable isotope ratios of the consumer (predator collagen) and its diet (prey collagen) and are the result of the discrimination of stable isotopes due to the behavior and physiology of the consumer (Bocherens et al., 2015; Dionne et al., 2016; Krajcarz et al., 2018). In both studies (**Publication 2 and 3**), TEF values (Δ^{13}C = 1.1 ± 1.1‰; Δ^{15}N = 3.2 ± 1.8‰) from a study on modern red fox by Krajcarz et al. (2018) were used. To get a robust statistical analysis, the MCMC (Markov Chain Monte Carlo, see Stock and Semmens (2016)) chain length was set to 1,000,000 with a burn-in of 500,000 in 3 chains. Verification of the model convergence was done with Gelman-Rubin and Geweke tests (for a detailed explanation, see Stock and Semmens (2016)). In brief, the Gelman-Rubin test shows model convergence if the values are near 1. In most analyses, values below 1.1 are acceptable (Gelman et al., 2014). Additionally, the Geweke test compares the mean of the first part of each chain with the mean of the second part, using a two-sided z-test. If both means are the same, the model is convergent (Geweke, 2004; Stock and Semmens, 2016). Results of the model convergence verification can be found in **publication 2 and 3**. All niche modeling (SIBER) and diet reconstructions (MixSIAR) were done using R Version 3.6.1.

4.3. Combining quantity and quality analyses

To find out how a particular fox niche responds in relation to human activity, I correlated them with the two indices, fox/LH and hare/LH, respectively. However, first of all, the value for the fox niches must be determined. I have calculated this value for each site and period as follows: the number of foxes in the respective niche divided by the NISP of foxes.

I then plotted the values obtained against the fox/LH and hare/LH indices, which were combined into three groups. The values were grouped into " <0.1", "0.1-0.5" and ">0.5". The correlation of the indices against the respective niches was then performed using the Bayesian normal linear model (lm) in R (Version 3.6.1 and R package arm; Gelman and Hill (2006)) and the adj. r^2 value was calculated. More information about Bayesian statistical methods in chapter 4.1.2.

5. Results and Discussion

In this chapter, I would like to discuss my research questions and examine the hypotheses formulated in chapter 2. For this purpose, I mainly refer to the research results of my three publications (attached as **publications 1-3**).

5.1. Fox exploitation by Palaeolithic hunter-gatherers in the Swabian Jura

To answer my first research question, namely, how people exploited foxes in the Middle and Upper Palaeolithic, I refer primarily to the results of my study on "The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany)", submitted to Archaeological and Anthropological Sciences on February 21, 2020, and attached to this thesis as **publication 1**. My first focus will be on the abundance of fox remains in zooarchaeological assemblages of the Swabian Jura, then on the use of foxes in the respective archaeological periods and finally on potential hunting methods.

5.1.1. Abundance of fox remains

In most archaeological assemblages of the Swabian Jura cave sites, fox remains make up 1 to 5%$_{\text{NISP}}$ of the faunal material (Bertacchi, 2017; Boessneck et al., 1973; Boger et al., 2014; Conard et al., 2013a; Kitagawa, 2014; Kitagawa et al., 2012; Krönneck, 2012; Lykoudi, 2017; Münzel, 2019; Napierala et al., 2014; Niven, 2006; Weinstock, 1999; Wong et al., 2017). Only in Kogelstein Cave are more than 37%$_{\text{NISP}}$ fox remains found in the faunal assemblage (Böttcher et al., 2000). However, I will not go into further details about this site as it was primarily used by hyenas and there is little evidence of human use. For more detailed information, see **publication 1**. Nevertheless, in all of the other assemblages, an increase in the relative abundance of foxes within the carnivore sub-assemblages (%fox of Carnivora), as well as in the relation to large herbivores (fox/LH index) from MP to the Magdalenian layers is recognizable (Table 11, Fig. 3). Since large herbivores were the main prey of Paleolithic hunter-gatherers, this index indicates how fox remains are related to the main prey of humans, and thus possibly gives a proxy for the importance of foxes in the prey spectrum of humans. However, other factors, such as the preservation of remains, excavation techniques, or natural death of the foxes in the cave play an important role and cannot be excluded in this index.

Table 11: *Important indices, calculated for foxes and hares. LH = Large herbivores, A = Aurignacian, G = Gravettian, G/A = Gravettian/Aurignacian transition layer, M = Magdamenian, MP = Middle Palaeolithic.*

(Period) Site	%Fox of Carnivora	Fox/LH	Hare/LH
(M) Brillenhöhle	76%	0.58	1.69
(M) Geißenklösterle	52%	0.72	0.33
(M) Helga Abri	100%	0.08	0.29
(M) Hohle Fels	77%	0.13	0.39
(M) Langmahdhalde	67%	0.09	0.13
(M) Vogelherd	67%	0.02	0
Magdalenian (n = 6)	**70%**	**0.21**	**0.48**
(G) Bockstein	33%	0.02	0.03
(G) Brillenhöhle	83%	0.51	2.07
(G) Geißenklösterle	85%	0.14	0.31
(G) Hohle Fels	59%	0.05	0.36
(G) Sirgenstein	60%	0.3	1.74
Gravettian (n = 5)	**73%**	**0.14**	**0.59**
(G/A) Fetzershaldenhöhle	66%	0.22	0.25
(G/A) Hohle Fels	50%	0.07	0.1
G/A Transition (n = 2)	**64%**	**0.18**	**0.21**
(A) Bockstein	33%	0.05	0.06
(A) Brillenhöhle	43%	0.13	0.25
(A) Geißenklösterle	59%	0.02	0.03
(A) Hohle Fels	42%	0.03	0.04
(A) Hohlenstein-Stadel	33%	0.34	0.29
(A) Sirgenstein	39%	0.09	0.29
(A) Vogelherd	37%	0.01	0.01
Aurignacian (n = 7)	**44%**	**0.02**	**0.03**
(MP) Bockstein	24%	0.04	0.01
(MP) Geißenklösterle	45%	0.12	0.04
(MP) Große Grotte	70%	0.07	0.15
(MP) Hohle Fels	33%	0.05	0
(MP) Hohlenstein-Stadel	18%	0.07	0.03
Middle Palaeolithic (n = 5)	**25%**	**0.06**	**0.03**

The fox/LH index increases slowly from an average of 0.06 in the MP layers to an average of 0.02 in the Aurignacian layers and an average of 0.14 in the Gravettian layers, up to an average of 0.21 in the Magdalenian layers.

However, there are some layers with a very high proportion of fox remains as well, such as in the Magdalenian layer of Geißenklösterle, with a fox/LH index of 0.72. The majority of fox bones in all sites are from adult animals. In total 28 remains (from an NISP of 1239) came from foxes younger than one year, most of them (n = 17) originating from the MP layers of Hohlenstein-Stadel (Kitagawa, 2014). This may be due, on the one hand, to the preservation, since unfused bones of juveniles are more susceptible to taphonomic processes, and, on the other hand, to the excavation method, since only single finds have been included in this study. The wet-sieved material of most of the sites had not yet been analyzed. However, missing juvenile remains may indicate that the caves were not used as natural fox dens and that foxes did not (or only rarely) breed there. Finally, the absence of juveniles could also indicate a human selection on adult foxes (see chapter 5.1.3 for more information).

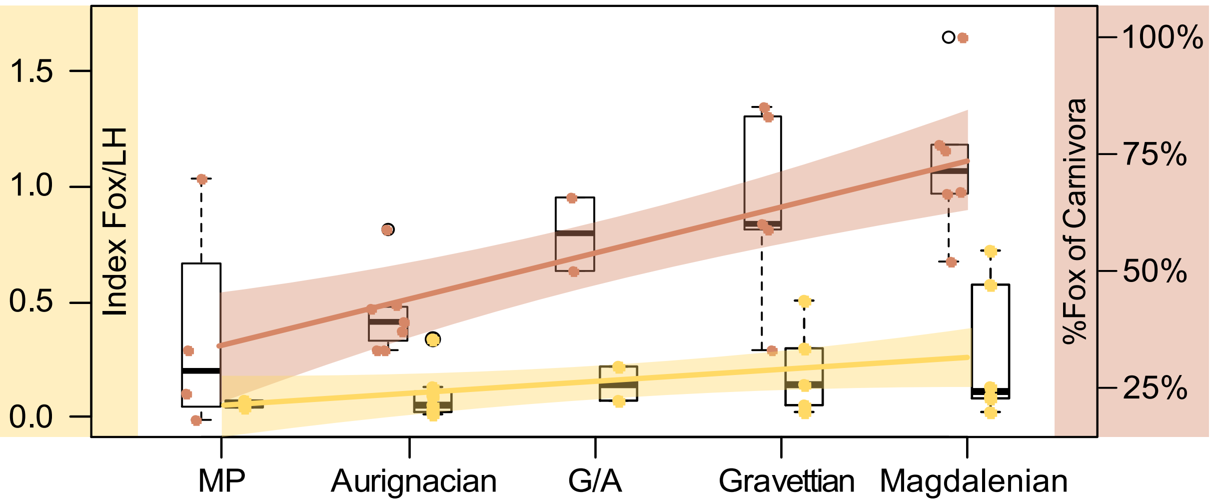

***Fig. 3:** Index of the relationship between foxes and large herbivores (LH) (yellow) and relative abundance of foxes in relation to other carnivores (red). Solid lines show the calculated mean regressions based on Bayesian linear model, shaded areas show 95% credibility interval. All values are based on NISP data. MP = Middle Palaeolithic, G/A = Gravettian/Aurignacian transition layer.*

5.1.2. Human modifications and the use of foxes

Human modifications, such as cut marks on fox bones are generally rare in the Palaeolithic, even if foxes are well-represented in assemblages (Lipecki and Wojtal, 2015; Street and Turner, 2013; Wilczyński et al., 2015; Wojtal and Wilczyński, 2015b; Wojtal et al., 2012), and the sites of the Swabian Jura are no exception: cut marks were found on only ten of the studied fox bones across the layers, respectively one in MP layer (Krönneck, 2012), five in Aurignacian layers (Conard et al., 2013a; Hahn, 1988; Münzel, 2019; Niven, 2006), two in Gravettian layers (Conard et al., 2013a) and two in Magdalenian layers (Napierala et al., 2014; Wong et al., 2017). Fox bones, showing cut marks, indicate both the skinning and use of the fur (n = 3), as well as butchering and use of meat (n = 7). However, not every cut leaves a mark and analysts have shown that experienced hunters or butchers leave hardly any marks on bone during the butchering process (Andersson and Paulsson, 1993; Binford, 1981; Charles, 1997). Furthermore, cut marks are often found on small bones, such as phalanges, which, due to their small size, are usually only recovered using finer methods of excavation, such as wet-sieving (Charles, 1997).

The most studied fox remains modified by humans are teeth (Fig. 4), which were used as pendants in Aurignacian (n = 15) and Gravettian (n = 9) periods by AMHs. Canines were most commonly perforated for this purpose (Camarós et al., 2016; Conard, 2003a; Hahn, 1992), although at least one incisor (Hahn, 1992) was used as an ornament, as well. Besides fox teeth, teeth from other carnivores were also used as pendants (Camarós et al., 2016; Conard, 2003a; Kitagawa et al., 2012; Langguth and Malina, 2003; Pacher, 2005). Together, the number of perforated teeth from the Aurignacian and Gravettian increases through time in archaeological assemblages (Camarós et al., 2016; Conard et al., 2013a; Kitagawa et al., 2012). If only foxes are considered, however, more ornaments are found in the Aurignacian than Gravettian layers. However, the number of fox tooth ornaments and ornament fragments may increase if the finds from wet-sieving are eventually included. Based on the current evidence, fox tooth ornaments might have been more important in the Aurignacian than later in the Gravettian, where ornaments of other carnivores became more abundant.

Summarizing, Paleolithic humans living in the Swabian Jura likely considered foxes to be both food resources and sources of raw material, such as fur and teeth. Other studies have come to similar conclusions, with Camarós et al. (2016) focusing on their use for food and Conard et al. (2013a) highlighting their use for fur.

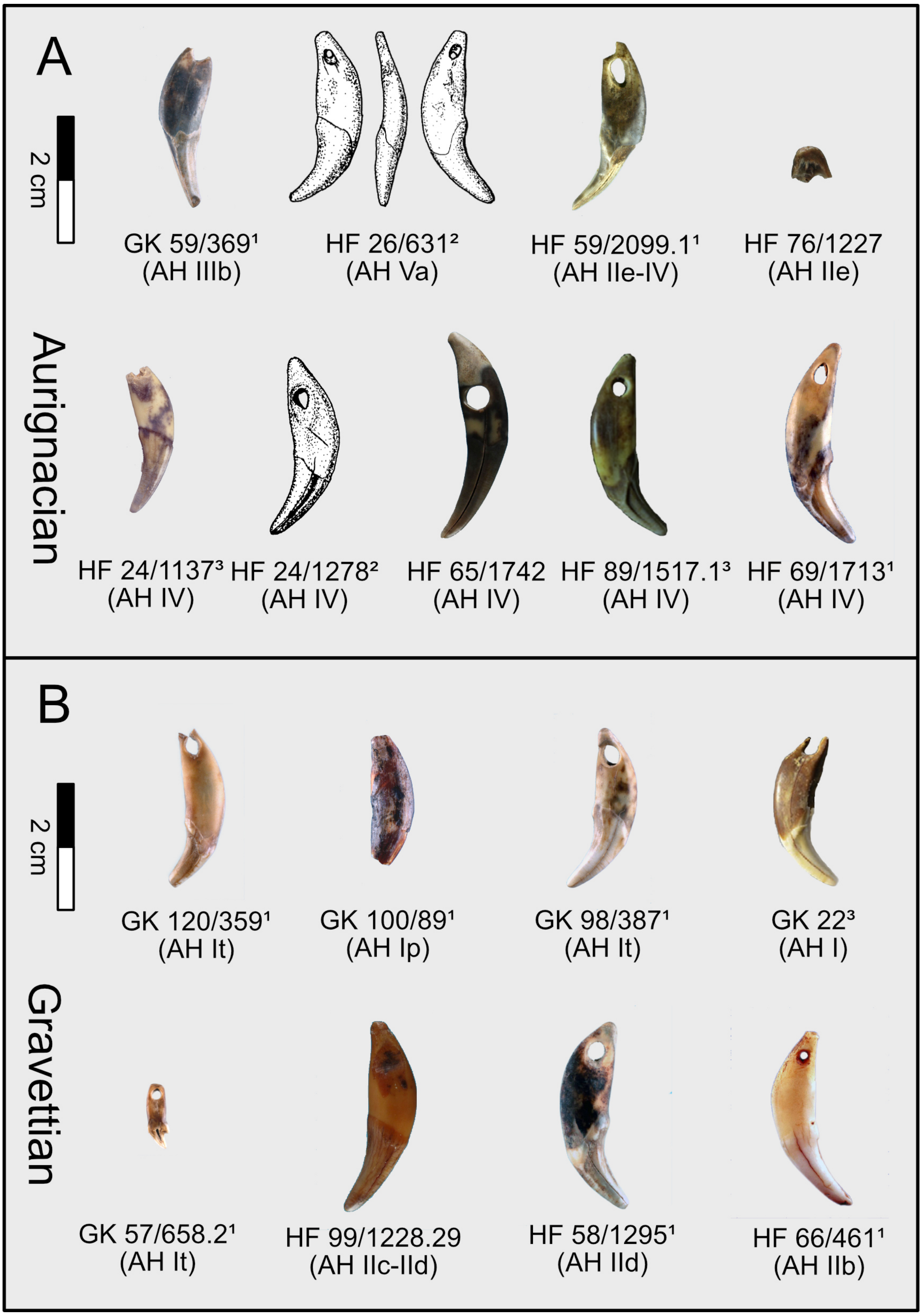

Fig. 4: A) *Nine fox tooth ornaments from the Aurignacian layers of Geißenklösterle (GK) and Hohle Fels (HF). Photos/drawings taken from [1]Langguth and Malina (2003), [2]Conard (2003) and [3]Camarós et al. (2016). Photos taken by Hilde Jenssen. AH = Archaeological horizon.*

B) *Eight fox tooth ornaments from the Gravettian layers of Geißenklösterle (GK) and Hohle Fels (HF). Photos/drawings taken from [1]Langguth and Malina (2003), [2]Conard (2003) and [3]Camarós et al. (2016). Photos taken by Hilde Jenssen. AH = Archaeological horizon.*

5.1.3. Hunting methods

Having now clarified the abundance of fox remains and proven their use by humans, we come to the important question: How were the foxes hunted?

It is informative to see that not only the NISP ratio of foxes to large herbivores, the main prey of humans, changed from Middle to Upper Palaeolithic but also the ratio of hares to large herbivores (hare/LH index, Tab 11). This conclusion is important for two primary reasons. Firstly, Conard et al. (2013a) combined hares and foxes in one category, recording a significant increase them from MP to Gravettian layers and thus proving the change in the diet breadth of AMHs in the Swabian Jura, which was described by Stiner et al. (2000) for the transition from the (European) Middle to the Upper Palaeolithic in general. This change required additional hunting techniques that Neanderthals did not use (or at least not to this extent) and leads us to the second reason. Hares are good comparison taxa to foxes as they have similar size and habitat requirements and are primarily nocturnal (Averianov et al., 2003; Pulliaines, 1993; Thulin and Flux, 2003; Wandeler and Lüps, 1993). With respect to their body proportions, we could, therefore, rank both taxa similarly in terms of caloric return and handling costs (Broughton et al., 2011). We assumed that the difference in hunting methods in relation to the prey choice model (PCM) would only be noticeable in the search time. Due to a negative correlation between the two indices fox/LH and hare/LH, we did not assume systematic hunting of foxes or hares by Neanderthals in the MP of the Swabian Jura ($n = 5$, adj. adj. $r^2 = -0.26$). With reference to Yeshurun et al. (2009), we only investigated the periods for hunting methods that showed a positive correlation, namely the Aurignacian ($n = 7$, adj. $r^2 = 0.50$), Gravettian ($n = 5$, adj. $r^2 = 0.88$) and Magdalenian ($n = 5$, adj. $r^2 = 0.99$). To investigate the most likely scenario for the Upper Paleolithic hunting of foxes, we have repeatedly compared the expected ratio of hares to foxes in each scenario with the archaeological ratios. In our study, we discussed four potential hunting scenarios:

1. A hunt for individual foxes and hares with long-range weapons such as a throwing spear, throwing stick, sling, or bow and arrow.
2. The use of traps, set up at game passes in an open landscape, which are used by small game.
3. The use of traps, set up near fox dens, for a selective fox hunt.
4. The use of traps with meat as bait for a selective fox hunt.

Table 12: *Assumptions of the four scenarios and results obtained from the archaeological periods. [1](Averianov et al., 2003; Pulliaines, 1993; Wandeler and Lüps, 1993; Watson and Hewson, 1973; Watson et al., 1973), [2](Bögel et al., 1974; Jensen and Nielsen, 1968; Lloyd et al., 1976; Van Haaften, 1970; Wandeler and Lüps, 1993).*

	Ratio fox : hare	Age distribution of foxes	Search time
Modern habitats	About 1 : 20[1]	49 to 77% juveniles[2]	
Scenario 1	About 1 : 20	Mainly adults	Depending on the environment
Scenario 2	About 1 : 20	Mainly adults	Low search time (set up traps)
Scenario 3	Mainly foxes	49 to 77% juveniles	Low search time (set up traps)
Scenario 4	Mainly foxes	Mainly adults	Low search time (set up traps)
Aurignacian	About 1 : 1		
Gravettian	About 1 : 4 to 1 : 7		
Magdalenian	About 1 : 2		

I have summarized the assumptions of the individual scenarios and the results obtained from the archaeological layers of the Upper Palaeolithic in Table 12. For more detailed information, see **publication 1**.

During the Middle Palaeolithic, the majority of the fox remains were likely deposited in the cave sites naturally, while humans were only sporadically involved. For the Upper Palaeolithic, we hypothesized in **publication 1** a combination of scenarios 2 and 4, meaning that foxes were caught primarily at game passes with traps and snares, partially baited with food remains. Although in the Magdalenian to a lesser extent than in the Aurignacian and Gravettian. Due to the low occupation density in some of the studied Magdalenian layers compared to the early Upper Palaeolithic (Conard, 2019; Münzel, 2019; Niven, 2006; Taller et al., 2014; Weniger, 1987a; Weniger, 1987b), more fox remains may have been introduced naturally as well. However, we could not exclude scenario 3, because the studied data did not include the wet-sieved materials and therefore did not provide an accurate assessment of the abundance of juvenile foxes.

Thus I can confirm my hypothesis that there are differences in the hunting of foxes and their exploitation between Neanderthals and AMHs in the Swabian Jura. While the found fox remains from the MP layers most likely entered the caves naturally, a hunt for foxes can be assumed from the Aurignacian onwards. The number of foxes is constantly increasing, which cannot be explained by taphonomic processes but is rather due to more intensive use of the fox as a resource for meat, fur, and teeth. Hunting at game passes was most likely performed with traps, partly baited with human food waste.

5.2. Trophic behavior of Late Pleistocene foxes

My second research question, which trophic behavior is shown by Late Pleistocene foxes and whether humans influenced this behavior in archaeological periods, I will discuss in this chapter. While the isotopic data for the pre-LGM are taken from the study "Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems", submitted to PLoS One on 27 February 2020 (**publication 2**), the results for the Magdalenian are taken from the published paper Baumann et al. (2020): “Dietary niche partitioning among Magdalenian canids in southwestern Germany and Switzerland”, attached as **publication 3**. First, I will present the newly obtained isotope data of the two studies and verify their association with single specimens. Then, I will present the two reconstructed isospaces and explain the trophic niches the foxes occupy.

The $\%N_{bone}$ values measured on 80 carnivore samples and three hare samples confirmed the favorable conditions of preservation (0.6 – 3.8%), establishing quantitatively that collagen is preserved in the samples. Moreover, the atomic $C:N_{coll}$ ratios of all analyzed carnivores (3.2 - 3.5), hares (3.3) and the newly analyzed 42 rodent samples (3.2 - 3.6), showed that the preservation of collagen was appropriate for the interpretation of the isotopic analysis in palaeobiological terms (Tables 13 and 14).

Table 13: *New carnivore samples used for isotopic analysis. AH = Archaeological horizon, A = Aurignacian, G = Gravettian, M = Magdalenian, MP = Middle Palaeolithic, BS = Bockstein, GK = Geißenklösterle, Gn = Gnirshöhle, HF = Hohle Fels, HS = Hohlenstein-Stadel, Ksl = Kesslerloch, Si = SIrgenstein, VH = Vogelherd.*

Publication	Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	Yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
Publication 2	PLC-79	MP	BS	BS 550825-35	BT VIII	*Canis lupus*	Radius	1.7	56.0	34.0	11.8	3.4	-20.1	10.6
Publication 2	PLC-35	MP	HS	HS 18/13-2806	MP R	*Canis lupus*	Ulna	2.2	64.7	35.2	12.4	3.3	-20.0	7.7
Publication 2	PLC-37	MP	HS	HS 13/10-8071	MP U	*Canis lupus*	Mandibula	1.1	33.8	34.6	12.1	3.3	-20.1	8.5
Publication 2	PLC-38	MP	HS	HS 17/11-4075	MP U	*Canis lupus*	Mandibula	2.1	74.4	33.6	11.8	3.3	-19.4	10.0
Publication 2	PLC-48	MP	VH	Vg VIII 7773	VIII	*Canis lupus*	Astragalus	2.4	104.5	38.8	13.6	3.3	-19.2	8.3
Publication 2	PLC-49	MP	VH	Vg VIII 12692	VIII	*Canis lupus*	Tibia	2.3	119.2	42.2	14.4	3.4	-19.7	7.3
Publication 2	PLC-76	MP	BS	BS 340813-6	BS V	*Vulpes lagopus*	Mandibula	0.9	27.3	40.0	13.3	3.5	-21.4	1.0
Publication 2	PLC-80	MP	BS	BS 340912-10	BS III	*Vulpes vulpes*	Tibia	0.8	41.7	26.4	9.1	3.4	-19.7	10.0
Publication 2	PLC-82	MP	BS	BS 340818-13	BS IV	*Vulpes vulpes*	Radius	1.5	71.5	42.5	15.0	3.3	-20.2	7.8
Publication 2	PLC-83	MP	BS	BS 330828-59	BS II	*Vulpes vulpes*	Humerus	2.7	135.2	43.1	15.3	3.3	-20.4	8.2
Publication 2	PLC-84	MP	BS	BS 340911-37	BS III	*Vulpes vulpes*	Mandibula	0.9	34.0	26.7	9.2	3.4	-20.1	9.0
Publication 2	VLP-10	MP	HF	HF 68/2989	VI	*Vulpes vulpes*	Tibia	3.7	73.2	42.0	14.9	3.3	-21.1	3.0
Publication 2	PLC-39	MP	HS	HS 13/9-8156	MP U	*Vulpes vulpes*	Mandibula	2.8	142.4	39.8	14.0	3.3	-20.3	8.4
Publication 2	PLC-40	MP	HS	HS 14/8-10670	MP U	*Vulpes vulpes*	Ulna	2.5	103.5	41.7	14.6	3.3	-19.9	8.6
Publication 2	PLC-78	A	BS	BS 550824-22	BT VI	*Canis lupus*	Tibia	2.9	107.0	41.0	14.6	3.3	-19.5	8.5
Publication 2	JK2175	A	HF	HF 24/1035	IIIa	*Canis lupus*	Ulna	2.5	67.2	34.4	12.2	3.3	-19.5	10.7
Publication 2	JK2180	A	HF	HF 89/1553	IV	*Canis lupus*	Humerus	3.1	110.3	40.9	14.6	3.3	-18.6	8.3
Publication 2	JK2184	A	HF	HF 79/2563	IV	*Canis lupus*	Metacarpal IV	3.4	96.8	40.2	14.3	3.3	-18.9	10.0
Publication 2	PLC-24	A	HS	HS 19/2-9285		*Canis lupus*	Mandibula	1.0	43.6	17.2	6.1	3.3	-19.1	9.5
Publication 2	PLC-25	A	HS	HS 19/2-9312		*Canis lupus*	Mandibula	0.6	14.9	34.8	12.2	3.3	-19.0	9.6
Publication 2	PLC-29	A	HS	HS 19/6-1435		*Canis lupus*	Ulna	2.8	108.4	41.8	14.8	3.3	-19.4	10.7
Publication 2	PLC-30	A	HS	HS 12/5-8905		*Canis lupus*	Atlas	2.5	85.0	40.1	14.1	3.3	-19.7	9.2
Publication 2	PLC-31	A	HS	HS 19/3-2467		*Canis lupus*	Ulna	1.9	74.7	42.2	14.6	3.4	-19.0	9.8
Publication 2	PLC-32	A	HS	HS 18/4-3805		*Canis lupus*	Humerus	3.2	158.8	41.9	14.8	3.3	-19.5	8.5
Publication 2	PLC-2	A	VH	Vg IV 9059	IV	*Canis lupus*	Radius	3.2	145.1	41.7	14.7	3.3	-20.2	9.1
Publication 2	PLC-3	A	VH	Vg IV/V 8200	IV/V	*Canis lupus*	Atlas	0.9	27.9	35.9	12.5	3.3	-21.0	9.4
Publication 2	PLC-44	A	VH	Vg V 12645	V	*Canis lupus*	Metacarpal	2.8	127.0	42.8	14.9	3.3	-18.9	9.6
Publication 2	PLC-45	A	VH	Vg IV 10685	IV	*Canis lupus*	Tibia	1.6	63.4	41.7	14.7	3.3	-20.4	9.5
Publication 2	PLC-46	A	VH	Vg IV 1732	IV	*Canis lupus*	Ulna	3.2	132.7	40.7	14.5	3.3	-19.7	9.3
Publication 2	PLC-47	A	VH	Vg IV 7214	IV	*Canis lupus*	Ulna	2.3	77.4	38.1	13.4	3.3	-19.2	8.9
Publication 2	PLC-62	A	Si	Si 1631	IV	*Gulo gulo*	Femur	2.1	67.3	34.8	12.4	3.3	-19.1	9.4
Publication 2	PLC-17	A	GK	GK 69/540	IIb	*Lynx lynx*	Phalanx		117.6	40.0	14.1	3.3	-19.3	7.7
Publication 2	PLC-23	A	HS	HS 18/7-11629		*Lynx lynx*	Humerus	2.6	79.8	40.4	14.2	3.3	-19.3	10.2
Publication 2	PLC-63	A	Si	Si 3892		*Lynx lynx*	Tibia	2.9	132.7	43.2	15.1	3.3	-19.8	7.0
Publication 2	VLP-1	A	GK	GK 35/206	III	*Vulpes lagopus*	Tibia	3.1	105.3	43.8	15.4	3.3	-20.6	9.1
Publication 2	VLP-3	A	HF	HF 25/1111	VAA	*Vulpes lagopus*	Radius	2.8	76.0	43.1	15.1	3.3	-19.9	8.6
Publication 2	PLC-22	A	HS	HS 17/4-5119		*Vulpes lagopus*	Mandibula	2.9	133.8	42.8	14.7	3.4	-20.2	5.4
Publication 2	PLC-28	A	HS	HS 19/7-11526		*Vulpes lagopus*	Mandibula	2.1	62.9	35.9	12.6	3.3	-19.7	8.6
Publication 2	PLC-55	A	HS	HS 17/7 7067		*Vulpes lagopus*	Mandibula	1.6	31.2	16.9	6.1	3.2	-20.1	8.9
Publication 2	PLC-1	A	VH	Vg IV 7213	IV	*Vulpes lagopus*	Tibia	2.6	113.6	41.9	14.6	3.4	-18.4	8.7

Table 13: *Continuing.*

Publication	Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	Yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
Publication 2	PLC-16	A	VH	Vg IV 245	IV	*Vulpes lagopus*	Mandibula	1.2	50.6	32.7	11.6	3.3	-19.4	9.4
Publication 2	PLC-15	A	VH	Vg IV 12782	IV	*Vulpes* sp.	Mandibula	1.4	56.7	35.1	12.2	3.4	-20.4	8.9
Publication 2	PLC-85	A	BS	BS 34-19		*Vulpes vulpes*	Tibia	2.5	112.4	43.9	15.5	3.3	-20.2	8.3
Publication 2	PLC-26	A	HS	HS 19/2-9298		*Vulpes vulpes*	Mandibula	0.8	30.9	27.2	9.6	3.3	-19.8	8.1
Publication 2	PLC-27	A	HS	HS 19/2-9359		*Vulpes vulpes*	Humerus	0.6	23.9	17.2	6.2	3.2	-20.2	8.2
Publication 2	PLC-66	A	Si	Si 3360	IV	*Vulpes vulpes*	Mandibula	1.8	76.3	40.5	13.8	3.4	-20.3	8.0
Publication 2	PLC-67	A	Si	Si 3361	IV	*Vulpes vulpes*	Mandibula	2.6	143.8	42.2	14.8	3.3	-21.0	8.2
Publication 2	PLC-68	A	Si	Si 3448	IV	*Vulpes vulpes*	Humerus	2.7	138.6	42.6	14.8	3.4	-20.4	6.0
Publication 2	PLC-69	A	Si	Si 3446	IV	*Vulpes vulpes*	Tibia	3.2	150.0	43.4	15.1	3.4	-20.0	4.8
Publication 2	PLC-10	A	VH	Vg IV 7245	IV	*Vulpes vulpes*	Tibia	1.1	36.2	37.7	13.1	3.4	-19.2	8.2
Publication 2	PLC-11	A	VH	Vg IV 7259	IV	*Vulpes vulpes*	Radius	3.2	148.2	42.3	14.9	3.3	-19.6	9.1
Publication 2	PLC-13	A	VH	Vg IV 12776	IV	*Vulpes vulpes*	Mandibula	2.3	112.6	38.9	13.6	3.3	-20.0	4.7
Publication 2	PLC-14	A	VH	Vg IV 12780	IV	*Vulpes vulpes*	Mandibula	1.1	42.8	34.1	11.9	3.4	-20.0	5.5
Publication 2	PLC-8	A	VH	Vg IV/V 11675	IV/V	*Vulpes vulpes*	Femur	2.8	58.4	40.7	14.4	3.3	-20.1	8.3
Publication 2	PLC-9	A	VH	Vg IV 3551	IV	*Vulpes vulpes*	Tibia	1.6	44.7	31.6	11.2	3.3	-19.4	5.7
Publication 2	JK2174	G	HF	HF 56/1965	IIC	*Canis lupus*	Scapula	3.5	144.8	39.6	14.1	3.3	-20.2	9.7
Publication 2	JK2183	G	HF	HF 59/1390	IIcf	*Canis lupus*	Calcaneus	3.4	155.7	40.9	14.4	3.3	-20.2	9.3
Publication 2	PLC-70	G	Si	Si 983	I	*Gulo gulo*	Scapula	3.1	165.1	41.7	14.8	3.3	-19.1	7.6
Publication 2	PLC-18	G	GK	GK 9/3	Ir	*Lynx lynx*	Rib	2.0	96.2	42.5	14.8	3.3	-19.5	8.4
Publication 2	PLC-19	G	GK	GK 121/93	Ir	*Lynx lynx*	Mandibula	3.6	137.2	42.6	14.8	3.3	-18.7	8.0
Publication 2	PLC-77	G	BS	BS 530924-15	BT IV/V	*Vulpes lagopus*	Ulna	2.2	97.6	41.6	14.7	3.3	-20.1	8.7
Publication 2	PLC-42	G	Si	Si 776	I	*Vulpes lagopus*	Mandibula	2.8	138.2	42.4	14.8	3.3	-20.3	7.6
Publication 2	VLP-4	G	GK	GK 508/70	I	*Vulpes vulpes*	Tibia	3.2	109.8	44.2	15.3	3.4	-19.7	7.1
Publication 2	VLP-5	G	GK	GK 15/106	I	*Vulpes vulpes*	Tibia	3.1	109.7	44.3	15.3	3.4	-19.7	9.7
Publication 2	PLC-43	G	Si	Si 773	I	*Vulpes vulpes*	Mandibula	3.2	166.9	43.9	15.1	3.4	-19.7	4.0
Publication 2	PLC-71	G	Si	Si 2862	I	*Vulpes vulpes*	Humerus	3.1	157.9	43.0	14.7	3.4	-20.5	6.0
Publication 2	PLC-72	G	Si	Si 2550	I	*Vulpes vulpes*	Mandibula	2.6	139.4	42.5	14.7	3.4	-19.4	6.7
Publication 2	PLC-73	G	Si	Si 2214	I	*Vulpes vulpes*	Humerus	2.8	135.5	44.0	14.9	3.4	-19.6	3.7
Publication 2	PLC-75	G	Si	Si 2213	I	*Vulpes vulpes*	Tibia	1.5	54.4	32.3	11.2	3.4	-20.3	9.2
Publication 3	JK2177	M	HF	HF 59/912	IIAD	*Canis lupus*	Tibia	3.3	148.3	41.5	14.6	3.3	-19.0	8.9
Publication 3	PLC-21	M	Gn	Gn2 P/22-171		*Vulpes vulpes*	Femur	1.7	65.9	40.1	14.0	3.3	-20.6	4.5
Publication 3	PLC-12	M	VH	Vg III 17185	III	*Vulpes vulpes*	Ulna	3.0	147.5	42.6	14.8	3.3	-19.7	8.2
Publication 3	VLP-6	M	GK	GK 78/17	AH Io	*Vulpes vulpes*	Tibia	2.5	53.2	43.2	14.8	3.4	-20.6	5.1
Publication 3	VLP-8	M	HF	HF 56/211	AH 0	*Vulpes lagopus*	Tibia	3.1	111.4	43.6	15.3	3.3	-20.6	5.3
Publication 3	JK2176		HF	HF 55/1250.1	-IIB	*Canis lupus*	Metacarpus II	3.7	169.4	41.6	14.7	3.3	-19.6	8.6
Publication 3	JK2179		HF	HF 55/1250.2	-IIB	*Canis lupus*	Carpus	3.8	173.5	39.9	14.2	3.3	-19.5	9.1
Publication 3	JK2181	M	HF	HF 100/530	IIB	*Canis lupus*	Cranium	3.3	147.1	40.9	14.6	3.3	-19.4	7.4
Publication 3	KLS-44	M	Ksl	M001:189		*Canis l. familiaris*	Palatinum	1.8	73.0	38.9	13.8	3.3	-19.2	5.9
Publication 3	M 58	M	Ksl	M001:58		*Canis lupus*	Mandibula			29.0	9.8	3.5	-20.1	7.1
Publication 3	M 62	M	Ksl	M001:62		*Canis lupus*	Maxilla			45.4	15.7	3.4	-20.0	7.9

Table 14: *New Small mammal samples used for isotopic analysis. AH = Archaeological horizon, A = Aurignacian, G = Gravettian, M = Magdalenian, MP = Middle Palaeolithic, GK = Geißenklösterle, HF = Hohle Fels.*

Publication	Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
Publication 2	SJM-7	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandibula		61.0	33.1	11.7	3.3	-21.2	5.5
Publication 2	SJM-8	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandibula		42.1	29.7	10.7	3.2	-21.0	6.7
Publication 2	SJM-9	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandibula		70.1	32.9	11.6	3.3	-21.2	7.1
Publication 2	SJM-11	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandibula		86.8	25.1	8.0	3.6	-25.1	-1.5
Publication 2	SJM-1	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		52.3	34.7	12.2	3.3	-21.8	5.9
Publication 2	SJM-2	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		60.1	33.6	11.8	3.3	-22.2	4.8
Publication 2	SJM-3	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		44.8	32.7	11.5	3.3	-20.7	6.5
Publication 2	SJM-4	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		55.4	35.4	12.2	3.4	-22.0	5.8
Publication 2	SJM-5	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		69.5	33.8	11.7	3.4	-21.9	7.3
Publication 2	SJM-6	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		72.0	32.0	11.4	3.3	-21.8	6.8
Publication 2	SJM-12	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		54.7	30.9	11.3	3.2	-23.1	1.0
Publication 2	SJM-13	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		70.3	31.1	11.3	3.2	-23.2	5.2
Publication 2	SJM-14	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		68.0	25.3	9.2	3.2	-24.9	-0.6
Publication 2	SJM-15	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		86.0	27.7	9.3	3.5	-24.6	1.0
Publication 2	SJM-16	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		70.5	26.0	8.4	3.6	-24.5	0.6
Publication 2	SJM-17	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		79.3	28.5	10.5	3.2	-22.9	2.5
Publication 2	SJM-18	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandibula		60.2	26.7	8.9	3.5	-23.5	2.5
Publication 2	SJM-10	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		63.1	30.4	10.9	3.3	-22.4	7.3
Publication 2	SJM-29	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		44.3	27.8	9.4	3.5	-22.5	7.9
Publication 2	SJM-30	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		48.2	25.7	9.0	3.3	-22.1	4.5
Publication 2	SJM-31	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		30.1	25.2	8.6	3.4	-22.6	6.7
Publication 2	SJM-32	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		59.3	26.9	9.2	3.4	-23.0	7.4
Publication 2	SJM-33	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		45.1	25.7	8.7	3.4	-23.1	5.4
Publication 2	SJM-34	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		67.1	21.4	7.9	3.2	-22.0	5.7
Publication 2	SJM-35	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		47.3	25.1	8.8	3.3	-22.7	4.4
Publication 2	SJM-36	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		59.3	23.2	7.9	3.5	-22.2	5.9
Publication 2	SJM-37	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		65.6	22.6	8.2	3.2	-21.8	5.7
Publication 2	SJM-38	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/agrestis	Mandibula		63.1	23.4	8.4	3.2	-23.0	6.2

***Table 14:** Continuing.*

Publication	Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
Publication 2	SJM-54	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandibula		33.4	31.3	11.3	3.2	-21.2	6.4
Publication 2	SJM-55	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandibula		41.5	29.5	10.6	3.2	-20.3	7.1
Publication 2	SJM-56	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandibula		68.6	23.9	8.7	3.2	-20.9	5.2
Publication 2	SJM-57	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandibula		51.0	36.8	13.0	3.3	-21.4	5.2
Publication 2	SJM-58	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandibula		47.6	27.7	9.7	3.3	-22.8	6.6
Publication 2	SJM-59	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandibula		59.5	28.4	10.1	3.3	-21.6	3.9
Publication 2	SJM-60	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandibula		57.5	30.1	10.6	3.3	-20.9	5.6
Publication 2	SJM-61	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandibula		51.9	32.2	11.5	3.3	-21.7	4.2
Publication 2	SJM-62	A	HF	HF Eimer-719 (Qu 32, AH IV)	AH IV	Microtus arvalis/agrestis	Mandibula		31.2	21.9	7.6	3.4	-22.1	3.8
Publication 2	SJM-63	A	HF	HF Eimer-1277 (Qu 31, AH IV)	AH IV	Microtus arvalis/agrestis	Mandibula		41.3	23.3	8.0	3.4	-21.8	4.5
Publication 2	SJM-50	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Dicrostonyx sp.	Mandibula		64.5	31.9	11.5	3.2	-21.1	3.6
Publication 2	SJM-51	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Dicrostonyx sp.	Mandibula		75.6	32.4	11.4	3.3	-21.3	6.1
Publication 2	SJM-52	G	HF	HF Eimer-1429 (Qu 112, AH IIc)	AH IIc	Dicrostonyx sp.	Mandibula		71.8	34.7	12.3	3.3	-20.2	3.5
Publication 2	VLP-12	G	GK	GK 99/458	It	*Lepus* sp.	Tibia	3.0	92.2	43.4	15.3	3.3	-20.4	2.8
Publication 2	VLP-13	G	GK	GK 86/17	Ir	*Lepus* sp.	Tibia	2.6	59.1	43.6	15.5	3.3	-20.2	3.5
Publication 2	SJM-53	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Microtus arvalis/agrestis	Mandibula		20.4	30.9	11.1	3.2	-21.7	3.0
Publication 3	VLP-15	M	GK	GK 76/76	AHIo	*Lepus sp.*	Tibia	2.9	116.4	43.5	15.2	3.3	-20.8	1.9

Among the isotopic values in the SJ pre-LGM isospace, we found only minor differences between the average of wolves (δ^{13}C = -19.6 ± 0.6‰ and δ^{15}N = +9.1 ± 0.9‰), lynx (δ^{13}C = -19.3 ± 0.4‰ and δ^{15}N = +8.5 ± 1.2‰) and wolverines (δ^{13}C = -19.1 ± 0.0‰ and δ^{15}N = +8.5 ± 1.2‰). Compared to each other, red foxes (δ^{13}C = -20.0 ± 0.4‰ and δ^{15}N = +7.3 ± 1.9‰) and Arctic fox (δ^{13}C = -20.0 ± 0.8‰ and δ^{15}N = +7.6 ± 2.6‰) were also very similar in their average isotope values. In contrast to the other carnivores, both fox species yielded a slightly lower average δ^{13}C and δ^{15}N values and there was one outlier for each species among the Middle Palaeolithic specimens (PLC-76 and VLP-10). Among the CE Mag isospace, we found a clear difference between foxes (red and Arctic fox), wolves, and dogs. Both fox species showed δ^{13}C values of −20.6‰ and their δ^{15}N values ranged from +4.5 to +5.3‰. The only exception was the red fox PLC-12 from Vogelherd, with higher values in both isotopes (δ^{13}C = −19.7‰ and δ^{15}N = +8.2‰). This fox fell within the range of the wolves (δ^{13}C = −20.1 to −19.0‰ and δ^{15}N = +7.1 to +9.1‰). The δ^{13}C and δ^{15}N values of the analyzed dog fragment from Kesslerloch were −19.2‰ and 5.9‰, respectively.

The rodents average isotopic values of Arctic lemming (δ^{13}C = -21.3 ± 1.4‰ and δ^{15}N = +5.0 ± 2.6‰), Norway lemming (δ^{13}C = -22.5 ± 1.2‰ and δ^{15}N = +4.2 ± 2.4‰) and vole (δ^{13}C = -22.4 ± 0.5‰ and δ^{15}N = +5.6 ± 1.4‰) covered a wide range of the SJ pre-LGM isospace, and were quite similar to each other. In contrast, the analyzed hare samples (δ^{13}C = -20.3 ± 0.2‰ and δ^{15}N = +3.2 ± 0.4‰) showed slightly higher δ^{13}C and lower δ^{15}N values than the lemming species and the voles.

5.2.1. Age of death and intra-individual variation of the samples

Before I discuss the two reconstructed isospaces, I would like to briefly deal with the topics of age at death and intra-individual variation of the sampled specimens.

Due to the lack of juvenile fox bones in the cave sites of the Swabian Jura described in chapter 5.1.1, only adult fox specimens could be sampled. This also applies to the other newly sampled bones, as none of the postcranial bones were unfused and the permanent dentition was completely visible in mandible and maxilla samples. For this reason, I can assume that we do not have any differentiation in the niches due to the consumption of breast milk.

In 19 of 80 newly investigated carnivore isotope samples, the intra-individual variability could not be excluded (Red fox: 11 of 30; wolf: 6 of 30; lynx: 2 of 5; Table 15), resulting in a total MNI of 71. This conclusion is based on new genetic studies of wolves and foxes, as well as new direct dating of the samples. Unfortunately, some of the most significant results are from old excavations (Sirgenstein and Vogelherd) and could not be spatially assigned to find squares, which led to great uncertainty in the assignment to individual specimens. More detailed information on the pre-LGM specimens can be found in **publication 2**. The two HF wolf samples JK2176 and JK2179 (HF 55/1250.1 and HF 55/1250.2, respectively), published in Baumann et al. (2020), belongs to one individual due to subsequent genetic investigation (publication in preparation, personal communication with Saskia Pfrengle).

Table 15: *List of samples, probably affected by intra-individual variation. R = right, L = left, AH = Archaeological horizon.*

Site	Lab ID	Excav. No	AH/GH	Period	Taxon	Element	MNI
Geißenklösterle	PLC-18	GK 9/3	AH Ir	Gravettian	Lynx	Rib	1
	PLC-19	GK 121/93	AH Ir	Gravettian	Lynx	Mandible	
Hohlenstein-Stadel	PLC-26	HS 19/2-9298	Hieb 2	Aurignacian	Red fox	Mandible	1
	PLC-27	HS 19/2-9359	Hieb 2	Aurignacian	Red fox	Humerus	
Hohle Fels	JK 2176	HF 55/1250.1	-IIB		Wolf	Carpal	1
	JK 2179	HF 55/1250.2	-IIB		Wolf	Metacarpal II	
Sirgenstein	PLC-66	Si 3360	AH IV	Aurignacian	Red fox	Mandible (R)	1
	PLC-67	Si 3361	AH IV	Aurignacian	Red fox	Mandible (L)	
	PLC-43	Si 773	AH I	Gravettian	Red fox	Mandible (R)	1
	PLC-73	Si 2214	AH I	Gravettian	Red fox	Humerus (R)	
Vogelherd	PLC-2	Vg IV 9059	AH IV	Aurignacian	Wolf	Radius	2
	PLC-45	Vg IV 10685	AH IV	Aurignacian	Wolf	Tibia	
	PLC-46	Vg IV 1732	AH IV	Aurignacian	Wolf	Ulna (L)	
	PLC-47	Vg IV 7214	AH IV	Aurignacian	Wolf	Ulna (R)	
	PLC-10	Vg IV 7245	AH IV	Aurignacian	Red fox	Tibia	2
	PLC-11	Vg IV 7259	AH IV	Aurignacian	Red fox	Radius	
	PLC-15	Vg IV 12782	AH IV	Aurignacian	Fox	Mandible (R)	
	PLC-9	Vg IV 3551	AH IV	Aurignacian	Red fox	Femur	1
	PLC-13	Vg IV 12776	AH IV	Aurignacian	Red fox	Mandible (R)	

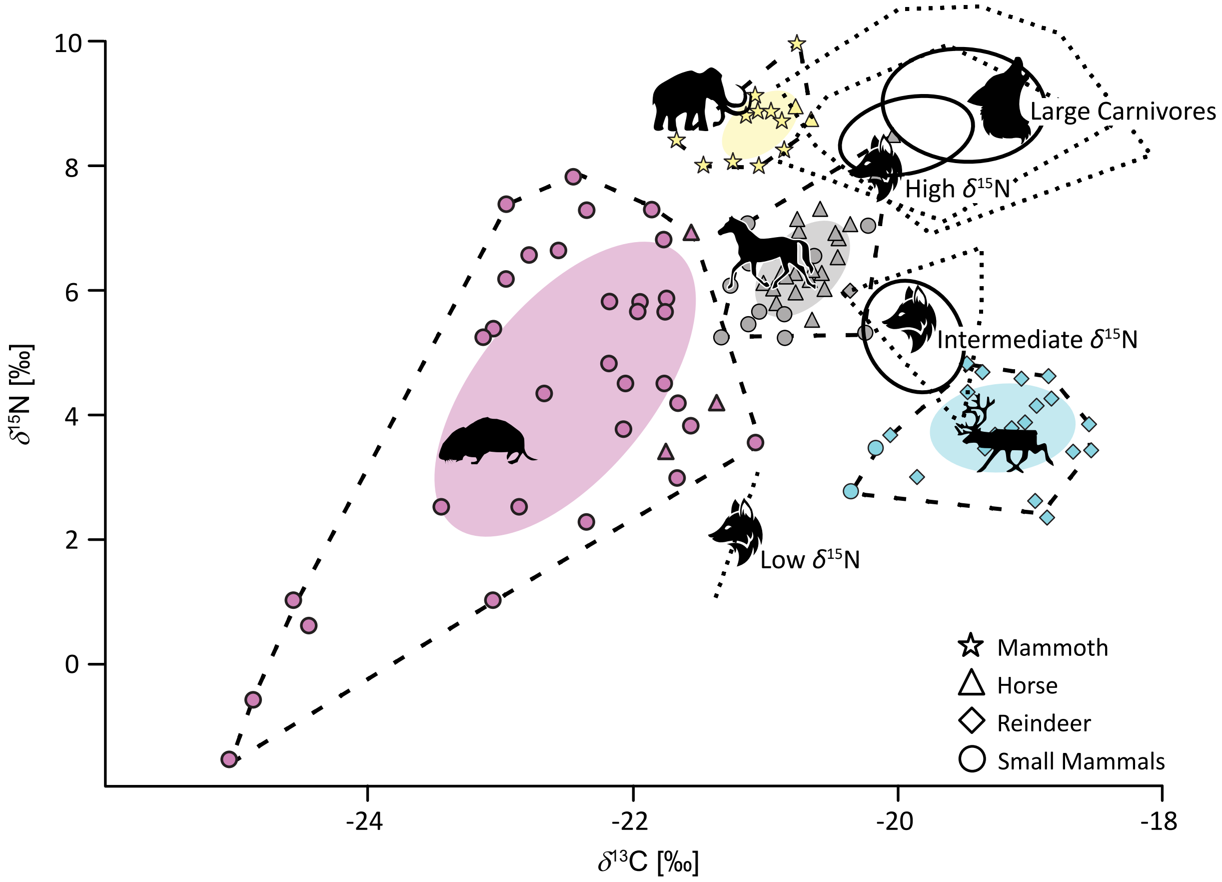

Fig. 5: *Isospace of the pre-LGM (Middle Palaeolithic, Aurignacian and Gravettian; SJ pre-LGM). The dashed lines each show the convex hulls (complete niches) while the ellipses (colored areas or as solid lines) show the Standard Ellypse Areas (core niches).*

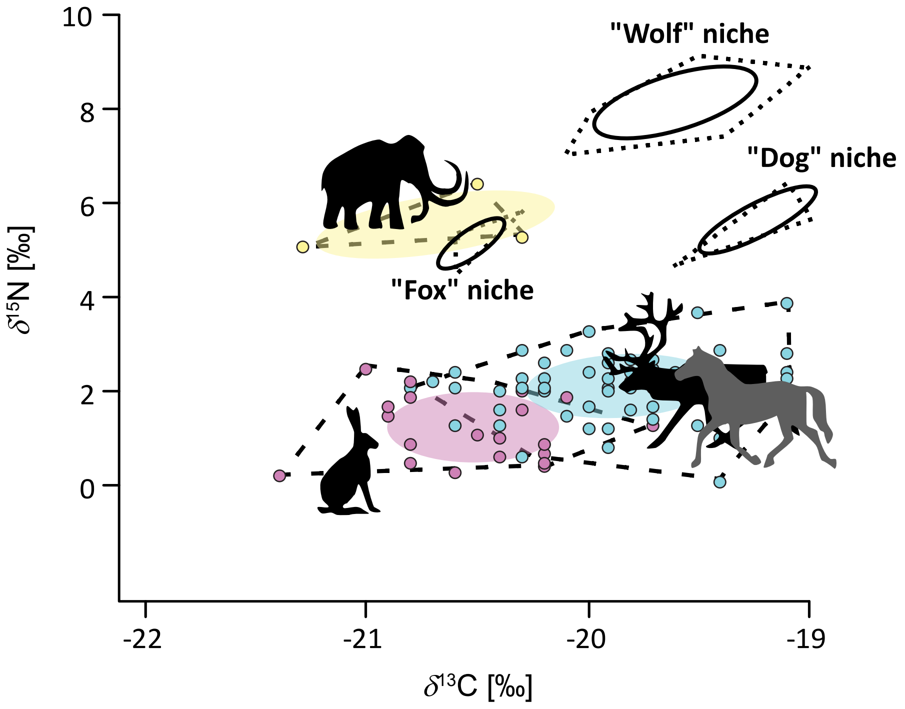

Fig. 6: *Isospace of the Magdalenian (CE Mag). The dashed lines each show the convex hulls (complete niches) while the ellipses (colored areas or as solid lines) show the Standard Ellipse Areas (core niches).*

Table 16: *Average isotope values of the individual calculated niches.*

Isospace	Period	Trophic niche	Number of samples	δ^{13}C	δ^{15}N
SJ pre-LGM	Middle Palaeolithic	low δ^{15}N foxes	2	-21.3 ± 0.2‰	+2.0 ± 1.4‰
		high δ^{15}N foxes	6	-20.1 ± 0.3‰	+8.7 ± 0.8‰
		large carnivores	7	-19.7 ± 0.4‰	+8.6 ± 1.2‰
	Aurignacian	intermediate δ^{15}N foxes	6	-20.0 ± 0.3‰	+5.4 ± 0.5‰
		high δ^{15}N foxes	15	-19.9 ± 0.6‰	+8.6 ± 0.4‰
		large carnivores	23	-19.5 ± 0.6‰	+9.3 ± 0.9‰
	Gravettian	intermediate δ^{15}N foxes	4	-19.8 ± 0.5‰	+5.1 ± 1.5‰
		high δ^{15}N foxes	5	-20.3 ± 0.3‰	+8.5 ± 1.1‰
		large carnivores	11	-19.4 ± 0.7‰	+8.8 ± 0.8‰
CE Mag	Magdalenian	"fox" niche	4	-20.5 ± 0.2‰	+5.2 ± 0.9‰
		"wolf" niche	7	-19.6 ± 0.8‰	+8.3 ± 1.1‰
		"dog" niche	4	-19.3 ± 0.4‰	+5.4 ± 1.0‰

5.2.2. Isospaces from the Middle to the Upper Palaeolithic

The two Isospace, namely SJ pre-LGM and CE Mag, were constructed as described in chapter 4.2.2. Table 10 shows which taxa are included in each prey group with how many specimens.

In the SJ pre-LGM isospace (Fig. 5), “reindeer” group has the highest δ^{13}C values (-19.3 ± 0.5‰) and the lowest δ^{15}N values (+3.8 ± 0.7‰). The “horse” group exhibits δ^{13}C values of -20.8 ± 0.3‰ and δ^{15}N values of +6.4 ± 0.7‰, while the “mammoth” group shows δ^{13}C values of -21.1 ± 0.3‰ and the highest δ^{15}N values (+8.7 ± 0.5‰). Finally, the “rodent” group exhibits δ^{13}C and δ^{15}N values of -22.5 ± 1.0‰ and +4.4 ± 2.3‰, respectively. For the CE Mag isospace (Fig. 6), we have recorded the following isotope values in the three calculated prey groups: "megafauna" showed the highest δ^{15}N values of +5.6 ± 0.7‰ and δ^{13}C values of -20.7 ± 0.5‰. The highest δ^{13}C values are present in the "Ungulates" group (δ^{13}C = -18.8 ± 0.4‰ and δ^{15}N = +2.1 ± 0.7‰). The "Small game" group has δ^{13}C and δ^{15}N values of -20.5 ± 0.4‰ and +1.2 ± 0.7‰, respectively.

For the SJ pre-LGM isospace, we calculated three niche types of foxes: foxes with high δ^{15}N values (range from +7.1 to +10.0‰), foxes with intermediate δ^{15}N values (range from +3.7 to +6.7‰), and foxes with low δ^{15}N values (range from +1.0 to +3.0‰). Additionally, the low δ^{15}N foxes show lower δ^{13}C values (range from -21.4 to -21.1‰) than the nearby intermediate δ^{15}N fox group (range from -20.5 to -19.4‰). This results in a total of six fox niches and three large carnivore groups, with respect to the three included pre-LGM periods (Table 16, Fig. 7a-9a). During all three pre-LGM periods the large carnivore groups overlapped with the high δ^{15}N fox niches to a large extent (Middle Pal. = 49.6%, Aurignacian = 39.0%, Gravettian = 41.0%). For the CE Mag isospace, three niches were calculated, including both foxes and large canids in all niches (Table 16, Fig. 10a). However, the niches did not overlap.

Despite the fact that we cannot exclude the inter-individual variation, there is no mixing of the samples beyond the Aurignacian and Magdalenian trophic niches. This means that the calculations of trophic niches, as we identified in our study, are still correct for the Aurignacian and Magdalenian, despite potential inter-individual variability. For the Gravettian, the situation is slightly different, since three samples of Sirgenstein could potentially belong together and thus extend beyond two niches. Unfortunately, no mtDNA was preserved in these samples (personal communication with Yumeko Tarusawa) and dating has not yet been possible either. Due to the great distance between the specimen in the SJ pre-LGM isospace (δ^{15}N = +6.0 and +6.7‰ to +9.2‰), an association to one individual is not very likely, but unfortunately not impossible. For the Gravettian, more samples are needed anyway to solidify the isospace, therefore we decided to continue with the calculated trophic niches for the time being.

5.2.3. Dietary reconstruction of fox niches and interpretation of fox trophic behavior

During pre-LGM, the diet of the high δ^{15}N foxes was quite similar to that of the large carnivores, which we can see by similar proportions (Tables 17-18 and Fig. 7b-9b) in the calculated diets and the niche overlap (39.0 to 49.6%) in all three periods. In the Magdalenian, only one of the sampled foxes (Table 21 and Fig. 10b) is found in a similar position. This leads to the conclusion that the high δ^{15}N foxes as well as PLC-12 (Vg III 17185 from VH) were commensal to large carnivores. The same behavior can be observed in modern red and Arctic foxes (Bassi et al., 2012; Dell'Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Macpherson, 1969; Murdoch et al., 2010; Pulliaines, 1993; Sidorovich et al., 2006; Soe et al., 2017; Van Haaften, 1970; Wandeler and Lüps, 1993; Wikenros et al., 2017) and is also suggested by morphological studies in Late Pleistocene red and Arctic foxes from Belgium (Szuma and Germonpré, 2019, 2020).

Another common trophic behavior in foxes is the diet on rodents and hares (Bassi et al., 2012; Dell'Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Murdoch et al., 2010; Sidorovich et al., 2006; Soe et al., 2017; Wandeler and Lüps, 1993). Both studies were able to prove this as well in the Late Pleistocene isospaces. In the SJ pre-LGM isospace, we found this behavior only in the Middle Palaeolithic, represented by the two low δ^{15}N foxes (Table 20 and Fig. 7b). For the CE Mag isospace, the “fox” niche is the equivalent of this (Table 22 and Fig. 10b).

The third trophic behavior that we were able to demonstrate in both studies was possibly influenced by humans (see chapter 5.4). During the Aurignacian and Gravettian, we have each a niche of intermediate δ^{15}N foxes, with a very restricted diet on reindeer and rodents (Table 19 and Fig. 8b-9b). We found a similar situation in the Magdalenian with a fox from Kesslerloch (Table 23, Fig. 10b). In the CE Mag isospace, this fox fell into the "dog" niche, in which three Kesslerloch canids fell, too. One of these canids was genetically (Loog et al., 2019) and morphologically (Napierala and Uerpmann, 2012) assigned a dog. We hypothesized in our studies that the fox showed synanthropic behavior (Baumann et al., 2020) and assumed similar results for the intermediate δ^{15}N foxes from the Aurignacian and Gravettian (**Publication 3**).

With these results, I can also confirm my second hypothesis. Firstly, three trophic behaviors of Late Pleistocene foxes could be determined and secondly, one of these behaviors seems to be influenced by humans. A more detailed evaluation will follow in the next chapter. This particular trophic behavior of some foxes indicates a restricted diet, while other dietary resources were available. As expected in my hypothesis, this niche could only be detected in the Upper Palaeolithic, and could, therefore, have been provided by AMHs.

Table 17: *Reconstructed dietary proportions for the different temporal large carnivore groups during the Middle Palaeolithic, Aurignacian and Gravettian.*

		n	Dietary source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
Large Carnivores		41	Horse	**35 ± 25%**	0.6%	1.4%	10.0%	**33.3%**	56.9%	74.3%	78.5%
			Mammoth	**25 ± 14%**	1.0%	2.5%	12.2%	**24.5%**	37.5%	46.3%	48.2%
			Reindeer	**30 ± 10%**	11.7%	14.2%	22.0%	**30.4%**	37.2%	44.1%	46.7%
			Rodents	**11 ± 5%**	2.8%	3.7%	7.6%	**10.7%**	14.1%	19.3%	21.5%
	Middle Pal.	7	Horse	**35± 25%**	0.6%	1.4%	10.0%	**33.6%**	56.4%	74.3%	78.3%
			Mammoth	**24 ± 14%**	1.1%	2.5%	12.3%	**24.4%**	36.8%	45.8%	47.9%
			Reindeer	**29 ± 9%**	11.0%	13.2%	21.4%	**29.6%**	36.3%	42.9%	45.0%
			Rodents	**12 ± 6%**	3.0%	4.0%	8.1%	**11.8%**	15.6%	22.0%	24.1%
	Aurignacian	23	Horse	**35 ± 26%**	0.5%	1.3%	10.0%	**34.6%**	57.9%	75.7%	80.1%
			Mammoth	**26 ± 15%**	0.9%	2.1%	12.7%	**26.1%**	39.7%	47.6%	49.5%
			Reindeer	**29 ± 9%**	11.1%	13.8%	21.4%	**29.3%**	35.7%	41.8%	43.6%
			Rodents	**10 ± 4%**	2.7%	3.5%	7.1%	**9.9%**	13.2%	17.8%	19.1%
	Gravettian	11	Horse	**34 ± 25%**	0.5%	1.3%	9.5%	**32.3%**	56.7%	74.3%	77.6%
			Mammoth	**24 ± 14%**	1.0%	2.4%	11.5%	**23.5%**	36.2%	44.6%	46.4%
			Reindeer	**31 ± 10%**	12.1%	15.0%	23.1%	**32.4%**	39.2%	46.2%	47.9%
			Rodents	**11 ± 5%**	2.8%	3.8%	7.3%	**10.5%**	14.0%	18.9%	20.5%

Table 18: *Reconstructed dietary proportions for the different temporal high δ^{15}N niches during the Middle Palaeolithic, Aurignacian and Gravettian.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
High δ^{15}N foxes		26	Horse	**24 ± 15%**	1.3%	2.7%	12.7%	**23.0%**	34.2%	50.2%	55.4%
			Mammoth	**22 ± 10%**	3.1%	5.1%	14.9%	**21.6%**	28.4%	36.7%	38.7%
			Reindeer	**25 ± 7%**	12.5%	14.3%	20.7%	**24.9%**	29.5%	35.7%	37.8%
			Rodents	**29 ± 6%**	18.6%	20.6%	25.4%	**29.0%**	32.8%	39.0%	41.0%
	Middle Pal.	6	Horse	**24 ± 15%**	1.2%	2.6%	12.5%	**22.3%**	33.7%	49.4%	54.1%
			Mammoth	**21 ± 9%**	2.6%	4.9%	14.2%	**21.1%**	27.7%	36.4%	38.2%
			Reindeer	**24 ± 6%**	11.5%	13.5%	19.7%	**23.9%**	28.2%	33.9%	35.7%
			Rodents	**31 ± 6%**	20.5%	21.8%	26.9%	**30.9%**	35.0%	42.7%	46.0%
	Aurignacian	15	Horse	**25 ± 15%**	1.3%	2.6%	13.1%	**23.8%**	35.3%	52.3%	57.8%
			Mammoth	**23 ± 10%**	3.0%	5.3%	15.8%	**23.1%**	30.2%	38.5%	40.7%
			Reindeer	**25 ± 6%**	12.7%	14.4%	20.6%	**24.5%**	28.6%	34.5%	36.1%
			Rodents	**28 ± 5%**	18.1%	19.5%	24.1%	**27.5%**	30.9%	35.9%	37.6%
	Gravettian	5	Horse	**24 ± 15%**	1.2%	2.5%	12.4%	**22.5%**	33.9%	50.3%	55.3%
			Mammoth	**21 ± 9%**	2.6%	4.9%	14.0%	**20.9%**	27.6%	35.6%	37.8%
			Reindeer	**26 ± 7%**	13.2%	15.3%	21.8%	**26.5%**	31.1%	37.5%	39.7%
			Rodents	**29 ± 6%**	18.4%	20.2%	25.3%	**28.8%**	32.4%	38.3%	40.4%

Table 19: *Reconstructed dietary proportions for the different temporal intermediate δ^{15}N niches during the Aurignacian and Gravettian.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
Intermediate δ^{15}N foxes		10	Horse	**4 ± 4%**	0.2%	0.5%	1.8%	**3.5%**	6.2%	11.2%	13.4%
			Mammoth	**3 ± 2%**	0.4%	0.5%	1.5%	**2.6%**	4.1%	7.4%	8.6%
			Reindeer	**46 ± 9%**	27.9%	31.3%	40.1%	**46.1%**	51.7%	60.1%	62.7%
			Rodents	**47 ± 9%**	30.9%	33.5%	41.2%	**46.4%**	52.0%	60.5%	64.4%
	Aurignacian	6	Horse	**5 ± 4%**	0.2%	0.5%	1.9%	**3.8%**	6.5%	12.2%	14.1%
			Mammoth	**3 ± 2%**	0.4%	0.6%	1.6%	**2.8%**	4.6%	7.7%	9.0%
			Reindeer	**47 ± 8%**	31.2%	33.7%	41.2%	**46.6%**	51.5%	59.0%	61.9%
			Rodents	**46± 7%**	31.3%	33.9%	40.7%	**45.2%**	50.3%	57.6%	60.1%
	Gravettian	4	Horse	**4 ± 4%**	0.2%	0.4%	1.8%	**3.5%**	5.9%	11.0%	13.1%
			Mammoth	**3 ± 2%**	0.3%	0.5%	1.4%	**2.4%**	3.9%	6.9%	8.1%
			Reindeer	**48 ± 8%**	30.6%	33.3%	42.2%	**47.6%**	52.9%	60.9%	63.4%
			Rodents	**45 ± 8%**	30.0%	32.7%	40.2%	**45.2%**	50.5%	58.5%	60.9%

Table 20: *Reconstructed dietary proportions for the low δ^{15}N niches during the Middle Palaeolithic.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
Low δ^{15}N foxes		2	Horse	**6 ± 6%**	0.3%	0.5%	2.1%	**4.5%**	8.5%	17.8%	21.3%
			Mammoth	**5 ± 4%**	0.4%	0.6%	1.9%	**3.8%**	6.5%	12.8%	15.4%
			Reindeer	**9 ± 8%**	0.9%	1.3%	3.8%	**7.2%**	13.1%	24.6%	28.5%
			Rodents	**80 ± 10%**	57.7%	61.9%	73.8%	**80.8%**	87.0%	93.0%	94.2%
	Middle Pal.	2	Horse	**6 ± 6%**	0.3%	0.5%	2.1%	**4.5%**	8.5%	17.8%	21.3%
			Mammoth	**5 ± 4%**	0.4%	0.6%	1.9%	**3.8%**	6.5%	12.8%	15.4%
			Reindeer	**9 ± 8%**	0.9%	1.3%	3.8%	**7.2%**	13.1%	24.6%	28.5%
			Rodents	**80 ± 10%**	57.7%	61.9%	73.8%	**80.8%**	87.0%	93.0%	94.2%

Table 21: *Reconstructed dietary proportions for the "Wolf" niche during the Magdalenian.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
"Wolf" niche		7	Megaherbivores	**74 ± 15%**	35.4%	46.8%	66.9%	**76.1%**	83.8%	92.4%	94.1%
			Small mammals	**15 ± 11%**	1.5%	2.3%	7.4%	**12.9%**	20.5%	34.8%	41.2%
			Ungulates	**11 ± 11%**	0.3%	0.5%	3.1%	**7.8%**	15.2%	34.1%	42.7%
	Wolf	6	Megaherbivores	**78 ± 11%**	53.8%	58.0%	70.7%	**78.8%**	85.7%	94.4%	96.1%
			Small mammals	**13 ± 9%**	0.9%	1.6%	6.2%	**11.4%**	18.3%	29.8%	33.6%
			Ungulates	**9 ± 9%**	0.1%	0.3%	2.2%	**6.6%**	13.5%	26.5%	31.6%
	Red fox	1	Megaherbivores	**69 ± 14%**	37.6%	45.6%	61.4%	**71.0%**	78.9%	88.0%	90.9%
			Small mammals	**21 ± 13%**	2.9%	4.5%	11.6%	**18.8%**	27.4%	44.0%	50.9%
			Ungulates	**10 ± 10%**	0.1%	0.3%	2.4%	**6.7%**	14.5%	29.2%	36.1%

Table 22: *Reconstructed dietary proportions for the "Fox" niche during the Magdalenian.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
"Fox" niche		4	Megaherbivores	**17 ± 14%**	1.6%	2.5%	7.4%	**13.3%**	21.2%	42.2%	57.4%
			Small mammals	**73 ± 19%**	15.2%	29.5%	66.5%	**78.3%**	86.3%	94.2%	95.6%
			Ungulates	**10 ± 13%**	0.3%	0.5%	2.4%	**5.4%**	12.2%	36.3%	49.7%
	Wolf	1	Megaherbivores	**20 ± 17%**	1.7%	2.8%	8.9%	**16.1%**	26.6%	52.7%	68.2%
			Small mammals	**70 ± 21%**	7.4%	24.7%	61.8%	**75.0%**	84.9%	94.1%	95.9%
			Ungulates	**10 ± 13%**	0.1%	0.3%	2.0%	**5.0%**	11.8%	36.3%	48.8%
	Arctic fox	1	Megaherbivores	**15 ± 15%**	0.4%	1.1%	5.8%	**11.8%**	19.6%	40.5%	60.0%
			Small mammals	**76 ± 20%**	8.8%	31.3%	69.3%	**80.4%**	88.5%	96.7%	98.3%
			Ungulates	**9 ± 14%**	0.1%	0.2%	1.6%	**4.5%**	10.9%	32.5%	48.8%
	Red fox	2	Megaherbivores	**12 ± 13%**	1.0%	1.7%	5.1%	**9.4%**	15.3%	29.6%	48.5%
			Small mammals	**81 ± 17%**	24.7%	50.1%	76.2%	**84.6%**	90.9%	96.4%	97.6%
			Ungulates	**7 ± 11%**	0.1%	0.2%	1.3%	**3.6%**	8.5%	23.0%	36.0%

Table 23: *Reconstructed dietary proportions for the "Dog" niche during the Magdalenian.*

		n	Prey source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
"Dog" niche		4	Megaherbivores	**29 ± 11%**	10.3%	12.9%	20.9%	**27.1%**	33.9%	49.0%	56.9%
			Small mammals	**50 ± 16%**	14.4%	21.1%	40.4%	**51.2%**	62.1%	75.4%	79.5%
			Ungulates	**21 ± 16%**	0.7%	1.5%	8.6%	**18.4%**	31.0%	50.5%	56.8%
	Wolf or dog	2	Megaherbivores	**27 ± 11%**	4.7%	9.7%	20.7%	**27.0%**	33.7%	44.3%	48.9%
			Small mammals	**47 ± 19%**	3.2%	10.1%	34.7%	**48.7%**	60.6%	74.1%	77.9%
			Ungulates	**26 ± 21%**	0.5%	1.1%	8.8%	**21.6%**	37.6%	67.9%	79.7%
	Dog	1	Megaherbivores	**27 ± 11%**	6.4%	10.5%	20.7%	**27.4%**	33.6%	44.8%	49.2%
			Small mammals	**48 ± 18%**	7.3%	14.8%	36.6%	**49.3%**	60.8%	74.7%	79.9%
			Ungulates	**25 ± 20%**	0.5%	1.1%	8.7%	**21.0%**	36.0%	61.2%	72.5%
	Red fox	1	Megaherbivores	**22 ± 10%**	6.3%	8.6%	15.6%	**21.3%**	27.6%	38.6%	43.5%
			Small mammals	**61 ± 17%**	22.2%	27.8%	50.3%	**62.4%**	73.3%	85.2%	88.3%
			Ungulates	**17 ± 15%**	0.2%	0.5%	4.8%	**12.9%**	25.7%	47.7%	56.5%

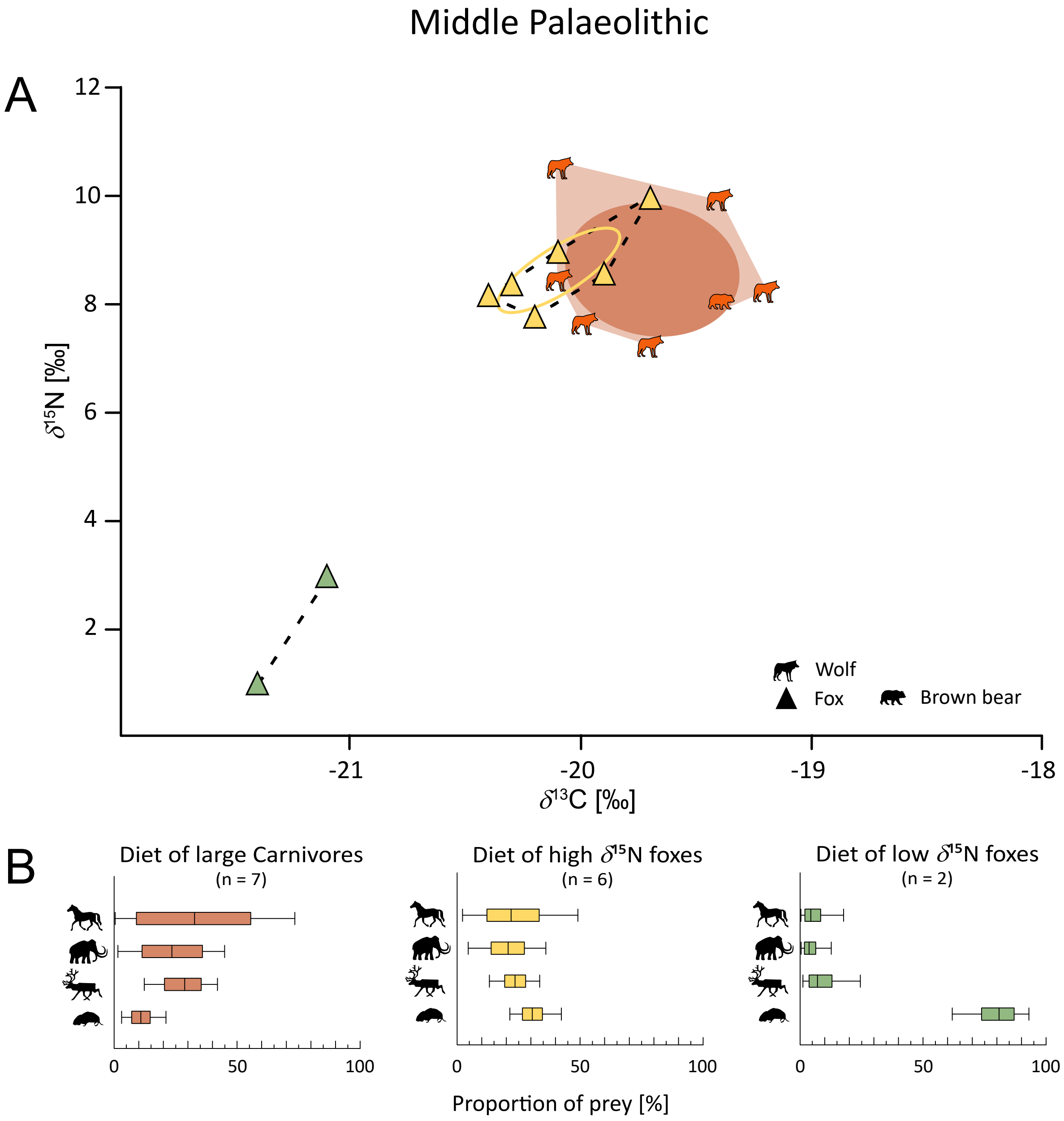

***Fig. 7: A)** Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Middle Palaeolithic with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (total niches). The solid lines and the dark collard ellipses show the calculated Standard Ellipse Area (core niches). **B)** Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.*

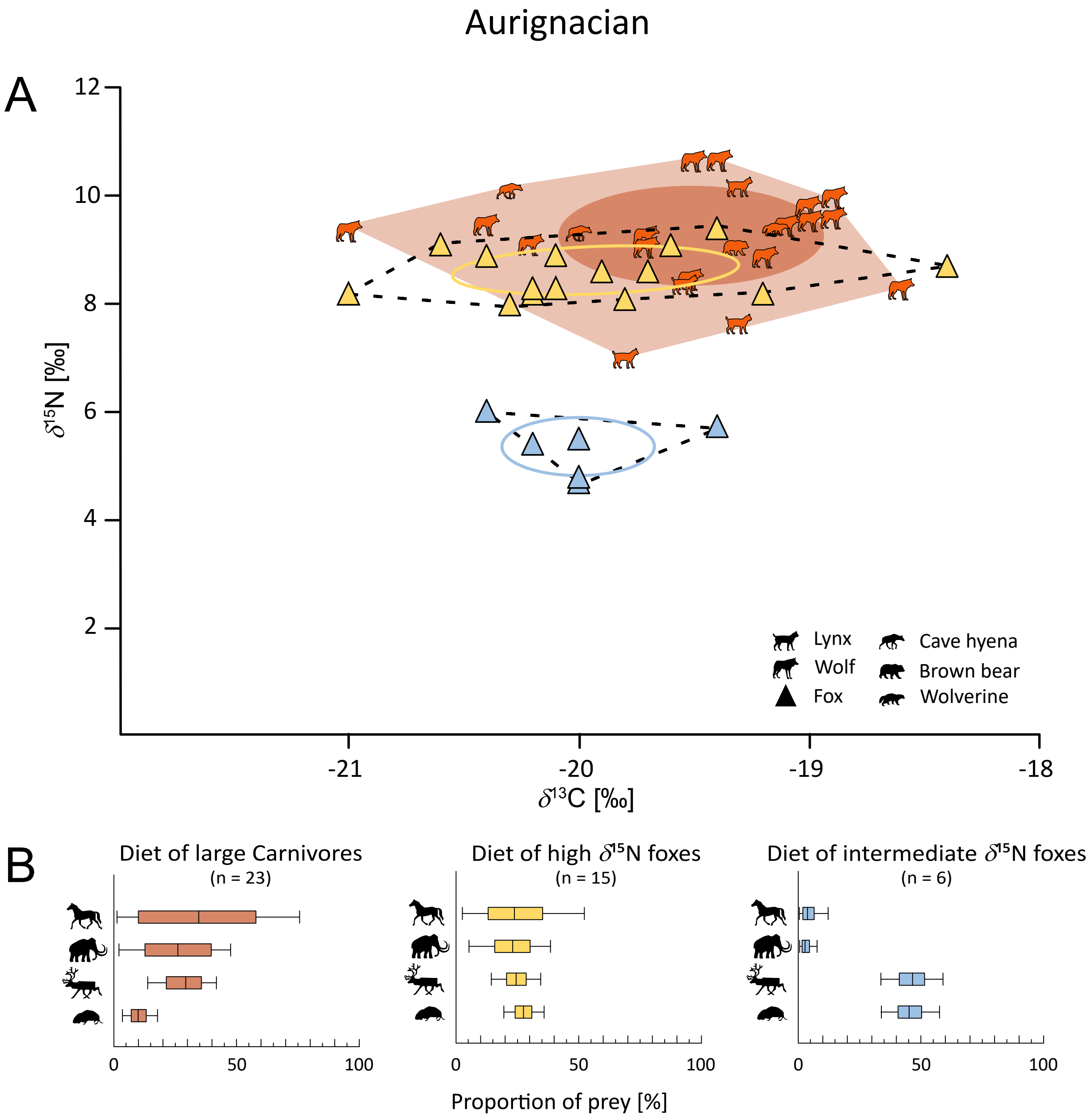

Fig. 8: A) *Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Aurignacian with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (total niches). The solid lines and the dark collard ellipses show the calculated Standard Ellipse Area (core niches).* ***B)*** *Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.*

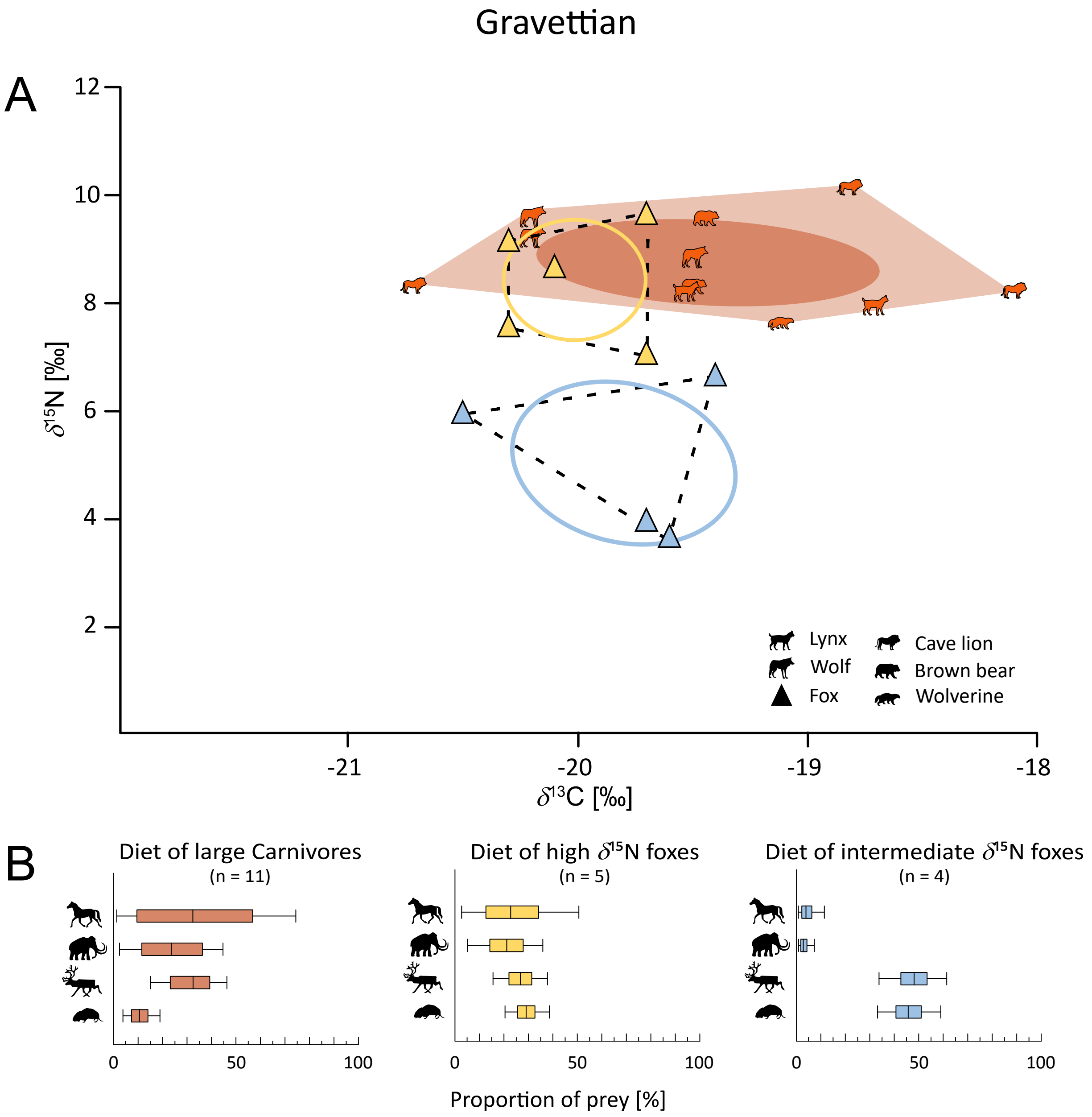

***Fig. 9: A)** Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Gravettian with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (total niches). The solid lines and the dark collard ellipses show the calculated Standard Ellipse Area (core niches). **B)** Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.*

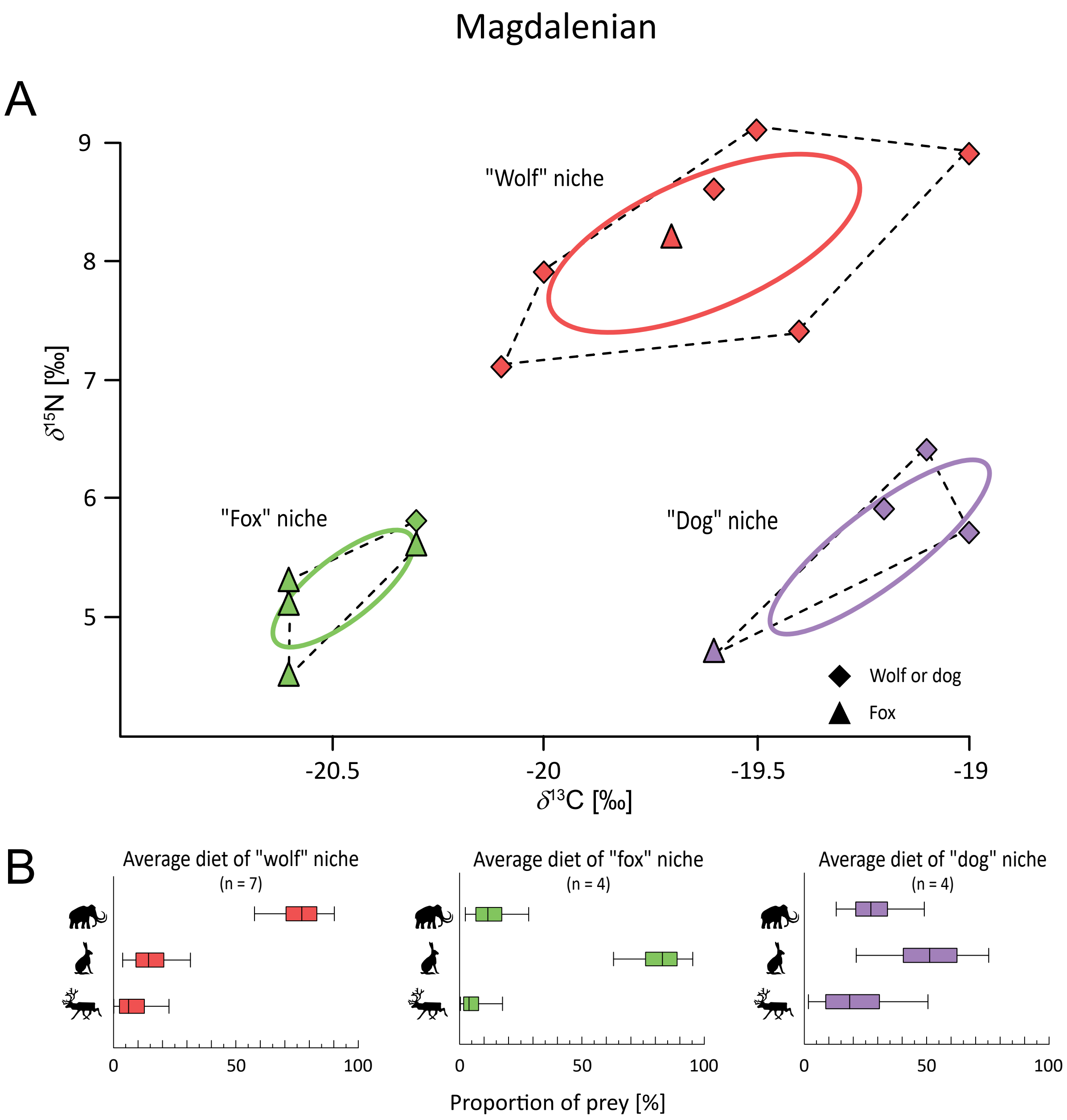

Fig. 10: A) *Calculated trophic niches of foxes (Triangles) and large canids (diamonds) from the Magdalenian with SIBER. Dashed lines show the convex hull (total niches), while solid lines show the calculated Standard Ellipse Area (core niches).* ***B)*** *Diet proportions calculated with MixSIAR of each niche. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.*

5.3. Could foxes indicate human impact on Late Pleistocene environment?

In this chapter, I would like to address my final research question of whether foxes can be used as a proxy for human behavior, population density, and interaction with the environment. For this purpose, I will try to combine all the results obtained from my studies. Starting with a consideration of how humans may have provided for specific niches, in particular what trophic resources they had made available. Then I will look at synanthropic behavior in foxes and try to correlate this with human occupation activities. Afterward, I will discuss the possibility that the observed patterns of abundance and niche allocation in foxes could be based on seasonality or natural factors. Finally, I will test my fox proxy hypothesis on other sites with published zooarchaeological and stable isotopic data.

5.3.1. What did Palaeolithic hunter-gatherer have to offer?

To pursue the question of whether and how foxes can be used as a proxy for human activities, for example, it must first be clarified what the trophic niche looked like, which humans created and to which some foxes adapted. For this, we consider how many people occupied the Swabian Jura and what they mainly hunted.

During the Middle Palaeolithic, the Swabian Jura was sparely populated by Neanderthals (Conard et al., 2013a), occupying the caves primarily in winter and spring (Münzel and Conard, 2004b). Common game species of Neanderthals, according to the zooarchaeological record, were horse and reindeer (Conard et al., 2013a; Kitagawa, 2014; Krönneck, 2012; Krönneck et al., 2004; Münzel, 2019; Münzel and Conard, 2004b). Isotope studies on the diet of Neanderthals from the Swabian Jura are still lacking. However, if we transfer the results from Central Europe studies (Bocherens, 2009; Bocherens et al., 2005b; Wißing et al., 2019; Wißing et al., 2016), we can assume that Neanderthals hunted and consumed mammoth in high proportions in the Swabian Jura as well.

The human population density in the Aurignacian was on average 3 people per 100 km², distributed in groups of 40 to 50 members (Schmidt and Zimmermann, 2019) and thus about 10 to 15 times higher than during the Middle Palaeolithic (Conard et al., 2013a). The zooarchaeological record indicates that, as in the Middle Palaeolithic, reindeer and horse were among the most important game species of the Palaeolithic hunters, but also a lot of mammoth and small game remains were found (Bertacchi, 2017; Conard et al., 2013a; Kitagawa, 2014; Krönneck, 2012; Münzel, 2019; Münzel and Conard, 2004b; Niven, 2006, 2007). Research on seasonality showed that the remains in the cave sites showed no preference for a particular season (Conard et al., 2013a; Gamble, 1979; Münzel, 2019; Münzel and Conard, 2004b; Niven, 2006). Probably they were visited all year round.

Although human population density in the Gravettian of the Swabian Jura has not yet been investigated in detail, there are some indications of decreasing population densities (Maier, 2017; Maier and Zimmermann, 2017). Nevertheless, there are faunal remains in the Gravettian layers, mainly in the cave sites of the Ach Valley, attributed to the presence of humans. This concerns mainly finds of favorite large game, such as reindeer, horse, and mammoth, but also small prey species such as hares, fish, and birds (Bertacchi, 2017; Conard et al., 2013a; Münzel, 2019).

The re-occupation of the Swabian Jura after the LGM probably took place quite quickly, although only short, irregular visits to the cave sites over a period of about 1000 years can be proven (Taller, 2014; Taller et al., 2014). In the Hegau Jura, Magdalenian people stayed longer, as numerous finds prove (Albrecht, 1979; Leesch and Müller, 2012; Napierala, 2008). Even if the main prey was reindeer and horse (Albrecht, 1979, 1983; Albrecht et al., 1977; Napierala, 2008), mammoth, although rare, existed in this region as direct dating of mammoth remains proved (Huber and Reinhard, 2016; Napierala, 2008).

In summary, it can be concluded that both Neanderthals in the Middle Palaeolithic and AMHs in the three periods of the Upper Palaeolithic hunted similar main prey, namely reindeer, horse, and mammoth. The latter was rare in the Magdalenian, although it cannot be excluded that it was well known among hunter-gatherers. In addition, the remains of small game increased since the Aurignacian, indicating a broader diet of AHM. Small game as well as animals up to the size of reindeer were brought to the cave sites and processed there (Niven, 2007), which could have created a potential food resource for foxes. Mammoths, in contrast, were butchered directly at the (human) kill sites and only certain parts were brought into the caves (Niven, 2007). This is another niche that could be used by foxes and other scavengers after humans have left the kill sites.

5.3.2. Signs of synanthropic behavior in foxes

The fact that modern foxes show synanthropic behavior and benefit from anthropogenic resources has already been proven in many studies (Amores, 1975; Dell'Arte et al., 2007; Jędrzejewski and Jędrzejewska, 1992; MacDonnald, 1977; Panek and Budny, 2017; Reshamwala et al., 2018; Sidorovich et al., 2006). The occupation of new trophic niches, which indicates the feeding on human food waste, was primarily used as the main argument.

If we refer to the main diet of humans and the identified fox niches, we find some parallels:

1. The high δ^{15}N foxes from the three pre-LGM periods show a high proportion of mammoth in their diets, similar to the large carnivore groups. In the Magdalenian, this trophic behavior is represented by the "wolf" niche. Both niches and the large carnivore group thus had unrestricted access to high δ^{15}N protein diet, such as mammoth meat, consumed by humans as well (Bocherens et al., 2005b; Drucker et al., 2017; Wißing et al., 2019; Wißing et al., 2016) and butchered at the kill sites (Niven, 2007). This leads to the hypothesis that specimens occupying these niches had regular access to kill sites and probably followed humans at a great distance.

2. For the intermediate δ^{15}N foxes of the Aurignacian and Gravettian, a diet was reconstructed, which primarily contains reindeer and rodents. Since foxes were not choosy in their scavenging, there must have been a reason for the dietary restriction to reindeer. My hypothesis is that they regularly fed directly on the food waste that humans produced while processing reindeer near the caves. Thus, these foxes would have shown synanthropic behavior. In the Magdalenian, we had identified a fox that also had a restricted diet and fell into a trophic niche together with potential dogs. Since the domestication of dogs in the Magdalenian is widely accepted (Germonpré et al., 2018; Thalmann and Perri, 2018), this suggested the hypothesis that the mentioned fox had scavenged from Magdalenian "dog food" and thus showed synanthropic behavior (Baumann et al., 2020).

However, synanthropic behavior also requires the regular presence of humans, otherwise, these niches would only be available for a short time and thus not be reflected in the stable isotope values of bone collagen (Bocherens et al., 1997; Bocherens and Drucker, 2003; Krajcarz et al., 2018). The study by Conard et al. (2012) provided first proxies for human occupation intensity, based on lithic artifact density. These values are comparable to fox remain density and show a positive strong correlation ($r^2 = 0.72$) of both indices in the early Upper Palaeolithic (Fig. 11). This allows the hypothesis that a higher settlement intensity leads to more foxes because they were either hunted more often or showed synanthropic behavior. The latter may also have led to an easier huntability of foxes, because synanthropic animals appear in larger groups than their non-synanthropic relatives and are therefore more tolerant to humans (Dell'Arte et al., 2007; Hulme-Beaman et al., 2016; Panek and Budny, 2017; Reshamwala et al., 2018; Wandeler and Lüps, 1993). If we refer to the PCM, this would be reflected in higher population densities within the vicinity of human-occupied areas and a decrease in search time. Therefore, synanthropic foxes could be hunted more often than non-synanthropic foxes and thus influence the ratio of fox to hare (see chapter 5.1.3).

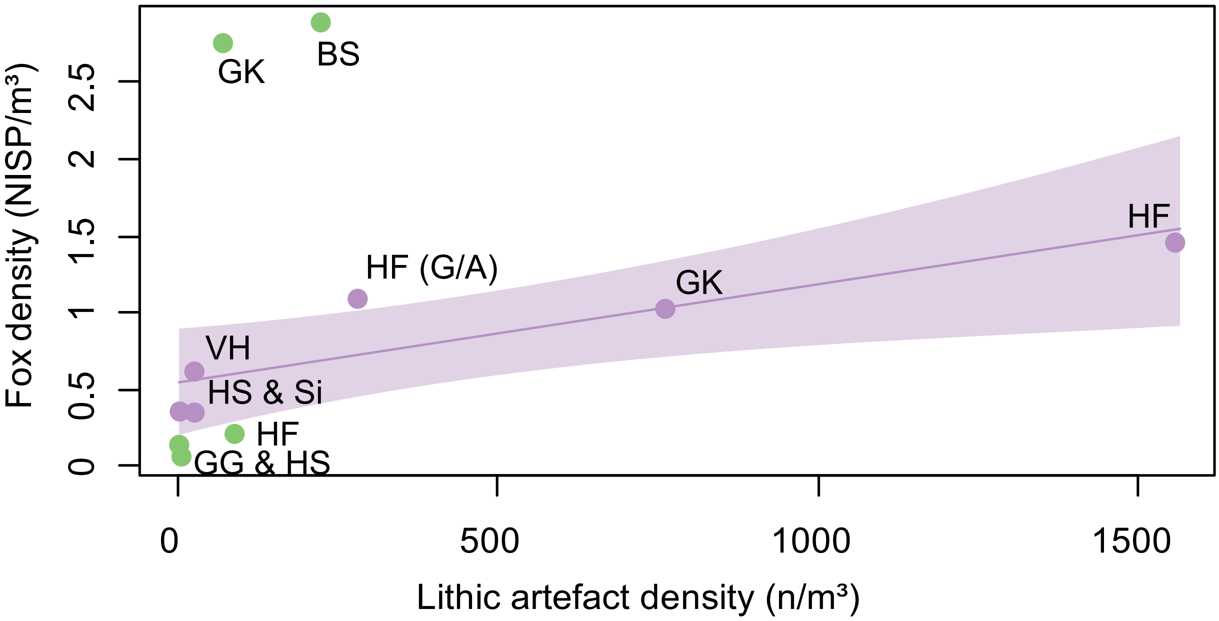

Fig. 11: *Relationship between lithic artifact density (published by Conard et al. (2012)) and the density of foxes. Orange points = Middle Palaeolithic sites. Blue points = Aurignacian sites (Exception: G/A = Gravettian/Aurignacian transition layer). Blue solid line shows the calculated mean regression based on Bayesian linear model, blue shaded area shows 95% credibility interval. GK = Geißenklösterle, BS = Bockstein, HF = Hohle Fels, VH = Vogelherd, HS = Hohlenstein-Stadel, Si = Sirgenstein, GG = Große Grotte, MP = Middle Palaeolithic.*

Another method to test human occupation intensity with the synanthropic fox niches is again the use of hares. While fox remains could have entered the caves naturally, as we assume for the MP layers, hares entered the caves mainly by hunting activities. Since the Aurignacian, AMHs have increasingly hunted hares and other small game and thus had a broader diet (Conard et al., 2013a). This may have been due to the over-hunting of the primary prey, but also to the human population size (Stiner et al., 2000; Stiner et al., 1999). The hare/LH index indicates the importance of this prey, representatively for small game, in the Swabian Jura and can be positively correlated (adj. $r^2 = 0.3$, Fig. 12A) with the intermediate $\delta^{15}N$ fox niches. In contrast, natural fox niches (high and low $\delta^{15}N$ fox niches together) do not correlate with hare abundance (adj. $r^2 = 0.03$, Fig. 12A). The same applies to the correlation of natural fox niches with the fox/LH index (adj. $r^2 = 0.02$, Fig. 12B) and the intermediate niche with the fox/LH index (adj. $r^2 = -0.08$, Fig. 12B). On the one hand, this indicates that the abundance of foxes in the archaeological sites studied does not come exclusively from synanthropic behavior, since they could enter the cave naturally. On the other hand, it also shows that synanthropic behavior positively correlates with human population density, represented by the abundance of hares under the assumption that the increase of small game in zooarchaeological assemblages correlates with human population growth (Stiner et al., 2000; Stiner et al., 1999).

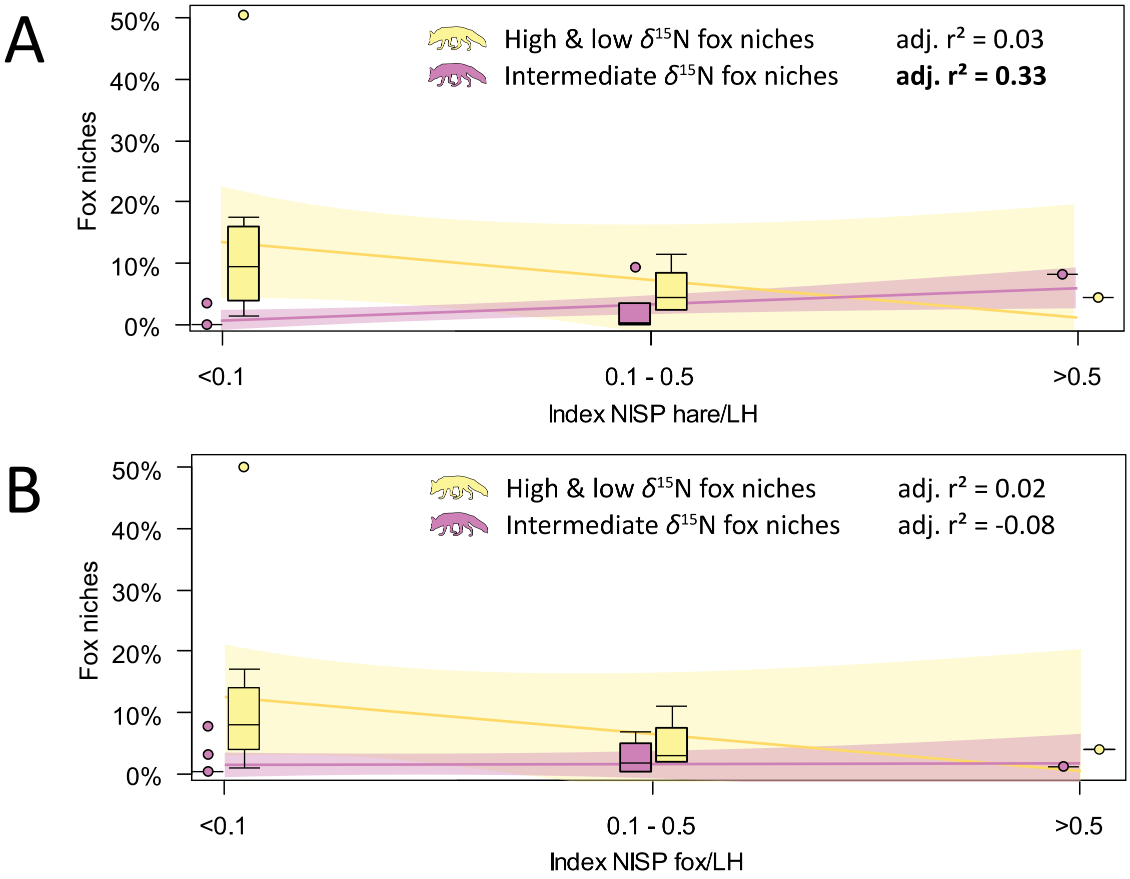

Fig. 12: A) *Relationship between hare/LH index and identified fox niches. Solid lines show the calculated mean regression based on Bayesian linear model, shaded areas show 95% credibility interval.* ***B)*** *Relationship between fox/LH index and identified fox niches. Solid lines show the calculated mean regression based on Bayesian linear model, shaded areas show 95% credibility interval. Bold adj. r^2 shows possitive correlation.*

In summary, I am able to correlate both the abundance of foxes with the lithic artifact density and the intermediate δ^{15}N fox niche with small game hunting during the early Upper Palaeolithic. Both correlations let me hypothesize that synanthropic behavior in foxes has been detectable since the Aurignacian and that this can be recognized by a restricted fox diet on human main prey.

5.3.3. Seasonality or natural death in caves?

There are different other approaches to explain how and when foxes came into the sites. Two of them I would like to discuss in more detail and verify them for my obtained results.

Seasonality

This hypothesis implies that Neanderthals and AMHs occupied the caves only during certain times or seasons (Conard et al., 2013a; Gamble, 1979; Münzel, 2019; Münzel and Conard, 2004b; Niven, 2006). Due to this discontinuous occupation behavior, many caves were alternately inhabited by humans and cave bears (Camarós et al., 2016; Kitagawa et al., 2012; Münzel and Conard, 2004a). When considering the isotopic results in this context, we have to keep in mind that seasonal or one-time events cannot be documented with isotope analysis from bone collagen (Bocherens et al., 1997; Bocherens and Drucker, 2003; Krajcarz et al., 2018). The carbon and nitrogen isotopic values rather integrate a larger time period over several years and show the average nutrition of the last years of the specimen's life. Conversely, this also means that these specimens must have had access to the calculated diet for several years before they died. However, the intermediate δ^{15}N fox niches from the early Upper Palaeolithic and the Kesslerloch fox from the Magdalenian "dog" niche, had restricted diets that could not be linked to scavenging from large predator kills or small mammal hunting. If humans were responsible for this restriction in the prey spectrum, it would mean that they must have done so for several years and not just seasonally.

Natural death

As already mentioned, the archaeological periods each contain several thousand years. During this time, the cave sites were not permanently occupied, thus there is always the chance that foxes died in the caves without human intervention. Especially for foxes from the Middle Palaeolithic layers, I consider this, based on both the two natural trophic niches (high and low δ^{15}N fox niches) and the bad correlation of fox abundance and human activities. During the early Upper Palaeolithic periods, (natural) low δ^{15}N fox niche is missing and intermediate δ^{15}N fox niches appeared, which cannot be of natural origin. Moreover, we have direct evidence that foxes of both niches were exploited by humans in the early Upper Palaeolithic by sampling two mandibles with cut marks. Of course, it can never be excluded that foxes from this niche also died naturally in the caves.

To sum up, natural death in the caves can never be excluded for foxes, as these caves could also have been used as a den. However, this is mainly to be expected in the "natural" niches, namely the low and high δ^{15}N fox niches. However, seasonality can be excluded, as it cannot be explained by the accumulation of stable isotopes in bone collagen of intermediate δ^{15}N foxes.

5.3.4. Foxes as a proxy for human behavior and niche construction

Opportunistic small predators, such as red and Arctic foxes, are very adaptable in their diet and can therefore easily change their trophic behavior (Bassi et al., 2012; Dell'Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Murdoch et al., 2010; Panek and Budny, 2017; Pulliaines, 1993; Reshamwala et al., 2018; Roth, 2003; Sidorovich et al., 2006; Van Haaften, 1970; Wandeler and Lüps, 1993). The same individuals that have hunted rodents alone for years can quickly adapt to scavenging and maintain this as a new trophic behavior as long as it is effective. This is especially evident in modern foxes, which live near villages and benefit from human food waste (Forsyth et al., 2014; Hulme-Beaman et al., 2016; Panek and Budny, 2017; Reshamwala et al., 2018; Soe et al., 2017). However, if this food source should dry up, they can easily change their trophic behavior and go back to hunt rodents.

This characteristic makes foxes an excellent food source indicator, and thus a proxy for the dietary resource provider (Fig. 13). Only if a certain trophic behavior can be maintained over several years, it can also be detected in the stable carbon and nitrogen isotopes in bone collagen (Bocherens et al., 1997; Bocherens and Drucker, 2003; Krajcarz et al., 2018). In the foxes I studied, this is especially true for the pre-LGM intermediate δ^{15}N foxes and the Kesslerloch fox from the Magdalenian "dog" niche.

The **"fox proxy" hypothesis** can also be applied to other sites, such as Předmostí (the Czech Republic, Gravettian period) or Buran-Kaya-III (Crimea, early Upper Palaeolithic).

Předmostí I

Archaeological studies showed that the open-air site Předmostí I was inhabited for a long time in the Gravettian (Svoboda et al., 1994). Mammoth remains are the most common, which also often show cut marks (Musil, 2010). However, the second most common species are wolves and Arctic foxes. Reindeer and horse are far less common. Předmostí I is therefore also interpreted as a seasonal mammoth hunting site (Svoboda et al., 1994). The high number of predators alone indicates a time slot that was free of humans so that these animals could scavenge. Bocherens et al. (2015) published the stable carbon and nitrogen isotope values of among others, large herbivores, wolves, and also six Arctic foxes from this site. The δ^{15}N values of these foxes are generally lower than other carnivores, although they also cluster together with individual wolves, wolverines and brown bears. Similar to the groups of the high δ^{15}N foxes from the Swabian Jura, the Předmostí I foxes seem to behave commensal to the local large carnivores. A special aspect of this site is the group of reindeer-consuming canids, which are considered as "Palaeolithic dogs" and was probably fed by humans (Bocherens et al., 2015; Germonpré et al., 2015; Germonpré et al., 2012; Germonpré et al., 2016). The diet of the Arctic foxes, on the other hand, indicates unrestricted scavenging. A direct synanthropic behavior, as suggested for the Swabian Jura early Upper Palaeolithic, is not visible in Předmostí I. This can be explained by the seasonal human occupation of the site and the resulting low continuity of such a trophic niche, but also by the occurrence of "Palaeolithic dogs", which probably kept other predators, including foxes, away from humans.

Buran-Kaya-III

The zooarchaeological record shows that in the rock shelter Buran-Kaya-III, especially in the layers 6-1 and 6-2 (both dated to 37.1 to 33.1 kyr cal BP, (Péan et al., 2013)) many saiga antelopes were killed and butchered by early Upper Palaeolithic hunters (Crépin et al., 2014; Lanoë et al., 2015). Based on this, Buran-Kaya-III was interpreted as a seasonal hunting camp, used only by humans during the annual migration of the saiga antelopes (Crépin et al., 2014; Lanoë et al., 2015). Besides saiga antelopes, bones of foxes, at least one wolf, and humans were also found and investigated in an isotope study (Drucker et al., 2017). Drucker et al. (2017) sampled among others five foxes (both red and Arctic foxes) from both layers. The main difference was observed in the $\delta^{13}C$ values between the foxes from layers 6-1 and 6-2. In addition to bulk collagen, the two amino acids phenylalanine and glutamic acid were also analyzed. It was shown that most of the foxes had been feeding on saiga antelope. Humans, on the other hand, had mammoth in their diet in addition to saiga antelopes. However, this diet did not apply to two foxes. They are also lower in their $\delta^{15}N$ values and fed on smaller prey such as hares (Drucker et al., 2017). If we now consider that it takes several years to generate $\delta^{15}N$ levels in bone collagen, most foxes should also have had several years of regular access to saiga antelope as a food resource. Similar to the reindeer in the Swabian Jura, the saiga antelope is a food resource for foxes, which at that time and in this site could mainly have been obtained by humans (Crépin et al., 2014; Drucker et al., 2017; Lanoë et al., 2015).

With the discussion of my last research question, I could also confirm my last hypothesis. A correlation between the abundance of foxes in the archaeological sites and the artifact density (representative for human population density), as well as a correlation of the synanthropic fox niches with the intensity of human activity (especially with the hunting of hares, representative for small game) was possible. Hereby I have shown that foxes can be used as a proxy for human activity. This **"fox proxy" hypothesis** could also be applied to other sites.

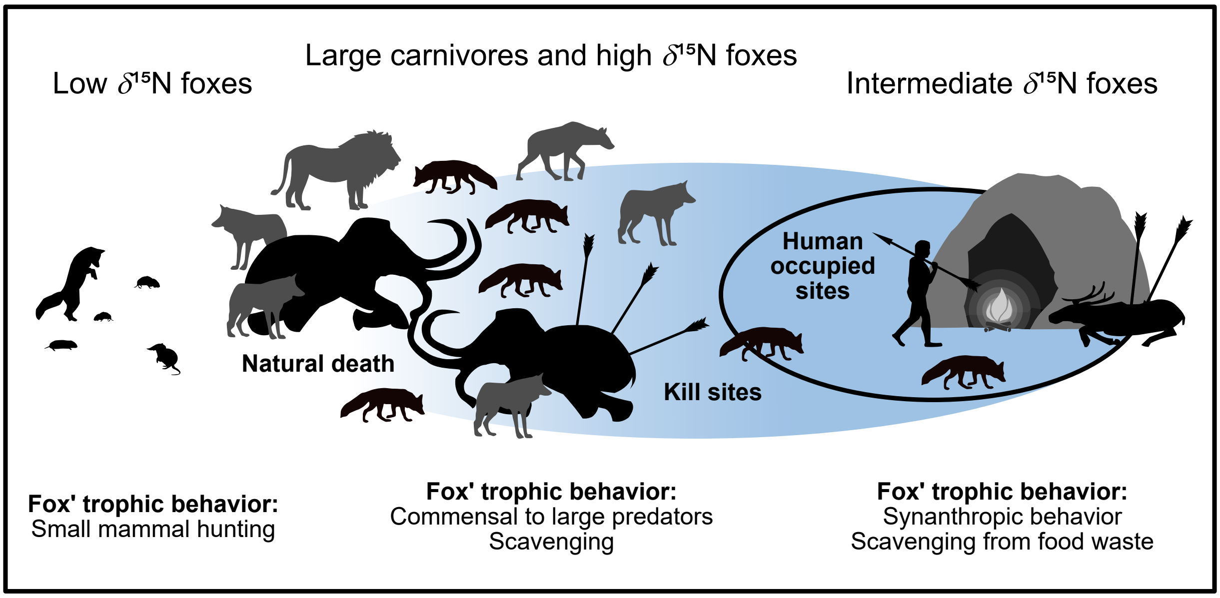

Fig. 13: *Graphical implementation of the* ***"fox proxy" hypothesis****. The blue coloured areas show the influence of humans on the foxes' diet and trophic behavior.*

6. Conclusion

With my thesis, I made a new consideration of the Late Pleistocene foxes of the Swabian Jura. Three aspects, in particular, played an important role for me:

1. What significance did foxes have in the archaeological periods of the Middle Palaeolithic, Aurignacian, Gravettian and Magdalenian, and how were they hunted?

   My study indicates that Neanderthals from the Swabian Jura had hardly hunted foxes and, therefore, foxes most likely entered the caves naturally during the Middle Palaeolithic. From the Aurignacian onwards, there was an increasing number of fox remains and evidence that they were hunted by AMHs. This hunt was probably carried out by trapping foxes at game passes in the vicinity of the inhabited caves, sometimes using traps, baited with food remains. Foxes were mainly exploited for their meat, fur, and teeth. The latter were processed into pendants during the Aurignacian and Gravettian.

2. What trophic behavior did Late Pleistocene foxes exhibit and did the hunting behavior of humans have an influence on this trophic behavior?

   As modern foxes, Late Pleistocene foxes showed different feeding strategies, resulting in three different trophic niches. While one fox niche was present in all investigated periods and could clearly be associated with a commensal behavior to large carnivores, two other niches could only be detected in specific periods. The niche of the small-mammal-hunting foxes was only found in regions and periods sparsely populated by humans, namely in the Middle Palaeolithic and Magdalenian of the Swabian Jura. During the Aurignacian and Gravettian of this region, as well as in the Magdalenian of the Kesslerloch, a fox niche with a clearly restricted diet appeared, which could be associated with human hunting behavior on large herbivores. This seems to be the earliest evidence of synanthropic behavior, well before the Neolithic.

3. Is it possible to use foxes as a proxy for human population density and activities?

   The positive correlation of fox abundance with artifact density on the one hand and the percentage of synanthropic fox niche occurrence with the abundance of small game on the other hand shows the strength of foxes to act as a proxy. In this context, the number of foxes in the zooarchaeological assemblage alone does not provide much information but becomes a good proxy for human population density and activities when considering the reconstructed trophic niches. This **"fox proxy" hypothesis** could also be applied to other sites.

My study proves that the influence of AMHs on the Late Pleistocene environment was stronger than that of Neanderthals. On the one hand, this may be due to the higher population density and group size of the AMHs, on the other hand, it may be due to improved hunting techniques. The fact that the influence on the mammoth steppe biome could be determined earlier than only at the time of the megafauna's extinction is also shown in studies on stable isotopes and trophic niche constructions of large herbivores (Drucker et al., 2015; Wißing et al., 2019). My trophic reconstructions of fox niches and thus the identified human influence on Late Pleistocene foxes' trophic behavior are a further indication of human impact on the environment, and thus joins the argument for an early start of the Anthropocene (Doughty et al., 2010; Haynes, 2018), beginning with the arrival of *Homo sapiens* in Europe.

To further verify my hypothesis, besides further isotope analyses of such strongly human-influenced sites, it is also necessary to integrate sites that are not directly connected to humans or have only a very low/irregular human occupation. This will help to gain a better understanding of the foxes' natural trophic niches and thus to better evaluate human influence. In the Swabian Jura, for example, these would be the two cave sites Fetzershaldenhöhle (Lone Valley; Conard et al., 2015b) and Kogelstein (Ach Valley; Böttcher et al., 2000), which are distinguished as hyena dens, as well as Bärenhöhle (near Sonnenbühl-Erpfingen; Rathgeber and Ufrecht, 2002) and Schafstall (near Veringenstadt; Conard et al., 2017; Conard and Toniato, 2018; Peters, 1936). I expect that further isotopic methods, such as the investigation of individual amino acids, will lead to a more detailed dietary reconstruction and, based on this, to a differentiated consideration of trophic niches. Consequentially, it will lead to a better interpretation of human influence on Pleistocene fox niches.

Furthermore, my studies show that it is profitable to take a closer look at animals that show synanthropic behavior today. This does not only apply to foxes but can also be initiated to other commensal scavengers. For example, the Czech sites Předmostí and Dolní Věstonice contain not only numerous foxes in the faunal assemblage, but also a lot of bones of corvids (Wertz et al., 2016). Especially modern crows and jackdaws have become adapted to humans and may have shown this synanthropic behavior much earlier.

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Appendix

The accepted publications and the submitted manuscript are listed in this appendix following the order in **List of Publications**.

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Appendix 1

The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany)

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ORIGINAL PAPER

The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany)

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Abstract

In this study, we examine the role of foxes in Palaeolithic economies, focusing on sites of the Middle Palaeolithic, Aurignacian, Gravettian and Magdalenian of the Swabian Jura. For this purpose, we used published faunal data from 26 assemblages from the region, including new information from the Magdalenian layers of Langmahdhalde. We explore how the abundance of foxes changes over time, how they were used by humans, and how they were deposited at the sites, with a special focus on fox hunting methods. To evaluate these hunting methods, we use the prey choice model of optimal foraging theory (OFT) and simulate possible hunting scenarios, which we test based on the published faunal assemblages. Our research indicates that foxes were hunted since the early Upper Palaeolithic for their meat, fur and teeth, possibly with traps. We find that the abundance of fox remains in the archaeological record of the region increased continuously starting in the Aurignacian, which cannot be explained by taphonomic factors. The trend of foxes to adapt to human-influenced environments with commensal behavior may also have contributed to them being hunted more often.

Keywords Fox hunting methods · Prey choice model · Aurignacian · Gravettian · Magdalenian · Middle Palaeolithic

Introduction

The transition from the Middle Palaeolithic, which was dominated by Neanderthals, to the Upper Palaeolithic, which is associated with the appearance of anatomically modern humans, is an important and very active field of research in archaeology (Arrighi et al. 2019; Benazzi et al. 2011; Fa et al. 2016; Jones et al. 2019; Jones et al. 2018; Morales et al. 2016; Peresani et al. 2016; Pirson et al. 2012; Pleurdeau et al. 2016; Richard et al. 2019; Romandini et al. 2019). In zooarchaeological studies, this transition is often interpreted as a change in human hunting behavior or an expansion of the food spectrum (Romandini et al. 2019; Starkovich 2012; Starkovich 2014; Stiner 2009; Stiner et al. 2000; Stiner et al. 1999). Although recent studies suggest that Neanderthals had a broad diet in some regions (Droke et al. 2020; Wißing et al. 2019; Wißing et al. 2016; Wroth et al. 2019; Yravedra et al. 2019), many sites in Europe and the Middle East have rapid increases in faunal diversity from their Middle to Upper Palaeolithic layers (Conard et al. 2013; Starkovich 2012; Starkovich 2014; Stiner 2009; Stiner et al. 2000), which can be interpreted as a result of a higher population density of modern humans and a resulting over-hunting of certain food resources (Stiner et al. 1999). In this context, representation of primarily small prey animals, such as hares, birds, fish and foxes, increases. While archaeological evidence strongly supports the use of hares, fish and birds as additional components of human diets (Conard et al. 2013; Stiner 2009; Stiner et al.

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2000; Stiner et al. 1999), the use of foxes for both fur and meat is less strongly supported but is likely to have occurred (Camarós et al. 2016; Conard et al. 2013; Yeshurun et al. 2009). In modern hunter-gatherer cultures, such as some Inuit tribes of the eastern Arctic (Eber 1989), it is common to consume foxes regularly only in times when no other food is available. This makes the presence of fox remains an important indicator for over-hunting of main prey and human population growth, following the hypothesis of Stiner et al. (1999). Furthermore, in some contexts, it is also possible that humans were not responsible for depositing fox remains at the sites. Our study focuses on the human use of foxes from the Middle Palaeolithic to the Magdalenian in the Swabian Jura of southwestern Germany, a region with some of the most well-researched Palaeolithic sites in Europe.

Researchers have studied the archaeofaunal remains from the Swabian Jura for decades. The sites are particularly famous for their rich Middle and Upper Palaeolithic layers. While the Middle Palaeolithic settlement of the region appears to have been sparse, most archaeological sites dating to the Upper Palaeolithic seem to have been used more intensively (Conard et al. 2012). In the Swabian Jura, the Upper Palaeolithic is represented by the Aurignacian (42,000–34,000 cal BP (Conard and Bolus 2003; Conard and Bolus 2008; Hahn 1982; Higham et al. 2012)), Gravettian (34,000–24,000 cal BP (Conard and Bolus 2008; Housley et al. 1997; Taller and Conard 2019)), and after the Last Glacial Maximum (LGM), the Magdalenian (16,300 to approximately 12,700 cal BP (Gaudzinski and Street 2003; Hahn 1995; Housley et al. 1997; Kind 2003; Taller et al. 2014)).

In general, archaeological sites in the Ach and Lone valleys of the Swabian Jura are dominated by remains of cave bear and ungulates throughout the Palaeolithic (e.g. Bertacchi (2017); Camarós et al. (2016); Conard et al. (2013); Kitagawa et al. (2012); Krönneck (2012); Lykoudi (2017); Münzel (2019); Münzel and Conard (2004a); Münzel and Conard (2004b); Napierala et al. (2014); Wong et al. (2017)). However, there are also small numbers of carnivore taxa in almost all of the sites, including red fox (*Vulpes vulpes*) and arctic fox (*Vulpes lagopus*) (Bertacchi 2017; Camarós et al. 2016; Conard et al. 2013; Kitagawa et al. 2012; Krönneck 2012; Lykoudi 2017; Münzel 2019; Münzel and Conard 2004a; Münzel and Conard 2004b; Napierala et al. 2014; Wong et al. 2017). We know that carnivores must have played an important role in the lives of Palaeolithic peoples, based on, among other things, the presence of perforated carnivore teeth in the archaeological record, which were most likely used as pendants (Camarós et al. 2016; Conard 2003; Hahn 1992; Langguth and Malina 2003; Münzel 2019). The earliest evidence of these pendants in the Swabian Jura comes from the Aurignacian layers of Hohle Fels and Geißenklösterle. In the Gravettian, perforated teeth of carnivores are found even more frequently (Camarós et al. 2016; Conard 2003). In addition to pendants made of carnivore teeth, felids and bears were illustrated in mobile art in hunting poses (Hahn 1986). Although no Palaeolithic figurines have been interpreted as depicting foxes, the regular presence of foxes in the faunal record, as well as the use of their teeth as pendants, indicates that these animals were important to humans during these periods. However, the nature of this relationship has not yet been studied in detail.

A particular behavior in foxes could be related to their occurrence in archaeological sites: commensalism. Commensal behavior is a symbiotic behavior between two species, which benefits one species and does not affect the other (Hulme-Beaman et al. 2016; Yeshurun et al. 2009). Modern foxes show two types of commensalism. In one type, they are commensal to large predators (Pulliaines 1993; Wandeler and Lüps 1993), such as wolves or polar bears and, and in the other type, they are commensal to humans (Jędrzejewski and Jędrzejewska 1992; Kidawa and Kowalczyk 2011; MacDonnald 1977; Panek and Budny 2017; Pulliaines 1993; Savory et al. 2014; Sidorovich et al. 2006; Soe et al. 2017; Wandeler and Lüps 1993). In both cases, the foxes benefit by obtaining food more easily without positively or negatively affecting the large predators or humans (Hulme-Beaman et al. 2016; Kays and Feranec 2011; Merkle et al. 2011; Murray et al. 2015; Newsome et al. 2010; Newsome et al. 2015; Warsen et al. 2014). Recent research has indicated that this phenomenon is not restricted to modern foxes (West and Yeshurun 2019; Yeshurun et al. 2009), but also likely occurred during the Magdalenian (Baumann et al. 2020).

This paper has three primary goals. First, we seek to determine how the abundance of foxes has changed from the Middle Palaeolithic to the Magdalenian in the Swabian Jura. Second, we explore how foxes were used during these different periods. Finally, we discuss the circumstances under which fox remains were likely deposited in the Palaeolithic sites of the Swabian Jura, including possible methods of fox hunting by humans. We address these goals by conducting a meta-analysis of previously published studies and presenting new data from recent excavations at Langmahdhalde. Furthermore, we interpret our results through the paradigm of human behavioral ecology and the prey choice model (Charnov 1976) in order to explore possible hunting scenarios Palaeolithic people might have used to procure foxes.

Material and methods

Our studied material consists of 26 assemblages from twelve different cave and rock shelter sites from the Ach and Lone valleys in the Swabian Jura that date to the Middle Palaeolithic (MP), Aurignacian (A), Gravettian/Aurignacian transition (G/A), Gravettian (G) and Magdalenian (M) (Fig. 1,

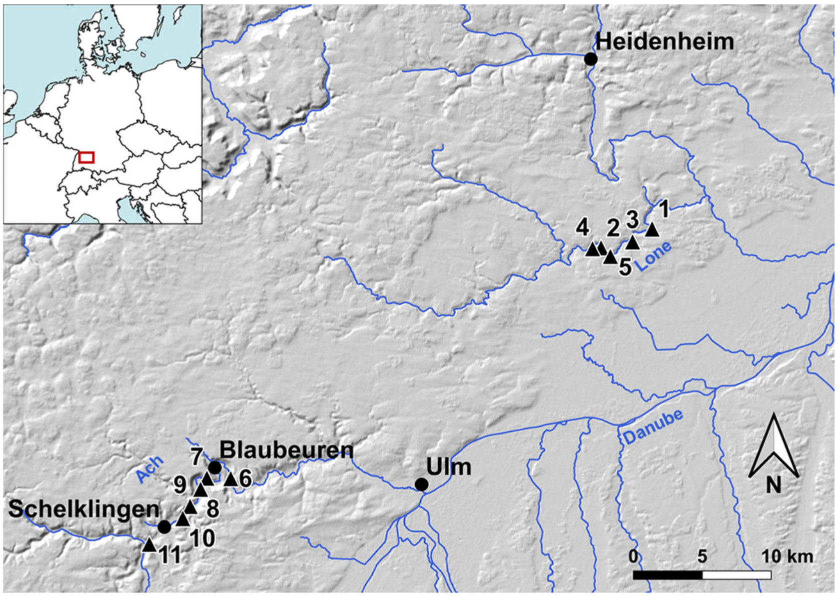

Fig. 1 Map of sites included in this study. 1 = Langmahdhalde; 2 = Fetzershaldenhöhle; 3 = Vogelherd; 4 = Bockstein; 5 = Hohlenstein-Stadel; 6 = Große Grotte; 7 = Brillenhöhle; 8 = Geißenklösterle; 9 = Sirgenstein; 10 = Hohle Fels and Helga Abri; 11 = Kogelstein. Map made in QGIS version 3.4 with topographic data from SRTM NASA version 3, hydrology data from the Landesanstalt für Umwelt Baden-Württemberg, administrative boundaries from ©EuroGeographics, and ocean data from Natural Earth

Table 1). From the Ach Valley, we have included Kogelstein, Hohle Fels, Helga Abri, Sirgenstein, Geißenklösterle, Brillenhöhle and Große Grotte, and the Lone Valley is represented by Hohlenstein-Stadel, Fetzershaldenhöhle,

Table 1 List of assemblages included in this study with key references. *AH* archaeological horizon, *MP* Middle Palaeolithic, *A* Aurignacian, *G/A* Gravettian/Aurignacían transition, *G* Gravettian, *M* Magdalenian

Region	Site	Assemblage	Period	Reference
Ach Valley	Brillenhöhle	AH IV AH V-VII	M G	Riek 1973; Boessneck et al. 1973
		AH XIV	A	
	Geißenklösterle	AH Io AH I	M G	Münzel 2019
		AH II-III	A	
		AH IV-VIII	MP	
	Große Grotte	AH II-XI	MP	Weinstock 1999
	Helga Abri	AH II F7-IIId	M	Münzel et al. (In prep.)
	Hohle Fels	AH 0-IIa (light)	M	Napierala et al. 2013
		AH IIb-cf AH IId-e	G G/A	Conard et al. 2013
		AH IIIa-Vb	A	
		AH VI-IX	MP	
	Kogelstein		MP	Böttcher et al. 2000
	Sirgenstein	AH I-III AH IV-VII	G A	Bertacchi 2017 (unpublished Master's thesis)
Lone Valley	Bockstein	BT IV-VI BT VII	G A	Krönneck 2012
		GH 3 & BS I-V	MP	
	Fetzershaldenhöhle	GH III	G/A	Lykoudi 2017 (unpublished Master's thesis)
	Hohlenstein-Stadel		A MP	Kitagawa 2014
	Langmahdhalde	AH IV-VI	M	Wong et al. 2017 and new data from this paper
	Vogelherd	AH III	M	Niven 2006
		AH IV/V & HL/KS	A	Boger et al. 2014; Niven 2006

Vogelherd, Langmahdhalde and Bockstein. We report the publications we used as sources for the NISP values (number of identified specimens, Grayson (2014); Lyman (2008)) in Table 1.

The data we present in this paper are based on both piece-plotted finds from excavations of the 1970s onwards and individual collected finds from excavations before this date. In the following, we will refer to them as "single finds". Even if many excavation sites were wet-sieved, the majority of these wet-sieved remains have not yet been published. The published NISP values for the Middle Palaeolithic assemblages of Kogelstein group the wet-sieved and single finds together; in order to address any biases this may introduce, we analysed Kogelstein separately. Wong et al. (2017) calculated the NISP values for the faunal remains from the Magdalenian site of Langmahdhalde using both single finds and wet-sieved material, but, as this site is still under excavation, these NISP values do not reflect the most current values. Therefore, supplementary Table S1 presents the most up-to-date NISP values from the Langmahdhalde Magdalenian assemblage for the taxonomic groups in this study and we use the values based only on single finds.

In general, fox remains are not well-represented at these sites compared to other mammalian taxa, except in Kogelstein, probably as a result of including screened materials. Calculating the relative abundance of foxes using percent NISP (%NISP) does not provide reliable results as the total number of foxes is very small in relation to the total NISP. Therefore, we use the ratio of the NISP of foxes to the NISP of large herbivores (fox/LH index), following Tchernov (1994) and Yeshurun et al. (2009). We only use faunal remains that are identified to the genus (i.e. *Vulpes* sp.) or species level (i.e. arctic fox: *Vulpes lagopus* and red fox: *Vulpes vulpes*). The category of large herbivore (LH) includes mammoth (*Mammuthus primigenius*), horse (*Equus ferus*), wooly rhinoceros (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), bison (*Bison* sp.), aurochs (*Bos primigenius*), ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*) and the size classes "mammoth/rhino", "horse" and "reindeer." Similarly, we calculated the ratio of hare (specimens identified to European hare, *Lepus europaeus*, mountain hare, *Lepus timidus* and *Lepus* sp.) to large herbivores (LH). It is possible that fox teeth are overrepresented in the single find material since they are easily identified during excavation. However, we have decided to include both postcranial and cranial elements, including teeth, in our analysis, because an overrepresentation of teeth is only present in the Magdalenian layers of Geißenklösterle (see Fig. S1), and because at some sites (e.g. Brillenhöhle and Große Grotte), no distinction was made between cranial and postcranial remains for fox or hare.

Another method we used to calculate the relative abundance of foxes is the ratio of foxes within the carnivores (NISP fox/NISP all carnivores, including foxes), or %fox of Carnivora. The carnivore category includes foxes, cave lion (*Panthera leo spelaea*), lynx (*Lynx lynx*), wild cat (*Felis silvestris*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), martens (*Martes* sp.), weasels (*Mustela* sp.), otter (*Lutra lutra*) and cave hyena (*Crocuta crocuta spelaea*). We excluded the European badger (*Meles meles*) from our analysis, because we could not exclude the possibility that modern badgers invaded the archaeological layers of some of the sites, such as Vogelherd (Niven 2006).

Moreover, we have excluded the cave bear (*Ursus spelaeus*), which belongs to the order Carnivora, but did not have a carnivorous diet (Bocherens et al. 1994; Münzel et al. 2014; Naito et al. 2016; Nelson et al. 1998; Pacher and Stuart 2009). Furthermore, due to their hibernation behavior, it is possible that cave bears died in the cave sites without human influence (Baca et al. 2016; Kitagawa et al. 2012; Münzel and Conard 2004a; Nelson et al. 1998; Pacher and Stuart 2009; Stiner 1999). To get an impression of whether the number of foxes is related to the human occupation density, we use fox density (NISP of fox/m^3 excavated sediment) and lithic artefact density (number of lithic artefacts/m^3 excavated sediment, from Conard et al. (2012)). The sites and values we include in this analysis are given in supplementary Table S2.

Since the sample size within archaeological assemblages is very small, we applied Bayesian statistics to measure fox and hare abundance. Bayesian statistics have the advantage that they provide usable probability and likelihood information even with small sample sizes ($n > 5$, Gelman et al. (2014)). Meanwhile, Bayesian statistics are increasingly used in archaeological studies (Borradaile 2003; Gearey et al. 2009; Halekoh and Vach 1999; Halekoh and Vach 2004; Otárola-Castillo and Torquato 2018). One way to evaluate the reliability of the statistical analysis is by using the credibility interval (CI; 95% by default) of the regression line. The narrower the CI, the more certain is the given regression trend.

For the correlation between fox and hare indices (fox/LH and hare/LH, respectively), the fox abundance within the carnivore sub-assemblages (%fox of Carnivora) between periods and the analysis of the relationship between fox density and lithic artefact density, we use a normal linear model (lm) analysis in a Bayesian framework (R package arm; Gelman and Hill (2006)), following the protocol of Korner-Nievergelt et al. (2015). The lm analysis gives an adjusted (adj.) r^2 value between 0 and 1, which can be used for the interpretation of the regression line (Korner-Nievergelt et al. 2015): positive values indicate a positive correlation and negative values indicate a negative correlation. The use of Bayesian statistics eliminates the need for the p value (probability value in frequency analyses), as this is generally too strongly biased by the sample size (Gelman et al. 2014; Halekoh and Vach 1999; Halekoh and Vach 2004; Korner-Nievergelt et al. 2015;

Otárola-Castillo and Torquato 2018). All Bayesian analyses were done with R Version 3.6.1.

Results

In this section, we present the relative abundance and frequency distributions of foxes from the Swabian Jura Middle Palaeolithic to Magdalenian. We also summarize incidences of human-made modifications on fox remains, such as cut marks and perforated tooth pendants, and the abundance of hares and foxes.

Fox representation from the Middle Palaeolithic to the Upper Palaeolithic

The majority of fox bones in all sites are from adult animals. We have recorded only 28 bones and teeth from foxes younger than 1 year. Seventeen juvenile fox bones/teeth come from the Middle Palaeolithic layers at Hohlenstein-Stadel (Kitagawa 2014), one from the Aurignacian of Vogelherd (Niven 2006), four from the Gravettian layer at Geißenklösterle (Münzel 2019) and six from the Magdalenien layers of Vogelherd and Langmahdhalde (1 and 5, respectively; Niven (2006)).

In most assemblages, fox remains make up only 1 to 5% of the faunal material (Bertacchi (2017); Boessneck et al. (1973); Boger et al. (2014); Böttcher et al. (2000); Conard et al. (2013); Kitagawa (2014); Kitagawa et al. (2012); Krönneck (2012); Lykoudi (2017); Münzel (2019); Napierala et al. (2014); Niven (2006); Weinstock (1999); Wong et al. (2017); Table S1). Only in the Middle Palaeolithic layers of Kogelstein Cave are foxes the dominant taxa by NISP count, with 418 specimens (37.5% of the assemblage) (Böttcher et al. 2000). Nevertheless, in all of the other assemblages, we see an increase in the relative abundance of foxes within the carnivore sub-assemblages (%fox of Carnivora) from the Middle Palaeolithic to the Magdalenian (Fig. 2a, Table 2). Similar to the increasing abundance of foxes within the carnivores, the fox/LH index increases from the Middle Palaeolithic to the Magdalenian layers, as does the hare/LH index (Fig. 2b, Table 2).

In five assemblages (Fig. S2, Table 2) from the Middle Palaeolithic layers (excluding Kogelstein), the index of both foxes and hares is very low (on average 0.06 and 0.03, respectively). In the Aurignacian layers, the average frequency of both taxa remained low, with the exception of the assemblages from Brillenhöhle, Hohlenstein-Stadel and Sirgenstein. In the faunal material of Hohlestein-Stadel, both indices clearly increased (on average 0.34 and 0.29, respectively). In the Brillenhöhle and Sirgenstein material, only the hare/LH index increased (0.25 and 0.29, respectively). With the transition to the Gravettian (i.e. the G/A layers from Hohle Fels and Fetzershaldenhöhle), as well as throughout the Gravettian, there is an increase in the two indices (G/A: on average 0.18 and 0.21, respectively; G: on average 0.14 and 0.59, respectively). The average frequency of hares in the faunal material was higher than that of foxes, both in the G/A transition and in the Gravettian. This was particularly evident in Brillenhöhle (hare/LH = 2.07) and Sirgenstein (hare/LH = 1.74), where hares outnumber large herbivores by NISP count.

When we look at the Magdalenian, we see that the average frequency of foxes continued to increase, while the average frequency of the hares decreased slightly. For the foxes, the highest value is from Geißenklösterle (fox/LH = 0.72). However, the number of faunal remains from the Magdalenian in Geißenklösterle is generally low (NISP = 229) compared to the other archaeological layers.

Previous studies have found that including fox teeth in fox abundance data leads to an overrepresentation of foxes in the assemblage of Geißenklösterle (Camarós et al. 2016; Conard et al. 2012; Conard et al. 2013; Hahn 1988; Münzel and Conard 2004b). For the Magdalenian in Geißenklösterle, for example, 20 out of 28 fox specimens are teeth. To test whether this is also true of the other assemblages, we calculated two fox/LH indices, one with and one without isolated teeth, and plotted them against each other (Fig. S1). We found that the abundance of fox remains from the Magdalenian of Geißenklösterle is particularly affected by tooth representation, but with all other assemblages, the difference between the two indices was minor. Based on these results and the fact that the published faunal results for the sites in this study do not all indicate how many isolated fox teeth are in the assemblages (e.g. in Hohlenstein-Stadel and Kogelstein), we consider only the fox/LH index that includes teeth in discussions below. In addition, we tested the inclusion of teeth (of foxes and hares) on the relationship between foxes and hares (Fig. S4). We found that the linear correlation for both taxa is lower when teeth are not included (all remains: adj. $r^2 = 0.13$, only postcranial: $r^2 = 0.05$). There are two reasons for this. Firstly, teeth and bone were not reported separately for all sites, which leads to a smaller sample size and thus to a higher uncertainty. Secondly, because of its high mineral content, enamel generally preserves better than bone and is thus represented in higher proportions. However, we consider including teeth to be useful because it enables us to compare even the sites that do not provide separate data on teeth and bone.

The increasing frequency of foxes through time seems to coincide with an increase in hare frequency. Examining fox frequency in relation to hare may yield some important insights, as these taxa are similar in size, share the same habitats and are nocturnal (Averianov et al. 2003; Pulliaines 1993; Thulin and Flux 2003; Wandeler and Lüps 1993). Figure 3 shows a comparison of the fox/LH index and the hare/LH index. In order to examine whether foxes and hares were captured in a similar manner, we analysed the correlation between

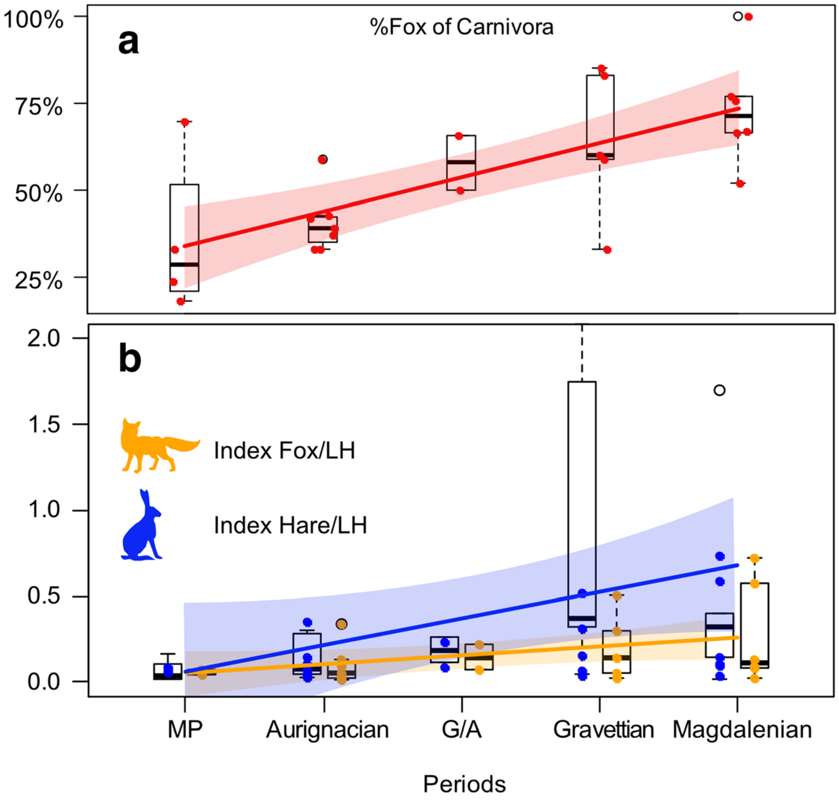

Fig. 2 **a** Relative abundance of foxes in relation to other carnivores. Red solid line shows the calculated mean regression based on Bayesian linear model, red shaded area shows 95% credibility interval. **b** Index of the relationship between foxes and large herbivores (LH) and between hares and large herbivores (LH). Solid lines show the calculated mean regressions based on Bayesian linear model, shaded areas show 95% credibility interval. All values are based on NISP data. MP = Middle Palaeolithic, G/A = Gravettian/Aurignacian transition layer

both indices for each period. If the correlation yields a positive linear relationship, it would mean that both taxa were caught in similar proportions to one another (Yeshurun et al. 2009). This could then indicate that humans used an unselective hunting strategy, such as snares on an open landscape, to catch these animals. For the Middle Palaeolithic ($n = 5$), we found a very low negative correlation (adj. $r^2 = -0.26$), while there is positive correlation for the Aurignacian ($n = 7$, adj. $r^2 = 0.50$) and a much higher positive correlation in the Gravettian ($n = 5$, adj. $r^2 = 0.88$). We also see a strong positive correlation for the Magdalenian ($n = 5$, adj. $r^2 = 0.99$); however, we had to exclude the data from Geißenklösterle, again because of the overrepresentation of fox teeth and the resulting bias to the index (see Fig. S1).

In order to investigate whether foxes became more frequent when humans were using the sites, we compared lithic artefact density to the density of fox remains in the Middle Palaeolithic and early Upper Palaeolithic (Fig. 4). The assemblages from the early Upper Palaeolithic ($n = 6$) show a strong positive correlation between lithic artefact density and fox density (adj. $r^2 = 0.72$). In contrast, the correlation in the Middle Palaeolithic sites ($n = 5$) is much lower (adj. $r^2 = 0.37$).

Human modification of fox remains in the Middle and Upper Palaeolithic

Cut marks on fox bones are generally rare in the Palaeolithic, even if foxes are well-represented in assemblages (Lipecki and Wojtal 2015; Street and Turner 2013; Wilczyński et al. 2015; Wojtal and Wilczyński 2015; Wojtal et al. 2012), and the sites of the Swabian Jura are no exception. Cut marks were found on only ten fox bones in our study. From the Middle Palaeolithic layer of Bockstein, Krönneck (2012) observed a phalanx with a circular cutting line. In the Aurignacian, there are five bones with cut marks: two mandibles from Vogelherd, one with cuts on the buccal side and the other with cuts on the lingual side (Niven 2006), a fifth metacarpal from Geißenklösterle (Hahn 1988; Münzel 2019) and a rib and an ulna from Hohle Fels (Conard et al. 2013). Additionally, the only two bones with butchering marks from the Gravettian come from Hohle Fels: a pelvis and a femur (Conard et al. 2013). There are two modified bones from the Magdalenian: an ulna from Hohle Fels (Napierala et al. 2014) and a mandible with parallel cuts from Langmahdhalde (Wong et al. 2017). While cut marks on the pelvis and femur can come from meat removal, cut marks on the outside of the mandible and on phalanges tend to come from skinning (Andersson and Paulsson 1993; Binford 1981; Valensi 1991).

The fox remains from Kogelstein Cave

The Middle Palaeolithic layer of Kogelstein is a special case in our analysed assemblages. It stands out from the other sites in our study because it has 418 fox specimens, a fox abundance in relation to other carnivores of approximately 70% and a fox/LH index of 1.05. As mentioned above, Böttcher et al.

Table 2 NISP data and the %fox of Carnivora, fox/LH and hare/LH indices of the different assemblages. *A* Aurignacian, *G/A* Gravettian/Aurignacían transition, *G* Gravettian, *M* Magdalenian, *LH* Large herbivores

Period/site	Fox	Hare	Other carnivores	Large herbivores (LH)	%Fox of Carnivora	Fox/LH	Hare/LH
M Brillenhöhle	63	183	20	108	75.9%	0.58	1.69
M Geißenklösterle	28	13	26	39	51.9%	0.72	0.33
M Helga Abri	4	15	0	51	100.0%	0.08	0.29
M Hohle Fels	41	122	12	313	77.4%	0.13	0.39
M Langmahdhalde	10	14	5	109	66.7%	0.09	0.13
M Vogelherd	2	0	1	97	66.7%	0.02	0.00
Magdalenian (*n* = 6)	**148**	**347**	**64**	**717**	**69.8%**	**0.21**	**0.48**
G Bockstein	8	11	16	356	33.3%	0.02	0.03
G Brillenhöhle	181	738	36	357	83.4%	0.51	2.07
G Geißenklösterle	109	240	19	782	85.2%	0.14	0.31
G Hohle Fels	74	497	52	1389	58.7%	0.05	0.36
G Sirgenstein	56	324	38	186	59.6%	0.30	1.74
Gravettian (*n* = 5)	**428**	**1810**	**161**	**3070**	**72.7%**	**0.14**	**0.59**
G/A Fetzershaldenhöhle	140	161	72	644	66.0%	0.22	0.25
G/A Hohle Fels	14	22	14	212	50.0%	0.07	0.10
G/A Transition (*n* = 2)	**154**	**183**	**86**	**856**	**64.2%**	**0.18**	**0.21**
A Bockstein	6	8	12	125	33.3%	0.05	0.06
A Brillenhöhle	3	6	4	24	42.9%	0.13	0.25
A Geißenklösterle	159	209	111	6700	58.9%	0.02	0.03
A Hohle Fels	29	37	40	876	42.0%	0.03	0.04
A Hohlenstein-Stadel	36	31	72	107	33.3%	0.34	0.29
A Sirgenstein	24	73	37	255	39.3%	0.09	0.29
A Vogelherd	122	133	212	9802	36.5%	0.01	0.01
Aurignacian (*n* = 7)	**379**	**497**	**488**	**17889**	**43.7%**	**0.02**	**0.03**
MP Bockstein	36	10	115	993	23.8%	0.04	0.01
MP Geißenklösterle	26	8	32	211	44.8%	0.12	0.04
MP Große Grotte	16	35	7	241	69.6%	0.07	0.15
MP Hohle Fels	2	0	4	37	33.3%	0.05	0.00
MP Hohlenstein-Stadel	50	22	223	739	18.3%	0.07	0.03
Middle Palaeolithic (*n* = 5)	**130**	**75**	**381**	**2221**	**25.4%**	**0.06**	**0.03**
MP Kogelstein	418	65	179	397	70.0%	1.05	0.16
Middle Palaeolithic (*n* = 6)	**548**	**140**	**560**	**2618**	**49.5%**	**0.21**	**0.05**

(2000) included wet-sieved material in the NISP counts of the faunal remains. Since small elements and fragments, such as phalanges and epiphysis fragments, are often not recovered without screening, this could explain why Kogelstein has such high NISP values for fox compared to the other sites. We would therefore assume that the hares and other small taxa would be represented in higher numbers in the Kogelstein faunal assemblage. However, this is not the case; Böttcher et al. (2000) report only 65 hare remains from the Middle Palaeolithic horizons at the site. This site is considered to have been a hyena den that had only a short human occupation during the Middle Palaeolithic (Böttcher et al. 2000), meaning that the fox remains were not necessarily deposited as the result of human activity. Therefore, factors other than the inclusion of wet-sieved material likely influenced the high representation of fox remains in the Middle Palaeolithic horizons of Kogelstein.

Discussion

We now consider Palaeolithic foxes from the Swabian Jura in a broader context and focus on three topics: the extent to which foxes were used as food or raw material sources by humans, the population structure of foxes and finally human hunting methods used in the Upper

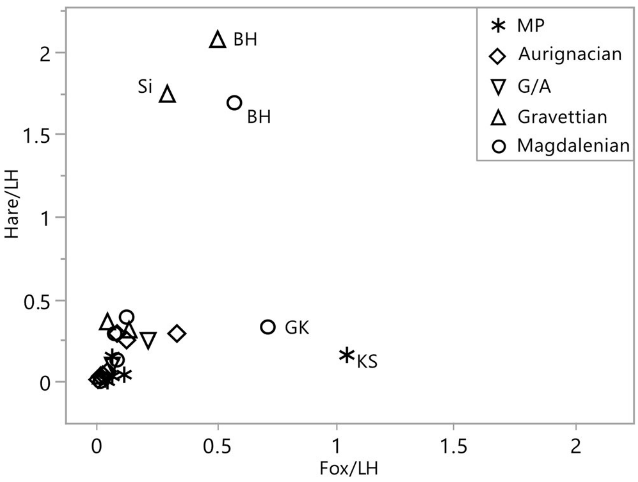

Fig. 3 Plot of the fox/large herbivore (LH) and hare/large herbivore (LH) indices. The cluster in the lower left corner indicates a balanced relationship between hare and fox remains in the assemblages. The Gravettian layer of Sirgenstein and both layers from Brillenhöhle (BH) show an overrepresentation in hares, while the two assemblages in the lower middle part indicate an overrepresentation in foxes. All values are based on NISP data (including teeth). GK = Geißenklösterle, Si = Sirgenstein, KS = Kogelstein, BH = Brillenhöhle, MP = Middle Palaeolithic, G/A = Gravettian/Aurignacian transition layer

Palaeolithic for foxes. For the first topic, we will compare our results with those of other studies in the Swabian Jura (Camarós et al. 2016; Conard et al. 2013; Kitagawa et al. 2012), Gönnersdorf (Street and Turner 2013) and the Gravettian sites of the Czech Republic (Wilczyński et al. 2015; Wojtal et al. 2012). In the second and third topics that deal with population structures and hunting methods, we will compare our results with modern behavioral studies of foxes and consider the prey choice model from optimal foraging theory (OFT) to explain human hunting behavior.

Fox use in the Central European Upper Palaeolithic

As we have shown in our study, humans living in the Swabian Jura during the Palaeolithic likely considered foxes to be both food resources and sources of raw material, such as fur and teeth. Other studies have come to similar conclusions, with Camarós et al. 2016 focusing on their use for food and Conard et al. (2013) highlighting their use for fur.

In our sample, we find only three specimens that suggest the use of foxes for their fur: one specimen from the Middle Palaeolithic at Bockstein, one from the Aurignacian at Vogelherd and one from the Magdalenian at Langmahdhalde. However, not every cut leaves a mark and analysts have shown that experienced hunters or butchers leave hardly any marks on bone during the butchering process (Andersson and Paulsson 1993; Binford 1981; Charles 1997). Furthermore, cut marks are often found on small bones, such as phalanges, which, due to their small size, are usually only recovered using finer methods of excavation, such as wet-sieving (Charles 1997). As this study does not consider wet-sieved finds, this may affect our results.

There have been several studies demonstrating that carnivore teeth were used as raw material for ornaments in the Swabian Jura during the Aurignacian and Gravettian (Camarós et al. (2016); Conard (2003); Hahn (1988); Hahn (1989); Hahn (1992); Kitagawa (2014); Kitagawa et al. (2012); Langguth and Malina (2003); Münzel (2019); Wehrberger (2007); Table 3, Fig. 5). This includes not only fox teeth, but also perforated cave lion, wolf and other carnivore teeth (Camarós et al. 2016; Conard 2003; Kitagawa et al. 2012; Langguth and Malina 2003; Pacher 2005). Together, the number of perforated teeth from the Aurignacian and Gravettian increases through time in archaeological assemblages (Camarós et al. 2016; Conard et al. 2013; Kitagawa et al. 2012). If only foxes are considered, however, more

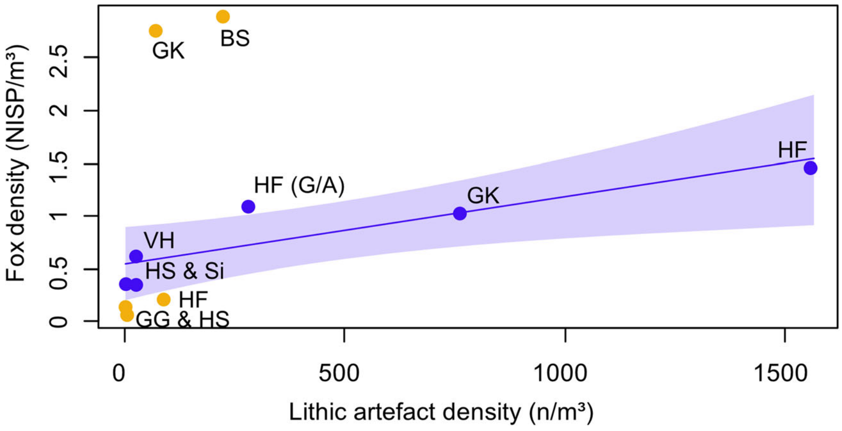

Fig. 4 Relationship between lithic artefact density (published in Conard et al. (2012)) and the density of foxes. Orange points = Middle Palaeolithic sites. Blue points = Aurignacian sites (Exception: G/A = Gravettian/Aurignacian transition layer). Blue solid line shows the calculated mean regression based on Bayesian linear model, blue shaded area shows 95% credibility interval. GK = Geißenklösterle, BS = Bockstein, HF = Hohle Fels, VH = Vogelherd, HS = Hohlenstein-Stadel, Si = Sirgenstein, GG = Große Grotte, MP = Middle Palaeolithic

Table 3 Number of fox tooth ornaments in the Swabian Jura, based on publications (Camarós et al. 2016; Conard 2003; Hahn 1988; Hahn 1989; Hahn 1992; Kitagawa 2014; Kitagawa et al. 2012; Langguth and Malina 2003; Münzel 2019; Wehrberger 2007). The values in brackets refer to the Archaeological Horizon (AH). *G/A* Gravettian/Aurignacían transition

	Geißenklösterle	Hohle Fels	Hohlenstein-Stadel
Gravettian	7 (AH I)	2 (AH IIb and IIc)	
G/A		1 (AH IId)	
Aurignacian	5 (AH III)	5 (AH IV)	5

ornaments are found in the Aurignacian than Gravettian layers. However, the number of fox tooth ornaments and ornament fragments may increase if the finds from wet-sieving are eventually included. Based on the current evidence, fox tooth ornaments might have been more important in the Aurignacian than later in the Gravettian, where ornaments of other carnivores became more abundant.

In order to understand whether the Swabian Jura is an exception in the case of fox use, we will examine other European Gravettian sites. The most suitable sites are Dolní Věstonice I

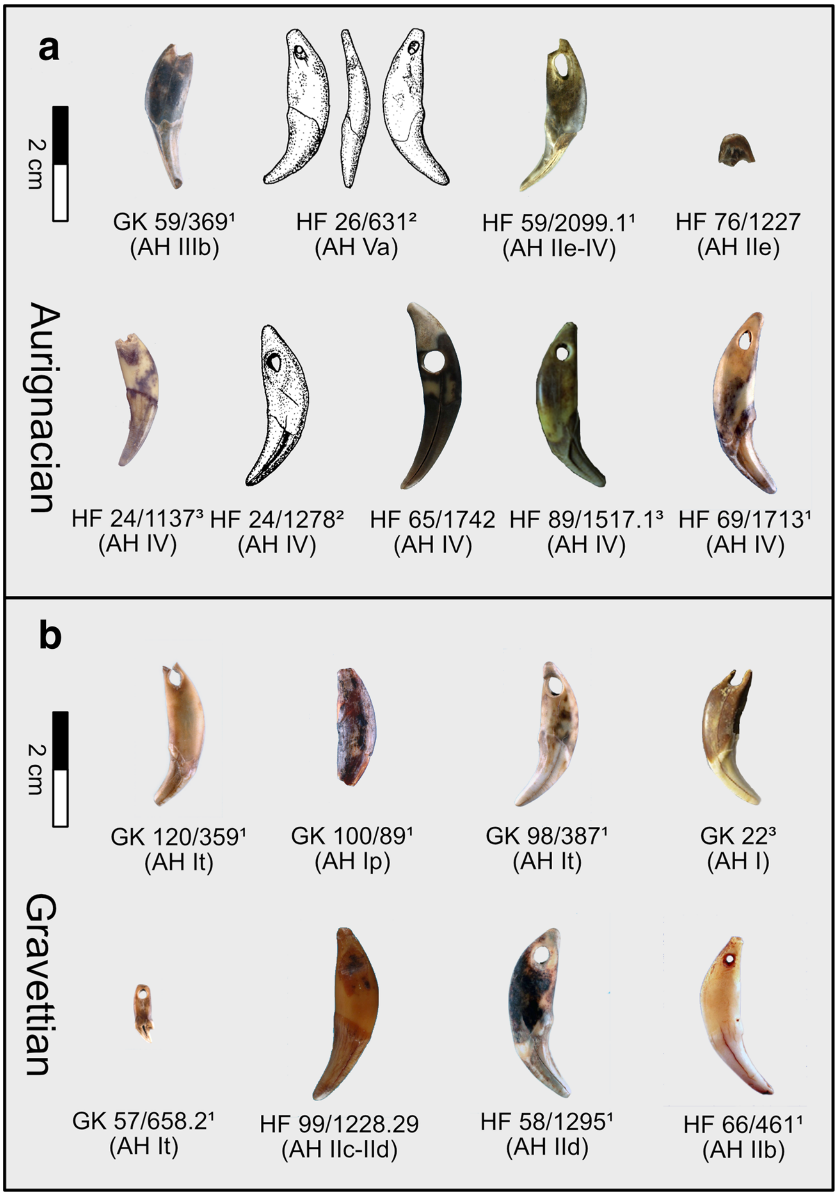

Fig. 5 **a** Nine fox tooth ornaments from the Aurignacian layers of Geißenklösterle (GK) and Hohle Fels (HF). Photos/drawings taken from (1) Langguth and Malina (2003), (2) Conard (2003) and (3) Camarós et al. (2016). Photos taken by Hilde Jenssen. AH = archaeological horizon. **b** Eight fox tooth ornaments from the Gravettian layers of Geißenklösterle (GK) and Hohle Fels (HF). Photos/drawings taken from (1) Langguth and Malina (2003), (2) Conard (2003) and (3) Camarós et al. (2016). Photos taken by Hilde Jenssen. AH = archaeological horizon

and Pavlov I of the Czech Republic, because they are well-researched and contain relatively high numbers of fox remains (NISP = 766 and 5460, respectively). Since for Pavlov I only the south-eastern area was evaluated, it is likely that the number of fox remains is even higher. Both sites are open-air sites. While Dolní Věstonice I has been described as a specialized mammoth hunting camp, Pavlov I has been described as a long-term base camp (Wilczyński et al. 2015; Wojtal et al. 2012). Only adult foxes, which are represented by all skeletal parts, have been found at Dolni Vestonice I (Wilczyński et al. 2015). No cut marks were found on fox bones at the site, making it unclear what purpose, if any, the humans that used the site had for these animals (Wilczyński et al. 2015).

Pavlov I shows a similar scenario, though the number of fox bones is much higher. Archaeologists recovered several fox bones with cut marks, which indicate that the animals were skinned and butchered. Furthermore, there are also very deep cuts on fox long bones from this assemblage, which could not be assigned to specific human activities (Wojtal et al. 2012). Both sites demonstrate that foxes were common faunal elements in Czech Gravettian open-air sites and, at least in Pavlov I, foxes were exploited by humans for both their fur and meat.

Pavlov I also provides evidence that carnivore teeth were a preferred material for making personal ornaments. In total, 284 perforated fox teeth and 65 perforated wolf teeth were found at this site. Dolni Vestonice I and Pavlov I include wet-sieved material (Wilczyński et al. 2015; Wojtal et al. 2012), which may account for the large number of small carnivore remains at these sites compared to those in the Swabian Jura.

Consider now the situation in the Magdalenian. For the sites of the Swabian Jura, the calculated indices (%fox of Carnivora and fox/LH) indicate a high abundance of foxes. However, only two cut marks indicate the use of these animals by humans. There is also no evidence for the use of fox teeth as ornaments or pendants. In order to contextualize these results, we compare the data of the Swabian Jura with the Magdalenian of Gönnersdorf, in western Germany. A large number of fox remains were found at this open-air site (Street and Turner 2013). These are mainly arctic fox (NISP = 2810), but 12 specimens are red fox. About half of the finds are cranial elements, including isolated teeth which dominate the fox remains from the site (NISP = 907). Similar to the Swabian Jura sites, in Gönnersdorf there are rarely cut marks indicating the use of these animals for fur. Despite the high representation of cranial elements, only five bones show cut marks which were clearly the result of skinning (Street and Turner 2013). A few more cut marks ($n = 30$), which indicate butchering, were found on long bones, the pelvis, ribs, vertebrae and scapulae. These modifications allowed Street and Turner (2013) to argue that hunter-gatherers at Gönnersdorf used the open skinning technique for the production of flat pelts. Furthermore, they suggest that different methods were used for butchering the foxes. As in the Swabian sites, it seems likely that foxes were also used as food at Gönnerdorf (Street and Turner 2013). Unlike in the Swabian Jura, perforated fox teeth occur in the Magdalenian layers of Gönnersdorf. While the fox ornaments of Geißenklösterle, Hohle Fels and Hohlenstein-Stadel were mainly limited to canines, both canines and other perforated teeth ($n = 45$), most frequently premolars, were found in the Gönnersdorf assemblage (Álvarez-Fernández 2000; Álvarez-Fernández 1999; Street and Turner 2013).

Population structure and the prey choice model

As discussed above, foxes were exploited by humans throughout the Upper Palaeolithic, which leads us to the question, what methods did humans use to hunt foxes? Fox hunting probably differed from large mammal hunting due to differences in social structure, diurnal vs. nocturnal behavior, and meat yield, among other factors. We explore this topic using optimal foraging theory (OFT) and, specifically, the prey choice model (Charnov 1976) which has been used to examine hunter-gatherer subsistence in many different contexts (e.g. Jones (2004); Nagaoka (2019); Starkovich (2014); Stephens and Krebs (1986); Stiner (2009)).

Following the prey choice model, we assume that foragers take into account the time and energy required to search for and handle a food resource when making decisions about which resources to pursue. Foxes and hares have approximately the same body proportions (Averianov et al. 2003; Pulliaines 1993; Thulin and Flux 2003; Wandeler and Lüps 1993), so we assume they have similar net energetic returns and are, therefore, ranked similarly in terms of caloric return (Broughton et al. 2011). Furthermore, we assume that the handling costs (i.e. the killing and processing of the prey) are similar for both taxa. The main difference between the two taxa would therefore be search time. To quantify search time for fox and hare, it is necessary to have a look at the ecology and population structure of these animals.

The number of red or arctic foxes living in an area and their reproductive rate is mainly determined by the food supply (Pulliaines 1993; Wandeler and Lüps 1993). Studies of the average population density of modern foxes find 4 to 18 red foxes and 0.03 to 2.5 arctic foxes per 10 km^2 (Pulliaines 1993; Wandeler and Lüps 1993). Within modern red fox populations, randomly taken samples have shown that 49 to 77% of the animals were younger than 1 year of age (Bögel et al. 1974; Jensen and Nielsen 1968; Lloyd et al. 1976; Van Haaften 1970; Wandeler and Lüps 1993). Modern red and arctic foxes in the wild have a maximum lifespan of 10 years (Pulliaines 1993; Wandeler and Lüps 1993).

Modern hares, in comparison, generally have much higher population densities and a shorter lifespan (maximum age of four years, Averianov et al. (2003); Thulin and Flux (2003)). On average, 200 to 300 European hares occur per 10 km^2 (Averianov et al. 2003) and mountain hare numbers vary strongly from 10 animals per 10 km^2 in Sweden (Bergengren 1969) to up to 2450 animals per 10 km^2 in some parts of Scotland (Watson and Hewson 1973; Watson et al. 1973). In both hare species, population densities can increase dramatically if conditions are favorable, such as mild winters and more food availability in the spring (Averianov et al. 2003; Thulin and Flux 2003). Based on this information, the average ratio of modern foxes to hares in the environment (Europe) is approximately one fox to 20 hares (Averianov et al. 2003; Pulliaines 1993; Wandeler and Lüps 1993; Watson and Hewson 1973; Watson et al. 1973).

In most of the Swabian Jura sites, we find higher NISP values for hare than fox in the assemblages, but not in all. In the Aurignacian layers of Hohlenstein-Stadel and the Magdalenian layers of Geißenklösterle and Vogelherd, as well as in all Middle Palaeolithic layers (except Große Grotte), foxes are more abundant than hares. In the case of the Middle Palaeolithic, this difference in hare and fox representation is probably due to the low number of small mammal remains overall and higher likelihood that foxes would enter the sites naturally. The values of the two Magdalenian layers of Geißenklösterle and Vogelherd can also be explained by the low number of hare and fox remains. At both sites, Magdalenian humans occupied the caves only for a short time (Münzel 2019; Niven 2006). With regard to the ratio of foxes to hares in the assemblages, we find a ratio of 1:7 in the Gravettian of Hohle Fels, which is the layer with the highest difference between foxes and hares. Some of the other layers in the Swabian Jura sites even have more fox than hare remains (Table 2). We hypothesize that there is a discrepancy between the relative abundance of fox and hare remains in the archaeological record and in the natural environment.

We do not assume that taphonomic processes and excavation methods provide a suitable explanation for this discrepancy because, as already mentioned, foxes and hares have similar body sizes and their bones are similarly proportioned. This means that post-depositional taphonomic processes and the time depth of the assemblage should affect both taxa similarly.

All the sites considered in our study show this discrepancy between the relative abundance of fox and hare remains in the faunal assemblages and in the natural environment, even those with very low human occupation densities. As we found at Kogelstein Cave, humans do not have to be involved in the accumulation of many foxes remains (Böttcher et al. 2000). Since this cave was a hyena den, the foxes could have been hunted by hyenas or could have lived commensal to them. Alternatively, foxes might have used the cave as a den behavior hyenas were not around. Similar commensal behavior to large predators has been demonstrated among modern foxes (Hartová-Nentvichová et al. 2010; Kidawa and Kowalczyk 2011; Murdoch et al. 2010; Pulliaines 1993; Roth 2003; Wandeler and Lüps 1993; Wikenros et al. 2017).

Another important point is that hares may also have been brought to the sites by carnivores, as described, for example, by Krajcarz and Krajcarz (2014). However, these bones should then show evidence of bite marks. This is the case in Kogelstein, Langmahdhalde, and in the archaeologically sterile layers of the other examined sites. In the layers of most of the sites we studied that showed considerable human activity, more cuts were found on the bones than bite marks. We can, therefore, assume that hares were introduced and used by humans rather than carnivores.

Kogelstein Cave and Langmahdhalde are exceptions for the sites examined in this study in this respect. At Kogelstein, fox and hare remains were deposited naturally. Further, at Langmahdhalde, there is evidence that some of the hare remains were deposited or scavenged by non-human predators in the form of puncture marks, bite marks and gnawing (Wong et al. in review). Therefore, we argue that fox behavior and human hunting methods can provide the best explanations for the large differences between the expected and observed ratios of hare and fox, assuming our expected ratio estimates are correct.

Palaeolithic fox hunting methods

As discussed above, we assume that the decision to hunt foxes vs. hares was made due to differences in the search time associated with each taxon. Therefore, we will now discuss four scenarios with different hunting methods that have a direct influence on search time. Scenario 1 is a hunt for individual animals with long-range weapons such as a throwing spear, throwing stick, sling or bow and arrow. In this case, the strongest influence on search time is the population size of the taxa, assuming these taxa are distributed similarly. Since hares occur in much higher population densities than foxes, hares would be taken more often than foxes because they would have been encountered more often. We would expect the ratio of hares to foxes in the archaeological assemblage be about the same as the natural population density ratio. Furthermore, we assume that mainly adult foxes (and hares) would be hunted, because adults are ranked higher than juveniles, based on their body size/weight (Broughton et al. 2011).

In the second scenario, traps are used to hunt both taxa. These are set up at game passes in an open landscape, which are used by small game. Since trap hunting only requires time to find the right place and set up the traps, there is no search time, unlike in scenario 1. Hares, which have higher population densities, should be more likely to be caught than foxes. We would therefore expect that in scenario 2, like scenario 1, the ratio between hare and fox remains in the archaeological assemblage would be similar to the population density ratio.

Furthermore, we assume that mainly adult foxes (and hares) would be hunted, because adults are more mobile than juveniles (Averianov et al. 2003; Pulliaines 1993; Thulin and Flux 2003; Wandeler and Lüps 1993).

Scenario 3 involves setting traps near fox dens. Similar to scenario 2, this would mean that search time is low. It would also mean that hares would be less likely to be caught in these traps. We would therefore expect foxes to be more common than hares in the faunal assemblages. Furthermore, trapping near fox dens would sample a fox population randomly and should result in trapping approximately 49 to 77% young animals (Bögel et al. 1974; Jensen and Nielsen 1968; Lloyd et al. 1976; Van Haaften 1970; Wandeler and Lüps 1993).

The fourth scenario is trapping with meat as bait. Similar to the third scenario, this is a specialized hunt for foxes (Monchot and Gendron 2011). Despite the higher population density of hares, they would be unlikely to be trapped because they would not be attracted to the bait. In this scenario, we would expect there to be more foxes in zooarchaeological assemblages than hares. Furthermore, the trapped foxes would be mostly adult individuals, because adults are more mobile than juveniles (Pulliaines 1993; Wandeler and Lüps 1993).

Looking at all the sites from the Aurignacian in the Swabian Jura, there is an almost balanced 1:1 ratio between fox and hare remains (Table 2). In the Gravettian, there is an average ratio of 1:4, in some sites even 1:6 (Sirgenstein) or 1:7 (Hohle Fels). This shows that hares have gained in importance as a food and/or fur source from the Aurignacian to the Gravettian. Nevertheless, foxes were also important prey animals, as their NISP values also rose from the Aurignacian to the Gravettian. In the Magdalenian, the ratio between these two taxa is approximately 1:2 on average. None of the time/cultural periods studied, therefore, have a fox to hare ratio corresponding to the natural population density of both taxa (approximately 1:20), indicating that scenarios 1 and 2 probably do not alone describe how foxes were hunted during the Palaeolithic in the Swabian Jura. In scenarios 3 and 4, the number of fox remains is higher than the number of hare remains, a situation that does not fit with our results from the Aurignacian or Gravettian. Furthermore, scenario 3 predicts more young foxes than adults, which we are unable to evaluate in this study. Currently, analysts have identified 28 bones and teeth from foxes younger than 1 year in the Swabian Jura, though it is likely this number will increase when wet-sieved finds are evaluated. However, the Czech sites reviewed above show that young animals are also underrepresented there, despite the analysis of wet-sieved materials (Wilczyński et al. 2015; Wojtal et al. 2012). Another reason may be the poorer preservation of juvenile bones and teeth as opposed to adult bones and teeth, as argued by Street and Turner (2013). For our discussion of hunting methods, we will therefore not look at juveniles any further.

If we now consider the data for the individual periods, it becomes apparent that there can be no general statement as to the agent of accumulation for the fox remains across all periods. During the Middle Palaeolithic, which has a large depth of time compared to the other periods studied here, most of the sites contained more fox remains than hare remains (Table 2). Additionally, human occupation at this time was less intense in the Swabian Jura (Conard et al. 2012), indicating that the majority of the fox remains were likely deposited in the cave sites naturally and that humans were only sporadically involved.

The data from the Aurignacian and Gravettian show an increase in fox and hare remains, and the importance of fox teeth as ornaments demonstrates clearly that foxes were used by humans. Therefore, we hypothesize that foxes, as well as hares, were caught primarily with traps and snares at game passes in the early Upper Palaeolithic of the Swabian Jura. Further, the higher number of foxes in the find material could reflect a partial baiting of the traps with food remains. However, we cannot exclude the targeted hunting of foxes at their dens because of the limited information about juveniles in the record.

With the exception of Geißenklösterle, the trend continues in the two indices fox/LH and hare/LH with a lower number of finds in the Magdalenian of the Swabian Jura. We assume that some foxes were also hunted by humans, but due to the low occupation density in some of the studied sites compared to the early Upper Palaeolithic (Conard 2019; Münzel 2019; Niven 2006; Taller et al. 2014; Weniger 1987a; Weniger 1987b), they may have been introduced naturally. For this period, we also hypothesize that humans used traps and snares to hunt foxes, although to a lesser extent than in the Aurignacian and Gravettian.

It is also possible that there was a behavioral change, such as the development of a commensal relationship between foxes and humans, during the Upper Palaeolithic that influenced how often humans encountered foxes versus hares in their territories.

Commensalism between foxes and humans could explain the number of fox remains in the Swabian Jura during some periods of the Palaeolithic and has been discussed to explain trends in Levantine sites (Yeshurun et al. 2009) and in the Late Holocene of Alaska (West and Yeshurun 2019). Modern commensal animals appear in larger groups than their non-commensal relatives and are therefore more tolerant of other species, including humans (Dell'Arte et al. 2007; Hulme-Beaman et al. 2016; Panek and Budny 2017; Reshamwala et al. 2018; Wandeler and Lüps 1993). Especially for foxes, this behavior is an adaptation to a human-influenced environment (Lord et al. 2019) and has been shown to have occurred at Kesslerloch, a Magdalenian site in Switzerland (Baumann et al. 2020).

If we refer to the prey choice model, commensal behavior in foxes changes the search time for foxes because commensal foxes would have higher population densities within the vicinity of human settlement areas. This decrease in search time associated with commensal foxes would increase the success rate of hunting these animals compared to non-commensal foxes, making them more likely to have been included as prey for Palaeolithic hunter-gatherers. The positive correlation of Aurignacian foxes with occupation density (Fig. 4) could also be an indication of commensal behavior during the Upper Palaeolithic in the Swabian Jura. It is likely that not only one factor was decisive, but several. Thus, commensal, food-habituated foxes may have been hunted more often with traps, alongside non-commensal animals that were trapped or occasionally hunted as single prey items.

Conclusion

In this paper, we have established that the abundance of foxes at sites in the Swabian Jura changed from the Middle Palaeolithic to the Magdalenian. While only a few foxes were found in most sites of the Middle Palaeolithic, NISP values of these animals increased steadily beginning in the Aurignacian. A similar phenomenon was observed with the hare remains. Based on the assumptions of the prey choice model, this indicates that the suppression of higher-ranked ungulate taxa in the Upper Palaeolithic led foragers to turn to lower-ranked prey or, alternatively, that the introduction of different hunting methods (i.e. snares or traps) or desire for different currencies (i.e. fur or fox teeth) influenced the abundance of different taxa at the sites.

Fox teeth, which were used as a raw material for the production of pendants and ornaments (Camarós et al. 2016; Conard 2003; Conard et al. 2013; Langguth and Malina 2003; Münzel 2019), appear to be an important aspect of the human use of foxes in the Swabian Jura during the Palaeolithic. However, we also found some evidence for the use of foxes as a source of fur and meat. Finally, we discussed the circumstances under which fox remains were likely deposited in the Palaeolithic sites of the Swabian Jura: while we found no clear evidence of humans hunting foxes during the Middle Palaeolithic, the data from the Aurignacian and Gravettian show a pattern that suggests primarily trap hunting. It is also possible that foxes became commensal to humans and were therefore hunted more often during these periods. In the Magdalenian of the Swabian Jura, the human occupation of the region appears to have been smaller than in the early Upper Palaeolithic, which is also reflected in the lower density of faunal remains at the sites. We hypothesize that foxes were hunted by humans during this period and were also introduced naturally to the sites.

With our study, we have shown that, since the early Upper Palaeolithic, the fox gained in importance as a resource, similar to hares, fish and birds. If we apply these results to the hypothesis of Stiner et al. (1999), we can predict an increase in the population density of humans from the Aurignacian onwards. This result is consistent with previous studies in the region (Conard et al. 2012; Schmidt and Zimmermann 2019).

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Authors' contributions The idea for this study originated from BMS, NJC and CB. The design of the study was discussed jointly by CB, BMS, SCM, GLW and NJC. Research and statistical analyses were conducted by CB. GLW analysed the new data for Langmahdhalde and SCM for Helga Abri. CB wrote the manuscript with the help of GLW. BMS, SCM and NJC provided helpful comments in the discussion. All authors contributed improvements and comments for the text flow. Language corrections were made by GLW and BMS.

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Availability of data and material All data used are accessible via the tables in this study or from the cited publications.

Compliance with ethical standards

Conflicts of interest/competing interests The authors declare that they have no competing interests.

Ethics approval Not applicable.

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Consent for publication Not applicable

Code availability Not applicable.

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The role of foxes in the Palaeolithic economies of the Swabian Jura (Germany)

Supplementary data

Supplementary Figures

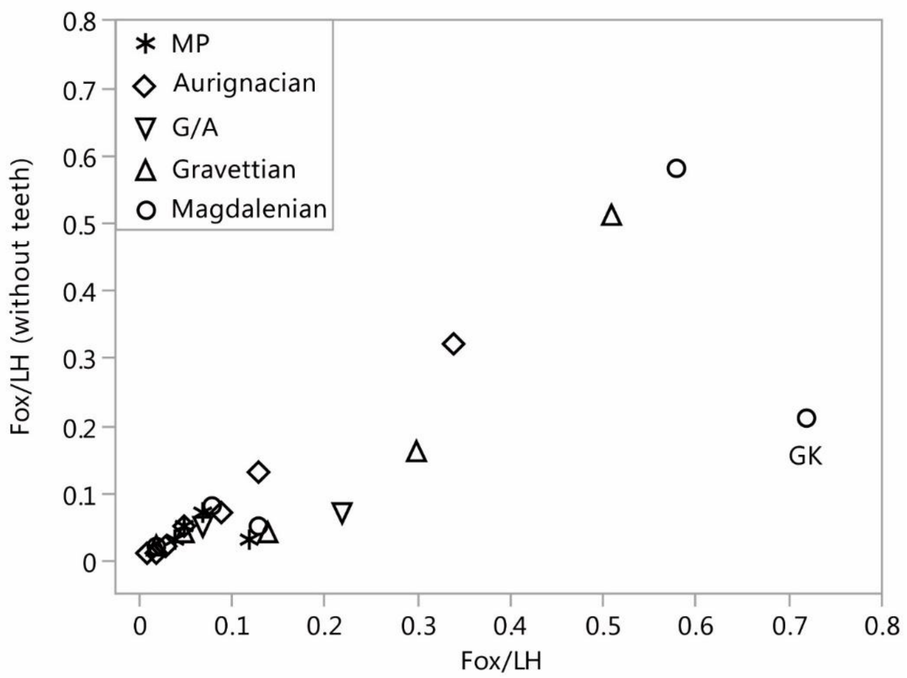

Figure S1: *Relationship between both indices of fox/LH, both including fox teeth and excluding them. On the x-axis, the index includes teeth and, on the y-axis, the index excludes teeth. Only the Magdalenian layer of Geißenklösterle was affected significantly by selecting teeth during the excavation. All values are based on NISP data. GK = Geißenklösterle, MP = Middle Palaeolithic, G/A = Gravettian/Aurignacian transition layer.*

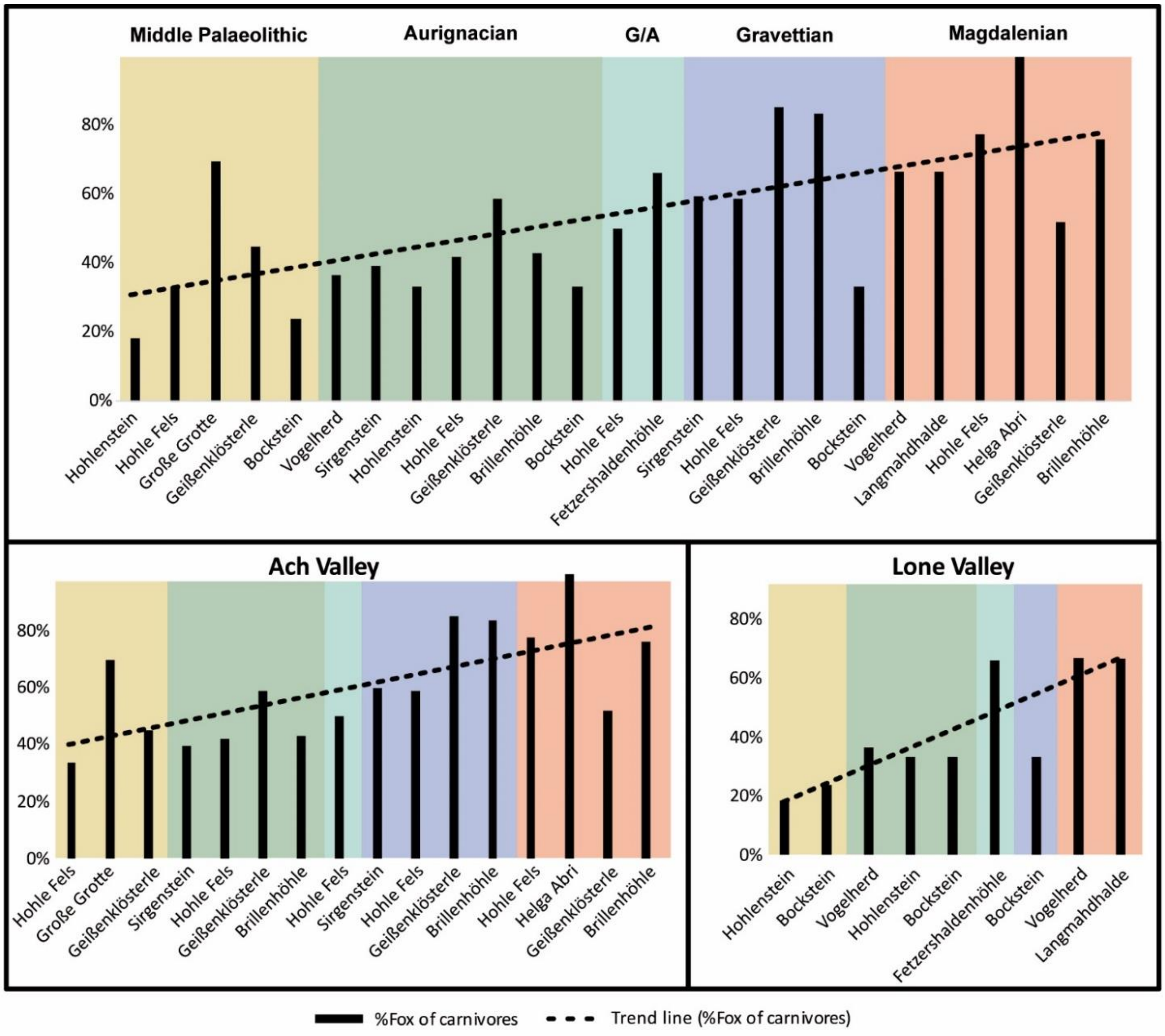

Figure S2: *Relative abundance of foxes in relation to other carnivores.*
All values are based on NISP data (including teeth). G/A = Gravettian/Aurignacian transition layer.

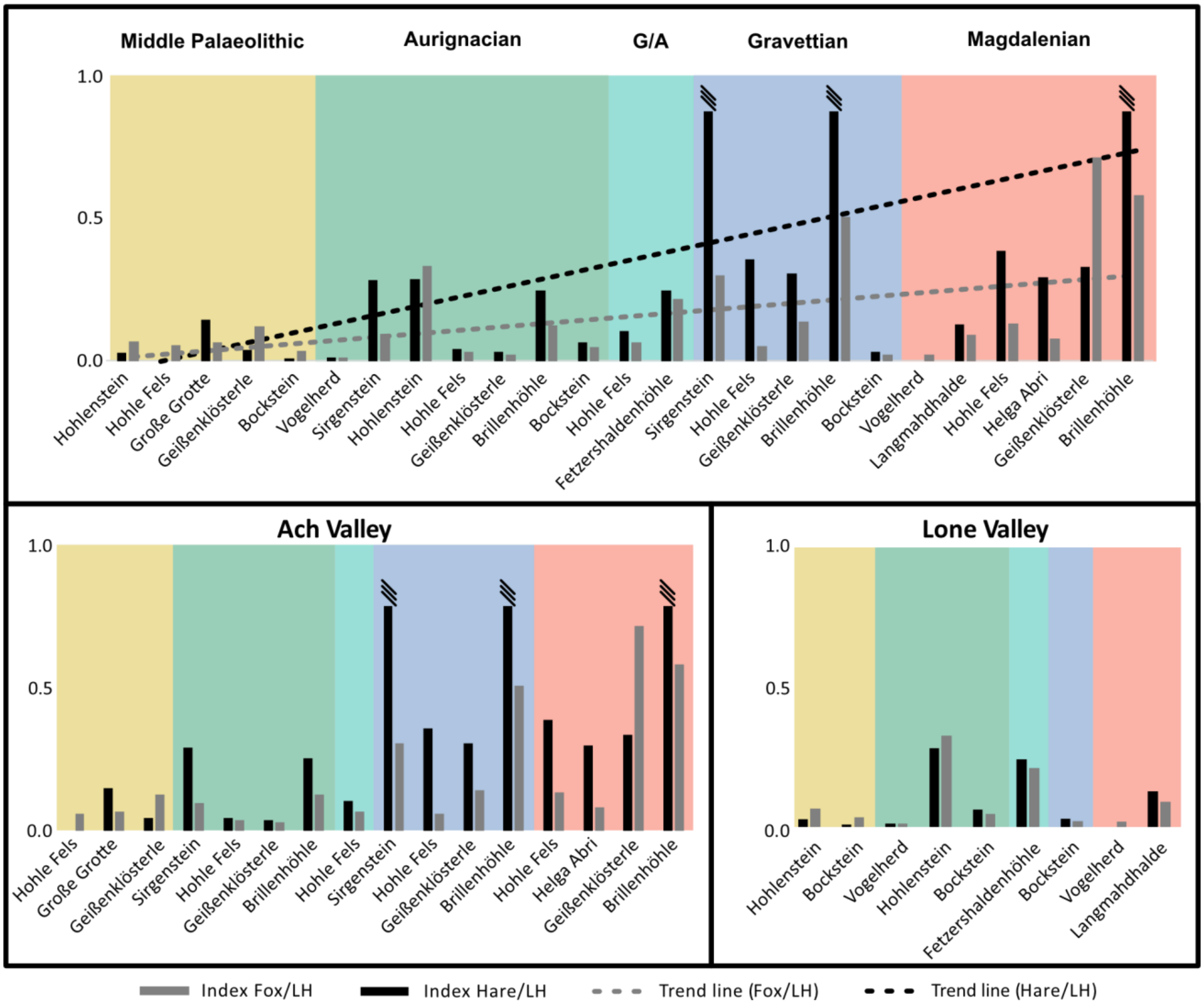

Figure S3: Index of the relationship between foxes and large herbivores (LH) and between hares and large herbivores (LH). The crossed lines indicate that the value is even higher than the axis of this figure (Table 2). All values are based on NISP data (including teeth). G/A = Gravettian/Aurignacian transition layer.

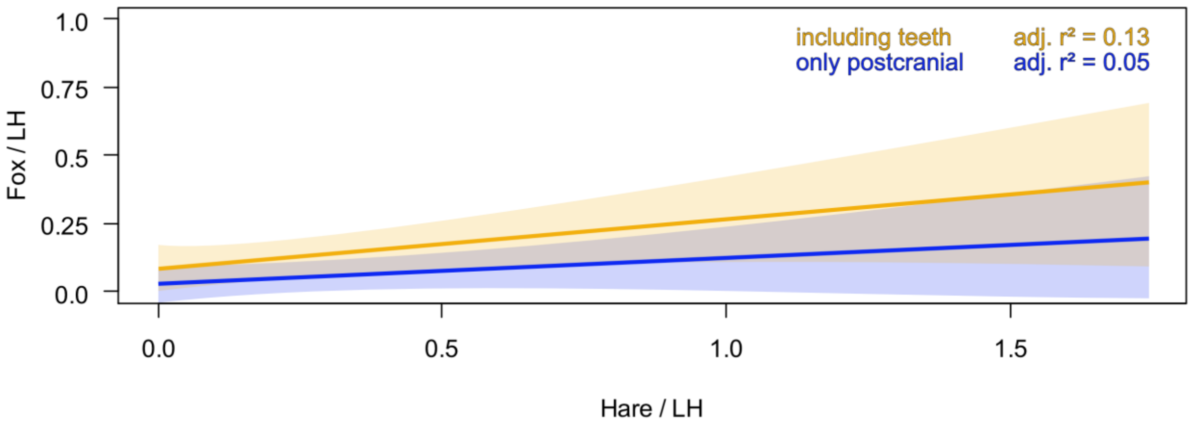

Figure S4: *Relationship between the indices Hare/LH and Fox/LH. Orange solid line shows the relation between the indices by using postcranial and teeth of both taxa, blue solid line shows this relation by using only the postcranial finds. Shaded areas show 95% credibility interval.*

Supplementary Tables

Table S1: *Langmahdhalde NISP values of taxa discussed in this paper. Values are from the following Magdalenian horizons of the site: AH IV, AH V, and AH VI. Data for "NISP" are based on all finds from the 2016 to 2018 field seasons. Data for "NISP -single finds only" are based only on measured finds from the 2016 to 2018 field seasons.*

Taxon	**NISP**	**NISP - single finds only**
Foxes		
Vulpes sp.	45	9
Vulpes lagopus	1	1
TOTAL	46	10
Hares		
Lepus sp.	156	13
Lepus europaeus	6	1
Lepus timidus	8	0
TOTAL	170	14
Large Herbivores		
Equus ferus	46	42
Cervus elaphus	11	10
Rangifer tarandus	80	52
Bos/Bison sp.	2	2
Capra ibex	3	2
Alces alces or *Megaloceros giganteus*	1	1
TOTAL	143	109
Other Carnivores		
Panthera spelaea	6	5
Martes martes	1	0
Mustela sp.	4	0
small Mustela sp. (M. erminea or M. nivalis)	34	0
Mustela putorius	1	0
Mustela erminea	1	0
TOTAL	47	5

Table S2: Compilation of the data used to calculate the fox density. Data for "Lithic artefact density" and "sediment" are based on Conard et al. (2012).

Site	Periode	Sediment (m³)	Lithic artefact density (n/m³)	Foxes (NISP)	Fox density (NISP/m³)
Geißenklösterle	Aurignacian	25.45	760	26	1.02
Hohle Fels	Aurignacian	19.95	1558	29	1.45
Sirgenstein	Aurignacian	71	27	24	0.34
Vogelherd	Aurignacian	202.5	27	122	0.60
Hohlenstein-Stadel	Aurignacian	100	3	36	0.36
Hohle Fels	G/A	12.75	280	14	1.10
Große Grotte	Middle Palaeolithic	274	7	16	0.06
Geißenklösterle	Middle Palaeolithic	9.45	70	26	2.75
Hohle Fels	Middle Palaeolithic	9.7	89	2	0.21
Hohlenstein-Stadel	Middle Palaeolithic	390	3	50	0.13
Bocksteinschmiede	Middle Palaeolithic	12.5	223	36	2.88

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Appendix 2

Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems.

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RESEARCH ARTICLE

Fox dietary ecology as a tracer of human impact on Pleistocene ecosystems

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Abstract

Nowadays, opportunistic small predators, such as foxes (*Vulpes vulpes* and *Vulpes lagopus*), are well known to be very adaptable to human modified ecosystems. However, the timing of the start of this phenomenon in terms of human impact on ecosystems and of the implications for foxes has hardly been studied. We hypothesize that foxes can be used as an indicator of past human impact on ecosystems, as a reflection of population densities and consequently to track back the influence of humans on the Pleistocene environment. To test this hypothesis, we used stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of bone collagen extracted from faunal remains from several archaeological sites located in the Swabian Jura (southwest Germany) and covering a time range over three important cultural periods, namely the Middle Palaeolithic (older than 42,000 years ago) attributed to Neanderthals, and the early Upper Palaeolithic periods Aurignacian and Gravettian (42,000 to 30,000 years ago) attributed to modern humans. We then ran Bayesian statistic systems (SIBER, mixSIAR) to reconstruct the trophic niches and diets of Pleistocene foxes. We observed that during the Middle Palaeolithic period, when Neanderthals sparsely populated the Swabian Jura, the niches occupied by foxes suggest a natural trophic behavior. In contrast, during the early Upper Palaeolithic periods, a new trophic fox niche appeared, characterized by a restricted diet on reindeer. This trophic niche could be due to the consumption of human subsidies related to a higher human population density and the resulting higher impact on the Pleistocene environment by modern humans compared to Neanderthals. Furthermore, our study suggests that, a synanthropic commensal behavior of foxes started already in the Aurignacian, around 42,000 years ago.

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Introduction

As soon as hominins started to kill large herbivores, around 2.5 Ma, they started a cascade of ecological reactions that led to vegetation and climate change [1, 2]. Late Pleistocene herbivorous megafauna extinction have been suggested to be at least partially caused by human impact

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[3, 4]. The impact of human on these large herbivores during the late Quaternary has been largely explored, but less is known about human influence on the ecology of carnivores. Some large carnivorous species may also have been impacted by hominin activities, leading to their extinction, through competition or extirpation [5–7]. However, one aspect that has been rarely addressed is the possibility that human hunting may have had a positive effect on some opportunistic species, through the subsidies that humans produced and that could have been exploited by some species. Especially small predators such as foxes could be one of these cases, considering the ability that both Arctic and red foxes (*Vulpes lagopus* and *Vulpes vulpes*) have to exploit the leftovers of other predators, including humans [8–14]. It is interesting to note that fox remains are often found in archaeological sites of the Late Pleistocene all over Europe [15–22]. To test the hypothesis that fox diet could have been influenced by subsidies from prehistoric hunter-gatherers, we used stable isotopic tracking of bone collagen in Middle and Upper Palaeolithic fossil bones from the Swabian Jura (southwestern Germany), documenting the replacement of Neanderthals (Middle Palaeolithic) by modern humans (Upper Palaeolithic).

The archaeological cave sites of the Swabian Jura, in particular the sites of the Ach and Lone valleys, are among the best scientifically investigated sites of the last glacial in Germany. Especially, the Middle and early Upper Palaeolithic layers (older than 42,000 to 30,000 years ago) contain important lithic and faunal assemblages [20, 23–25]. While during the Middle Paleolithic (from early to middle Würmian period and older than 42,000 years [26–28]) human occupation was spare in this region, it increased during the early Upper Palaeolithic [23]. The early Upper Palaeolithic is represented by the Aurignacian, dated from 42,000 to 34,000 cal BP [28–31] and the Gravettian, dated from 34,000 to 30,000 cal BP [28, 32, 33] in the Swabian Jura. Most of the pre-LGM sites (periods preceding the last glacial maximum) in the Swabian Jura are dominated by faunal remains of cave bear and ungulates [20, 34–41]. The relative abundance of skeletal remains of different species does not necessarily reflect the intensity of faunal exploitation. Niven [42] explained that mainly smaller ungulates, such as reindeer, were taken to the cave by humans as a whole, whereas large animals, such as mammoths, were butchered directly at the kill sites and only certain parts were transported to the cave. In return, this can explain why ivory was often found, but complete mammoth skeletons are missing. Remains of cave bears, which usually have died naturally in the caves during hibernation, do not necessarily relate to human activity, even if there are indications of cave bear hunting [35–37].

In addition to the herbivores, which accounted for the majority of the prey hunted by humans, remains of large and small carnivores have also been found in all of the sites [20, 34–41]. Remains of red foxes and Arctic foxes are particularly common among carnivores and increased from the Middle to the Upper Palaeolithic [17, 20]. The increasing occurrence of fox remains in the early Upper Palaeolithic layers can be explained to some extent by the behavior of foxes. Red and Arctic foxes are generally opportunists, using the food that is most easily accessible to them [43, 44]. Studies of modern red and Arctic foxes have shown that the closer they live to towns or villages, the more they feed on human food leftovers [8, 14, 45, 46]. However, this commensal behavior is not only shown in connection with humans, but also with large carnivores, such as bears and wolves [43, 44, 47, 48]. Without the influence of large predators or humans, both fox species feed mainly on small mammals [8, 9, 11, 12, 43, 44, 46, 48–50]. Studies on Late Pleistocene red and Arctic foxes from Belgium showed that they were slightly larger than today's foxes and lived much more carnivorous [15, 16, 51]. In addition, Szuma and Germonpré [15] concluded that Pleistocene foxes were more adapted to scavenging and thus were more likely commensal to large carnivores or even humans. Consequently, foxes could also have benefited from the prey of other predators during the Middle and early Upper Palaeolithic of the Swabian Jura, whether they were cave lions, brown bears or humans.

In order to understand the dietary behavior of animals, the use of stable carbon and nitrogen isotopes (δ^{13}C, δ^{15}N) from fossil bone collagen have proven to be extremely informative in recent decades [52–59]. In general, the collagen carbon and nitrogen isotopic values are reflecting the protein part of the diet for omnivores [60], and since meat is much higher in protein than plants, the impact of plant food will be negligible. Thus foxes could be treated in isotopic studies as predators, even if they are known to possibly include plant food in their diet [43, 44]. Especially, the δ^{15}N values in collagen are linked to the trophic level and indicate which prey were consumed in which proportions for carnivorous species [52, 61, 62]. Reconstructions of the trophic isospace, a two-dimensional space, based on the δ^{13}C and δ^{15}N values of consumers (e.g., carnivores) and sources (e.g., large herbivores and rodents), is the basis for determining trophic niches and food reconstructions by using Bayesian statistics [63–66]. Such reconstructions were also performed in archaeological sites of the Swabian Jura during the last years [52, 57, 67–69].

In this study, we firstly reconstruct the trophic niche of foxes over three important cultural time ranges, namely the Middle Palaeolithic, Aurignacian and Gravettian. Based on these results, we consider how a potential commensal to human behavior could be demonstrated and used as an indicator of human population densities and consequently to track back the influence of humans on the Pleistocene environment. To find an answer, we reconstructed the trophic niches and diet of Middle Palaeolithic, Aurignacian and Gravettian foxes from the Swabian Jura, based on their δ^{13}C and δ^{15}N isotopic values.

Material and methods

Material

In this study, we present 70 new δ^{13}C and δ^{15}N isotopic values of foxes and large carnivores from Middle Palaeolithic, Aurignacian and Gravettian layers of the Ach and Lone valleys (Table 1) as well as a set of 44 new small mammal isotopic values from the same periods (Table 2). No permits were required for the described study, which complied with all relevant regulations. All samples used in this study are stored in the storage facilities of the Institute for Scientific Archaeology (University of Tübingen), headed by Nicholas J. Conard. Preserved collagen samples are stored in the storage facilities of Biogeology (headed and managed by Hervé Bocherens), Department of Geosciences (University of Tübingen).

All newly analyzed specimens were most likely adult, distinguished by symphysial fusing and tooth characteristics. To exclude using samples from the same individual, most carnivore samples came from separate archaeological sites or layers. In total, our samples reflect a minimum of 62 single carnivore specimens (more information in the chapter "intra-individual variability" of S1 Text).

To generate a representative isospace we have added published isotope values of nine large predators and 51 large herbivores [54, 57, 69]. More detailed information is given in S1 Table. In total, we considered seven carnivore species. For the Middle Paleolithic we included wolf (*Canis lupus*), brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*) and Arctic fox (*Vulpes lagopus*). The Aurignacian is represented by wolf, wolverine (*Gulo gulo*), lynx (*Lynx lynx*), hyena (*Crocuta crocuta*), brown bear, red fox and Arctic fox. For the Gravettian, we considered the following carnivores: wolf, wolverine, lynx, cave lion (*Panthera leo spelaea*), brown bear, red fox and Arctic fox. As the isospaces for the different pre-LGM periods are quite similar [57], we can use the complete set of vole (*Microtus arvalis/agrestis*), Norway and Arctic lemmings (*Lemmus lemmus* and *Dicrostonyx torquatus*), horse (*Equus* sp.), hare (*Lepus* sp.), mammoth

Table 1. List of newly analyzed isotopic values of carnivores reported in this study.

Lab ID	Period	Location	Excav. No	AH	Taxon	Skeleton element	N_{bone} [%]	Yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
PLC-79	MP	BS	BS 550825–35		*Canis lupus*	Radius	1.7	56.0	34.0	11.8	3.4	-20.1	10.6
PLC-35	MP	HS	HS 18/13-2806	MP R	*Canis lupus*	Ulna	2.2	64.7	35.2	12.4	3.3	-20.0	7.7
PLC-37	MP	HS	HS 13/10-8071	MP U	*Canis lupus*	Mandible	1.1	33.8	34.6	12.1	3.3	-20.1	8.5
PLC-38	MP	HS	HS 17/11-4075	MP U	*Canis lupus*	Mandible	2.1	74.4	33.6	11.8	3.3	-19.4	10.0
PLC-48	MP	VH	Vg VIII 7773	VIII	*Canis lupus*	Astragalus	2.4	104.5	38.8	13.6	3.3	-19.2	8.3
PLC-49	MP	VH	Vg VIII 12692	VIII	*Canis lupus*	Tibia	2.3	119.2	42.2	14.4	3.4	-19.7	7.3
PLC-76	MP	BS	BS 13.8.34/6		*Vulpes lagopus*	Mandible	0.9	27.3	40.0	13.3	3.5	-21.4	1.0
PLC-80	MP	BS	BS 12.9.34/10		*Vulpes vulpes*	Tibia	0.8	41.7	26.4	9.1	3.4	-19.7	10.0
PLC-82	MP	BS	BS 18.8.34/13		*Vulpes vulpes*	Radius	1.5	71.5	42.5	15.0	3.3	-20.2	7.8
PLC-83	MP	BS	BS 28.8.33/59		*Vulpes vulpes*	Humerus	2.7	135.2	43.1	15.3	3.3	-20.4	8.2
PLC-84	MP	BS	BS 11.9.34/37		*Vulpes vulpes*	Mandible	0.9	34.0	26.7	9.2	3.4	-20.1	9.0
VLP-10	MP	HF	HF 68/2989	VI	*Vulpes vulpes*	Tibia	3.7	73.2	42.0	14.9	3.3	-21.1	3.0
PLC-39	MP	HS	HS 13/9-8156	MP U	*Vulpes vulpes*	Mandible	2.8	142.4	39.8	14.0	3.3	-20.3	8.4
PLC-40	MP	HS	HS 14/8-10670	MP U	*Vulpes vulpes*	Ulna	2.5	103.5	41.7	14.6	3.3	-19.9	8.6
PLC-78	A	BS	BS 24.8.55/22		*Canis lupus*	Tibia	2.9	107.0	41.0	14.6	3.3	-19.5	8.5
JK2175	A	HF	HF 24/1035	IIIa	*Canis lupus*	Ulna	2.5	67.2	34.4	12.2	3.3	-19.5	10.7
JK2180	A	HF	HF 89/1553	IV	*Canis lupus*	Humerus	3.1	110.3	40.9	14.6	3.3	-18.6	8.3
JK2184	A	HF	HF 79/2563	IV	*Canis lupus*	Metacarpal IV	3.4	96.8	40.2	14.3	3.3	-18.9	10.0
PLC-24	A	HS	HS 19/2-9285		*Canis lupus*	Mandible	1.0	43.6	17.2	6.1	3.3	-19.1	9.5
PLC-25	A	HS	HS 19/2-9312		*Canis lupus*	Mandible	0.6	14.9	34.8	12.2	3.3	-19.0	9.6
PLC-29	A	HS	HS 19/6-1435		*Canis lupus*	Ulna	2.8	108.4	41.8	14.8	3.3	-19.4	10.7
PLC-30	A	HS	HS 12/5-8905		*Canis lupus*	Atlas	2.5	85.0	40.1	14.1	3.3	-19.7	9.2
PLC-31	A	HS	HS 19/3-2467		*Canis lupus*	Ulna	1.9	74.7	42.2	14.6	3.4	-19.0	9.8
PLC-32	A	HS	HS 18/4-3805		*Canis lupus*	Humerus	3.2	158.8	41.9	14.8	3.3	-19.5	8.5
PLC-2	A	VH	Vg IV 9059	IV	*Canis lupus*	Radius	3.2	145.1	41.7	14.7	3.3	-20.2	9.1
PLC-3	A	VH	Vg IV/V 8200	IV/V	*Canis lupus*	Atlas	0.9	27.9	35.9	12.5	3.3	-21.0	9.4
PLC-44	A	VH	Vg V 12645	V	*Canis lupus*	Metacarpal	2.8	127.0	42.8	14.9	3.3	-18.9	9.6
PLC-45	A	VH	Vg IV 10685	IV	*Canis lupus*	Tibia	1.6	63.4	41.7	14.7	3.3	-20.4	9.5
PLC-46	A	VH	Vg IV 1732	IV	*Canis lupus*	Ulna	3.2	132.7	40.7	14.5	3.3	-19.7	9.3
PLC-47	A	VH	Vg IV 7214	IV	*Canis lupus*	Ulna	2.3	77.4	38.1	13.4	3.3	-19.2	8.9

(*Continued*)

Table 1. (Continued)

Lab ID	Period	Location	Excav. No	AH	Taxon	Skeleton element	N_{bone} [%]	Yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
PLC-62	A	Si	Si 1631	IV	*Gulo gulo*	Femur	2.1	67.3	34.8	12.4	3.3	-19.1	9.4
PLC-17	A	GK	GK 69/540	IIb	*Lynx lynx*	Phalanx		117.6	40.0	14.1	3.3	-19.3	7.7
PLC-23	A	HS	HS 18/7-11629		*Lynx lynx*	Humerus	2.6	79.8	40.4	14.2	3.3	-19.3	10.2
PLC-63	A	Si	Si 3892		*Lynx lynx*	Tibia	2.9	132.7	43.2	15.1	3.3	-19.8	7.0
VLP-1	A	GK	GK 35/206	III	*Vulpes lagopus*	Tibia	3.1	105.3	43.8	15.4	3.3	-20.6	9.1
VLP-3	A	HF	HF 25/1111	VAA	*Vulpes lagopus*	Radius	2.8	76.0	43.1	15.1	3.3	-19.9	8.6
PLC-22	A	HS	HS 17/4-5119		*Vulpes lagopus*	Mandible	2.9	133.8	42.8	14.7	3.4	-20.2	5.4
PLC-28	A	HS	HS 19/7-11526		*Vulpes lagopus*	Mandible	2.1	62.9	35.9	12.6	3.3	-19.7	8.6
PLC-55	A	HS	HS 17/7 7067		*Vulpes lagopus*	Mandible	1.6	31.2	16.9	6.1	3.2	-20.1	8.9
PLC-1	A	VH	Vg IV 7213	IV	*Vulpes lagopus*	Tibia	2.6	113.6	41.9	14.6	3.4	-18.4	8.7
PLC-16	A	VH	Vg IV 245	IV	*Vulpes lagopus*	Mandible	1.2	50.6	32.7	11.6	3.3	-19.4	9.4
PLC-15	A	VH	Vg IV 12782	IV	*Vulpes* sp.	Mandible	1.4	56.7	35.1	12.2	3.4	-20.4	8.9
PLC-85	A	BS	BS 34/19		*Vulpes vulpes*	Tibia	2.5	112.4	43.9	15.5	3.3	-20.2	8.3
PLC-26	A	HS	HS 19/2-9298		*Vulpes vulpes*	Mandible	0.8	30.9	27.2	9.6	3.3	-19.8	8.1
PLC-27	A	HS	HS 19/2-9359		*Vulpes vulpes*	Humerus	0.6	23.9	17.2	6.2	3.2	-20.2	8.2
PLC-66	A	Si	Si 3360	IV	*Vulpes vulpes*	Mandible	1.8	76.3	40.5	13.8	3.4	-20.3	8.0
PLC-67	A	Si	Si 3361	IV	*Vulpes vulpes*	Mandible	2.6	143.8	42.2	14.8	3.3	-21.0	8.2
PLC-68	A	Si	Si 3448	IV	*Vulpes vulpes*	Humerus	2.7	138.6	42.6	14.8	3.4	-20.4	6.0
PLC-69	A	Si	Si 3446	IV	*Vulpes vulpes*	Tibia	3.2	150.0	43.4	15.1	3.4	-20.0	4.8
PLC-10	A	VH	Vg IV 7245	IV	*Vulpes vulpes*	Tibia	1.1	36.2	37.7	13.1	3.4	-19.2	8.2
PLC-11	A	VH	Vg IV 7259	IV	*Vulpes vulpes*	Radius	3.2	148.2	42.3	14.9	3.3	-19.6	9.1
PLC-13	A	VH	Vg IV 12776	IV	*Vulpes vulpes*	Mandible	2.3	112.6	38.9	13.6	3.3	-20.0	4.7
PLC-14	A	VH	Vg IV 12780	IV	*Vulpes vulpes*	Mandible	1.1	42.8	34.1	11.9	3.4	-20.0	5.5
PLC-8	A	VH	Vg IV/V 11675	IV/V	*Vulpes vulpes*	Femur	2.8	58.4	40.7	14.4	3.3	-20.1	8.3
PLC-9	A	VH	Vg IV 3551	IV	*Vulpes vulpes*	Tibia	1.6	44.7	31.6	11.2	3.3	-19.4	5.7
JK2174	G	HF	HF 56/1965	IIC	*Canis lupus*	Scapula	3.5	144.8	39.6	14.1	3.3	-20.2	9.7
JK2183	G	HF	HF 59/1390	IIcf	*Canis lupus*	Calcaneus	3.4	155.7	40.9	14.4	3.3	-20.2	9.3
JK2178	G	HF	HF 99/1174	IIC	*Canis lupus*	Metacarpale II	3.7	11.9	40.6	14.5	3.3	-19.5	8.9
PLC-70	G	Si	Si 983	I	*Gulo gulo*	Scapula	3.1	165.1	41.7	14.8	3.3	-19.1	7.6
PLC-18	G	GK	GK 9/3	Ir	*Lynx lynx*	Rib	2.0	96.2	42.5	14.8	3.3	-19.5	8.4

(*Continued*)

Table 1. (Continued)

Lab ID	Period	Location	Excav. No	AH	Taxon	Skeleton element	N_{bone} [%]	Yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
PLC-19	G	GK	GK 121/93	Ir	*Lynx lynx*	Mandible	3.6	137.2	42.6	14.8	3.3	-18.7	8.0
PLC-77	G	BS	BS 24.9.53/15		*Vulpes lagopus*	Ulna	2.2	97.6	41.6	14.7	3.3	-20.1	8.7
PLC-42	G	Si	Si 776	I	*Vulpes lagopus*	Mandible	2.8	138.2	42.4	14.8	3.3	-20.3	7.6
VLP-4	G	GK	GK 508/70	I	*Vulpes vulpes*	Tibia	3.2	109.8	44.2	15.3	3.4	-19.7	7.1
VLP-5	G	GK	GK 15/106	I	*Vulpes vulpes*	Tibia	3.1	109.7	44.3	15.3	3.4	-19.7	9.7
PLC-43	G	Si	Si 773	I	*Vulpes vulpes*	Mandible	3.2	166.9	43.9	15.1	3.4	-19.7	4.0
PLC-71	G	Si	Si 2862	I	*Vulpes vulpes*	Humerus	3.1	157.9	43.0	14.7	3.4	-20.5	6.0
PLC-72	G	Si	Si 2550	I	*Vulpes vulpes*	Mandible	2.6	139.4	42.5	14.7	3.4	-19.4	6.7
PLC-73	G	Si	Si 2214	I	*Vulpes vulpes*	Humerus	2.8	135.5	44.0	14.9	3.4	-19.6	3.7
PLC-75	G	Si	Si 2213	I	*Vulpes vulpes*	Tibia	1.5	54.4	32.3	11.2	3.4	-20.3	9.2

AH = Archaeological horizon, MP = Middle Palaeolithic, A = Aurignacian, G = Gravettian, BS = Bockstein, HS = Hohlenstein-Stadel, HF = Hohle Fels, GK = Geißenklösterle, Si = Sirgenstein, VH = Vogelherd.

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(*Mammuthus primigenius*) and reindeer (*Rangifer tarandus*) samples as dietary sources to reconstruct the trophic niches of the carnivores. All of our studied material come from archaeological cave sites from the Ach Valley (Hohle Fels, Geißenklösterle and Sirgenstein) and the Lone Valley (Bockstein, Hohlenstein-Stadel and Vogelherd) (Fig 1).

The taxonomic determination of carnivore specimens was done following published morphological and metrical studies [24, 38, 40, 41, 70], as well as by comparing the bones with the zooarchaeological collection of the University of Tübingen. However, in the rest of study, we will combine red fox and Arctic fox as "fox", since they do not show a clear trophic niche differentiation in the Middle and Upper Palaeolithic of the Swabian Jura [67, 71] (see chapter “Statistical test for isotopic variance of both fox species” in S2 Text). The newly analyzed small mammals were determined by using published determination keys [72–74].

Elemental and isotope analyses

For the isotopic analysis of the larger bones (Lab codes: JK, PLC, VLP), bone samples (0.3–0.7 g) were cut using a Saeshin Forte 200 alpha micro-circular saw. After successive cleaning in Millipore water and acetone, the samples were ground to powder manually (grain size less than 0.7 mm). In the case of the rodent samples (Lab code: SJM), the complete mandible without teeth was taken for each specimen and grinded manually with a mortar, which resulted in a smaller grain size of the samples, but in a higher yield of bone powder. The collagen content of the bone was only measured for JK, PLC and VLP samples by performing a CNS elemental analysis following Bocherens [55]. This analysis was performed at the Hydrogeochemisty working group (University of Tübingen) using a Vario EL elemental analyzer. Sulfanilic acid from Merck was used as the international standard. The SJM samples did not have enough material to perform this preliminary analysis and were run directly for collagen extraction.

Table 2. List of newly analyzed isotopic values of rodents and hare reported in this study.

Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/ N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
SJM-54	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandible		33.4	31.3	11.3	3.2	-21.2	6.4
SJM-55	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandible		41.5	29.5	10.6	3.2	-20.3	7.1
SJM-56	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Dicrostonyx sp.	Mandible		68.6	23.9	8.7	3.2	-20.9	5.2
SJM-57	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandible		51.0	36.8	13.0	3.3	-21.4	5.2
SJM-58	A	HF	HF Eimer-1004 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandible		47.6	27.7	9.7	3.3	-22.8	6.6
SJM-59	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandible		59.5	28.4	10.1	3.3	-21.6	3.9
SJM-60	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandible		57.5	30.1	10.6	3.3	-20.9	5.6
SJM-61	A	HF	HF Eimer-1002 (Qu 11, AH Vab)	AH Vab	Lemmus lemmus	Mandible		51.9	32.2	11.5	3.3	-21.7	4.2
SJM-62	A	HF	HF Eimer-719 (Qu 32, AH IV)	AH IV	Microtus arvalis/ agrestis	Mandible		31.2	21.9	7.6	3.4	-22.1	3.8
SJM-63	A	HF	HF Eimer-1277 (Qu 31, AH IV)	AH IV	Microtus arvalis/ agrestis	Mandible		41.3	23.3	8.0	3.4	-21.8	4.5
SJM-50	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Dicrostonyx sp.	Mandible		64.5	31.9	11.5	3.2	-21.1	3.6
SJM-51	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Dicrostonyx sp.	Mandible		75.6	32.4	11.4	3.3	-21.3	6.1
SJM-52	G	HF	HF Eimer-1429 (Qu 112, AH IIc)	AH IIc	Dicrostonyx sp.	Mandible		71.8	34.7	12.3	3.3	-20.2	3.5
VLP-12	G	GK	GK 99/458	It	*Lepus* sp.	Tibia	3.0	92.2	43.4	15.3	3.3	-20.4	2.8
VLP-13	G	GK	GK 86/17	Ir	*Lepus* sp.	Tibia	2.6	59.1	43.6	15.5	3.3	-20.2	3.5
SJM-53	G	HF	HF Eimer-1225 (Qu 110, AH IIc)	AH IIc	Microtus arvalis/ agrestis	Mandible		20.4	30.9	11.1	3.2	-21.7	3.0
SJM-7	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandible		61.0	33.1	11.7	3.3	-21.2	5.5
SJM-8	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandible		42.1	29.7	10.7	3.2	-21.0	6.7
SJM-9	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandible		70.1	32.9	11.6	3.3	-21.2	7.1
SJM-11	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Dicrostonyx sp.	Mandible		86.8	25.1	8.0	3.6	-25.1	-1.5
SJM-1	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		52.3	34.7	12.2	3.3	-21.8	5.9
SJM-2	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		60.1	33.6	11.8	3.3	-22.2	4.8
SJM-3	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		44.8	32.7	11.5	3.3	-20.7	6.5
SJM-4	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		55.4	35.4	12.2	3.4	-22.0	5.8
SJM-5	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		69.5	33.8	11.7	3.4	-21.9	7.3
SJM-6	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		72.0	32.0	11.4	3.3	-21.8	6.8
SJM-12	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		54.7	30.9	11.3	3.2	-23.1	1.0

(*Continued*)

Table 2. (Continued)

Lab ID	Period	Location	Excav. No	AH	Taxon	Element	N_{bone} [%]	yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/ N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
SJM-13	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		70.3	31.1	11.3	3.2	-23.2	5.2
SJM-14	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		68.0	25.3	9.2	3.2	-24.9	-0.6
SJM-15	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		86.0	27.7	9.3	3.5	-24.6	1.0
SJM-16	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		70.5	26.0	8.4	3.6	-24.5	0.6
SJM-17	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		79.3	28.5	10.5	3.2	-22.9	2.5
SJM-18	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Lemmus lemmus	Mandible		60.2	26.7	8.9	3.5	-23.5	2.5
SJM-10	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		63.1	30.4	10.9	3.3	-22.4	7.3
SJM-29	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		44.3	27.8	9.4	3.5	-22.5	7.9
SJM-30	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		48.2	25.7	9.0	3.3	-22.1	4.5
SJM-31	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		30.1	25.2	8.6	3.4	-22.6	6.7
SJM-32	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		59.3	26.9	9.2	3.4	-23.0	7.4
SJM-33	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		45.1	25.7	8.7	3.4	-23.1	5.4
SJM-34	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		67.1	21.4	7.9	3.2	-22.0	5.7
SJM-35	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		47.3	25.1	8.8	3.3	-22.7	4.4
SJM-36	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		59.3	23.2	7.9	3.5	-22.2	5.9
SJM-37	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		65.6	22.6	8.2	3.2	-21.8	5.7
SJM-38	MP	HF	HF Eimer-1613 (Qu 26, AH IX WF)	AH IX WF	Microtus arvalis/ agrestis	Mandible		63.1	23.4	8.4	3.2	-23.0	6.2

AH = Archaeological horizon.

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Collagen extraction following the protocol of Bocherens [53] was performed in the Biogeology working group (University of Tübingen). Depending on the percentage of nitrogen in the bone powder (%N_{bone}) of each sample, as measured by the CNS analysis, we used 120 mg (4.0–4.5%N_{bone}) to 450 mg (0.4–1.0%N_{bone}) of bone powder for the extraction. In the case of the SJM samples we used the totality of the available powder, because the average sample size was only 40 mg. With respect to the smaller grain size of the SJM samples we have reduced the time in which the sample remains in 1 molar HCl solution from the 20 minutes recommended in the protocol to 15 minutes to avoid collagen damage for fine grain bone powder. The collagen extraction process included a step of soaking the bone powder in 0.125 M NaOH between the demineralization and gelatinization steps to achieve the elimination of lipids and humic acids. After this process, the samples were freeze-dried.

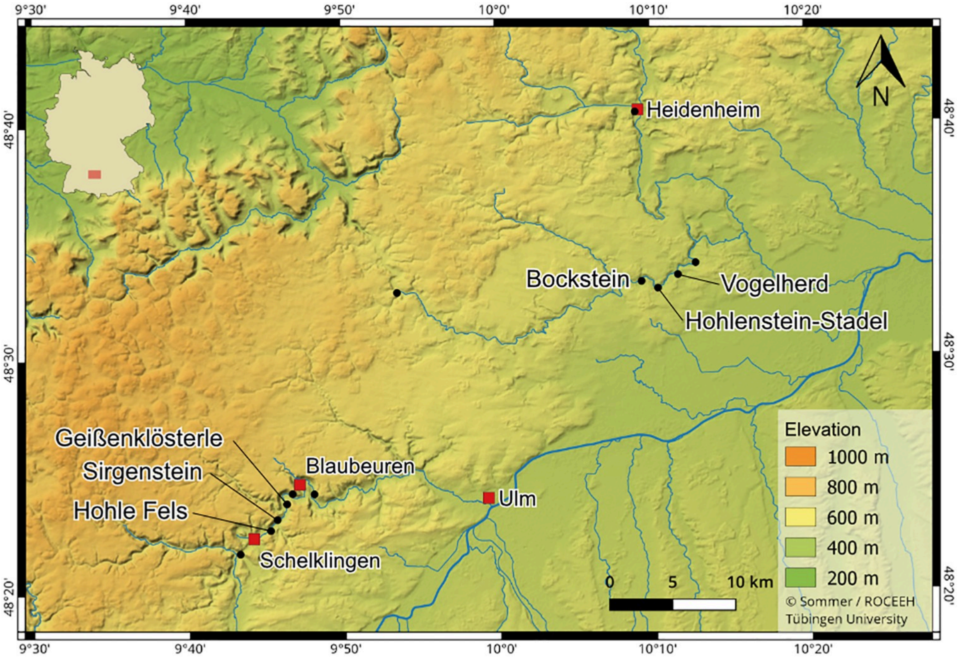

Fig 1. Map of the studied sites. Map of sites included in this study. https://doi.org/10.5281/zenodo.3460300 (CC BY 4.0 license).

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The elemental analyses (C_{coll}, N_{coll}) and isotopic measurements of collagen ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) for the VLP samples (n = 7) were performed at the Geochemical department of the University of Tübingen, using an elemental analyzer NC 2500 connected to a Thermo Quest Delta+XL mass spectrometer. While the elemental analyses and isotopic measurements for JK (n = 8), 38 PLC samples (PLC-1 –PLC-49) and 10 SJM samples (SJM-1 –SJM-10) were undertaken at the Laboratory of Chronology (Finnish Museum of Natural History), using an NC 2500 elemental analyzer coupled to a Thermo Delta V Plus isotope ratio mass spectrometer. For the 21 PLC samples (PLC-55 –PLC-85), and the 32 SJM samples (SJM-11 –SJM-63), the elemental analyses and isotopic measurements were performed in duplicate at the Institute of Environmental Science and Technology of the Universitat Autònoma de Barcelona (ICTA-UAB) using a Thermo Flash 1112 (Thermo ScientificVC) elemental analyzer coupled to a Thermo Delta V Advantage mass spectrometer with a Conflo III interface.

The samples analyzed in Tübingen and Helsinki were calibrated to $\delta^{13}C$ values of USGS-40 ($\delta^{13}C$ = -26.8‰, $\delta^{15}N$ = -4.7‰) and USGS-41 ($\delta^{13}C$ = +36.1‰, $\delta^{15}N$ = +46.7‰). Based on multiple measurements of matrix matched in-house reference materials, the reproducibility was ±0.19‰ for $\delta^{13}C$, ±0.24‰ for $\delta^{15}N$ values. The reproducibility error for the amounts of C and N was lower than 4%.

At the laboratory of Barcelona, the international laboratory standard IAEA 600 (caffeine) was used as well as two in-house reference materials (modern collagen of camel and elk). These same two in-house reference materials were also used for the isotopic analyses performed in Tübingen and Helsinki, assuring the comparability of all measured isotopic values independently of where they were performed. An analytical error below 0.2‰ (1σ) was determined for $\delta^{13}C$ and $\delta^{15}N$ in all the repeated analyses. The reproducibility error for the amounts of C and N was lower than 2%.

Following the recommendations of DeNiro [75] and Ambrose [76], we only used collagen samples with a carbon-to-nitrogen-ratio ($C{:}N_{coll}$) between 2.9 and 3.6 and a percentage of nitrogen higher than 5% for palaeoecological interpretations.

All commissioned laboratories measure the ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ relative to a standard (V-PDB for carbon and AIR for nitrogen). The isotopic ratios are expressed using the δ (delta) value as follows:

$$\delta^{13}C = \left[(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{reference} - 1\right] \text{ x } 1000\ (‰)$$

$$\delta^{15}N = \left[(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{reference} - 1\right] \text{ x } 1000\ (‰)$$

Trophic niche modeling

To reconstruct the fox trophic niches, we first applied a multivariate cluster analysis to the $\delta^{13}C$ and $\delta^{15}N$ isotopic values in JMP 14 with respect to the stratigraphic association, namely Middle Palaeolithic, Aurignacian and Gravettian. As a result, we obtained different clusters for each of the periods. We then used the R package SIBER (Stable Isotope Bayesian Ellipses in R) to calibrate the niches out of the clusters [65]. It was possible to reconstruct the complete niches (= convex hull or total area, TA, Layman [77]) that include all members of the clusters, given by the isotopic values of our samples. Furthermore, we calculated the core niches (= standard ellipse area, SEA, Jackson [65]) that explain 40% of all potential specimens that will fit into these niches, based on a most likelihood estimation in a Bayesian framework. While the complete niche is quite sensitive to the given sample size, the core niche is more reliable for analyzing small assemblages and is recommend by Jackson [65]. To examine the trophic niche overlap between foxes and large carnivores, we calculated, additionally to SEA and TA, the standard ellipse area corrected for sample size (SEAc). Based on this, the percentage of overlap in the respective core niches could be estimated. Throughout this study, we use the term "niche" for a trophic niche.

Dietary reconstruction

To build the isospace for the dietary reconstruction, we used prey groups, combined by their $\delta^{13}C$ and $\delta^{15}N$ isotopic values. Instead of using the individual species as groups, we formed the groups using a multivariable cluster analysis of their isotopic values with JMP 14. For further calculations it is necessary that the groups show a clear separation of the core niches (SEA), which we tested with the R package SIBER. To reconstruct the proportions of different prey group in the protein fraction of the carnivore diet, we used the R package MixSIAR (Bayesian Mixing Models in R, Stock and Semmens [66]). Initially, such Bayesian mixing models (e.g., MixSIAR, FRUITS, SIAR) were designed for ecologists who work with recent ecosystems and food chains but the model has been subsequently successfully applied to archaeological contexts [54, 67, 78–81].

MixSIAR allows the reconstruction of the most likely diet of the carnivores based on the nitrogen and carbon isotopes from their bone collagen relative to the isotopic values from their prey species. Essential for this calculation is the trophic enrichment factor (TEF) that quantifies the increase of $\delta^{13}C$ and $\delta^{15}N$ values in collagen from prey to predator. Indeed, the stable isotope composition of a predator differs from the composition of its prey in a predictable manner. The TEFs correspond to the difference between the stable isotope ratios of the consumer (predator collagen) and its diet (prey collagen) and are the result of the discrimination of stable isotopes due to the behavior and physiology of the consumer [54, 62, 82]. For our study, we used the same TEF values ($\Delta^{13}C$ = 1.1 ± 1.1‰; $\Delta^{15}N$ = 3.2 ± 1.8‰)[62] for all carnivores. To get a robust statistical analysis, we set the MCMC (Markov Chain Monte Carlo, see Stock and Semmens [66]) chain length to 1,000,000 with a burn-in of 500,000 in 3 chains. Verification of the model convergence was done with Gelman-Rubin and Geweke tests (for detailed explanation, see Stock and Semmens [66]). In brief, the Gelman-Rubin test shows model convergence if the values are near 1. In most analyses, values below 1.1 are acceptable [83]. Additionally, the Geweke test compares the mean of the first part of each chain with the mean of the second part, using a two-sided z-test. If both means are the same, the model is convergent [66, 84].

All niche modeling (SIBER) and diet reconstructions (MixSIAR) were done using R Version 3.6.1.

Results

Elemental and isotopic analyses

The $\%N_{bone}$ values measured on 71 carnivore samples and two hare samples confirmed the favorable conditions of preservation (0.6–3.8%), establishing quantitatively that collagen is preserved in the samples. Moreover, the atomic $C{:}N_{coll}$ ratios of all analyzed carnivores (3.2–3.5) and the small mammal samples (3.2–3.6), showed that the preservation of collagen was appropriate for the interpretation of the isotopic analysis in palaeobiological terms (Tables 1 and 2). Among the isotopic values, we found only minor difference between the average of wolves ($\delta^{13}C$ = -19.6 ± 0.6‰ and $\delta^{15}N$ = +9.1 ± 0.9‰), lynx ($\delta^{13}C$ = -19.3 ± 0.4‰ and $\delta^{15}N$ = +8.5 ± 1.2‰) and wolverines ($\delta^{13}C$ = -19.1 ± 0.0‰ and $\delta^{15}N$ = +8.5 ± 1.2‰). Compared to each other, red foxes ($\delta^{13}C$ = -20.0 ± 0.4‰ and $\delta^{15}N$ = +7.3 ± 1.9‰) and Arctic fox ($\delta^{13}C$ = -20.0 ± 0.8‰ and $\delta^{15}N$ = +7.6 ± 2.6‰) were also very similar in their average isotope values. In contrast to the other carnivores, both fox species yielded a slightly lower average $\delta^{13}C$ and $\delta^{15}N$ values and there was one outlier for each species among the Middle Palaeolithic specimens (PLC-76 and VLP-10).

The rodents average isotopic values of Arctic lemming ($\delta^{13}C$ = -21.3 ± 1.4‰ and $\delta^{15}N$ = +5.0 ± 2.6‰), Norway lemming ($\delta^{13}C$ = -22.5 ± 1.2‰ and $\delta^{15}N$ = +4.2 ± 2.4‰) and vole ($\delta^{13}C$ = -22.4 ± 0.5‰ and $\delta^{15}N$ = +5.6 ± 1.4‰) covered a wide range of the pre-LGM isospace, and were quite similar to each other. In contrast, the analyzed hare samples ($\delta^{13}C$ = -20.3 ± 0.2‰ and $\delta^{15}N$ = +3.2 ± 0.4‰) showed slightly higher $\delta^{13}C$ and lower $\delta^{15}N$ values than the lemming species and the voles.

Trophic niche modeling

To form the pre-LGM isospace, we need to define the herbivore groups that are the assumed prey of most carnivores. Because with species-related groups the overlap of TA and SEA was too high, we built isotope-related groups (Fig 2). Finally, we generated four different prey groups, named after the most abundant taxon in the group (S3 Table). The "reindeer" group has the highest $\delta^{13}C$ values (-19.3 ± 0.5‰) and the lowest $\delta^{15}N$ values (+3.8 ± 0.7‰) and includes beside reindeer (n = 15) also hare (n = 2) and one Arctic lemming. The "horse" group includes horse (n = 19), Arctic lemming (n = 8) and Norway lemming (n = 4) and exhibits $\delta^{13}C$ values of -20.8 ± 0.3‰ and $\delta^{15}N$ values of +6.4 ± 0.7‰. The "mammoth" group shows $\delta^{13}C$ values of -21.1 ± 0.3‰ and the highest $\delta^{15}N$ values (+8.74 ± 0.5‰) and contains beside mammoth (n = 12) also two horses. Finally, the "rodent" group includes Norway lemming (n = 15), vole (n = 15), horse (n = 3) and Arctic lemming (n = 2) with $\delta^{13}C$ and $\delta^{15}N$ values of -22.5 ± 1.0‰ and +4.4 ± 2.3‰, respectively.

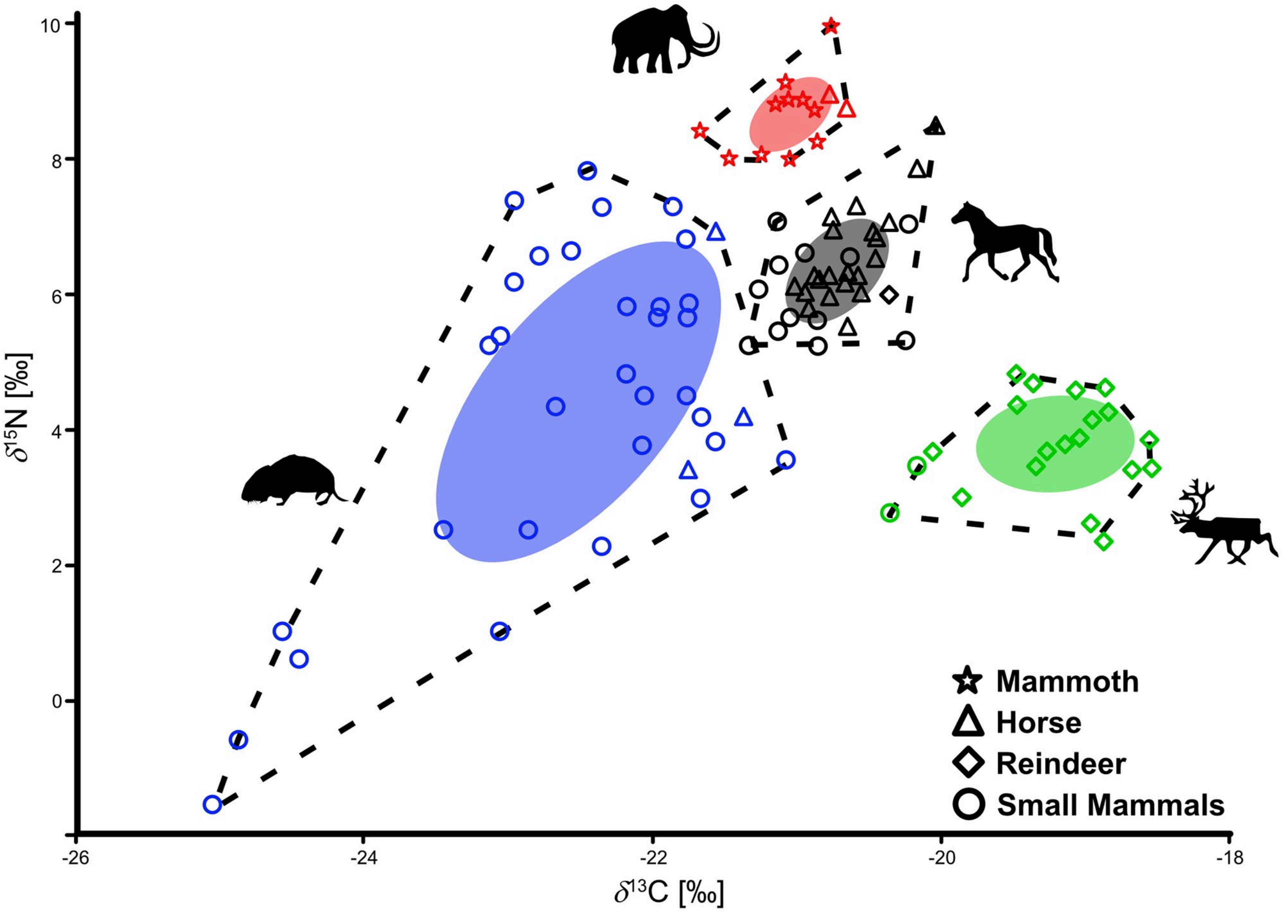

Fig 2. Dietary sources in the isospace. Dietary sources calculated with SIBER. Groups are named by the most abundant taxon. Dashed lines show the convex hull of the groups, while collard ellipses show the calculated Standard Ellipse Area (SEA).

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For the carnivores we have primarily distinguished between foxes and large carnivores. Both fox species are combined here, as they differ very little in their isotope values (see chapter "Statistical test for isotopic variance of both fox species" in S2 Text). We were able to calculate three niche types of foxes: First foxes with high δ^{15}N values (range from +7.1 to +10.0‰), then foxes with intermediate δ^{15}N values (range from +3.7 to +6.7‰), and finally foxes with low δ^{15}N values (range from +1.0 to +3.0‰). Additionally, the low δ^{15}N foxes show lower δ^{13}C values (range from -21.4 to -21.1‰) than the nearby intermediate δ^{15}N fox group (range from -20.5 to -19.4‰). Finally, we also found these niche types in the respective periods, although not all niches at once. This results in a total of six fox niches and three large carnivore groups (Figs 3–5, S3 Table). For the Middle Palaeolithic, we found a large carnivore group (δ^{13}C = -19.7 ± 0.4‰ and δ^{15}N = +8.6 ± 1.2‰), a high δ^{15}N fox niche (δ^{13}C = -20.1 ± 0.3‰ and δ^{15}N = +8.7 ± 0.8‰), and a low δ^{15}N fox niche (δ^{13}C = -21.3 ± 0.2‰ and δ^{15}N = +2.0 ± 1.4‰). The Aurignacian is represented by a large carnivore group (δ^{13}C = -19.5 ± 0.6‰ and δ^{15}N = +9.3 ± 0.9‰), a high δ^{15}N fox niche (δ^{13}C = -19.9 ± 0.6‰ and δ^{15}N = +8.6 ± 0.4‰), and an intermediate δ^{15}N fox niche (δ^{13}C = -20.0 ± 0.3‰ and δ^{15}N = +5.4 ± 0.5‰). Finally, in the Gravettian, we calculated a large carnivore group (δ^{13}C = -19.4 ± 0.7‰ and δ^{15}N = +8.8 ± 0.8‰), a high δ^{15}N fox niche (δ^{13}C = -20.3 ± 0.3‰ and δ^{15}N = +8.5 ± 1.1‰), and an intermediate δ^{15}N fox niche (δ^{13}C = -19.8 ± 0.5‰ and δ^{15}N = +5.1 ± 1.5‰) as well. In order

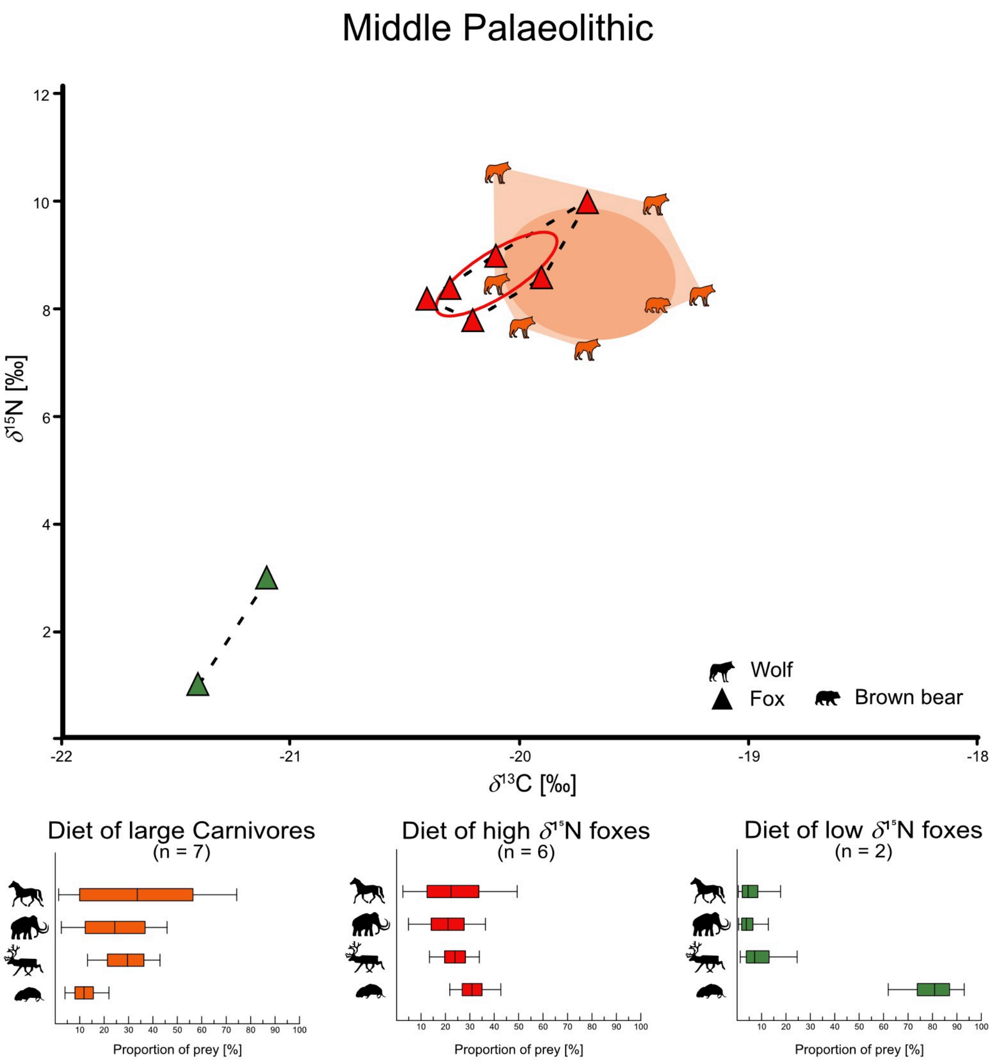

Fig 3. Trophic niches in the Middle Palaeolithic. Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Middle Palaeolithic with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (outline of the niches). The solid lines in the fox niches and the dark collard ellipses in the carnivore group show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. In the lower part of the figure is the reconstructed diet given. Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.

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to indicate trophic niche competition or approaches of commensal behavior of foxes to other carnivores, we have calculated the SEAc overlap of the large carnivore group and the high δ^{15}N foxes (Table 3, S3 Table for all calculated niche parameters). During all three periods the group of large carnivores overlaps with the high δ^{15}N fox niches to a large extent (Middle Pal. = 49.6%, Aurignacian = 39.0%, Gravettian = 41.0%).

Dietary reconstruction

The MixSIAR calculated model for dietary reconstructions showed convergence in both tests. Both diagnostics tested 127 variables of the model. In the Gelman-Rubin test, no variable was higher than 1.01. Additionally, the Geweke diagnostic revealed only three unequal variables in

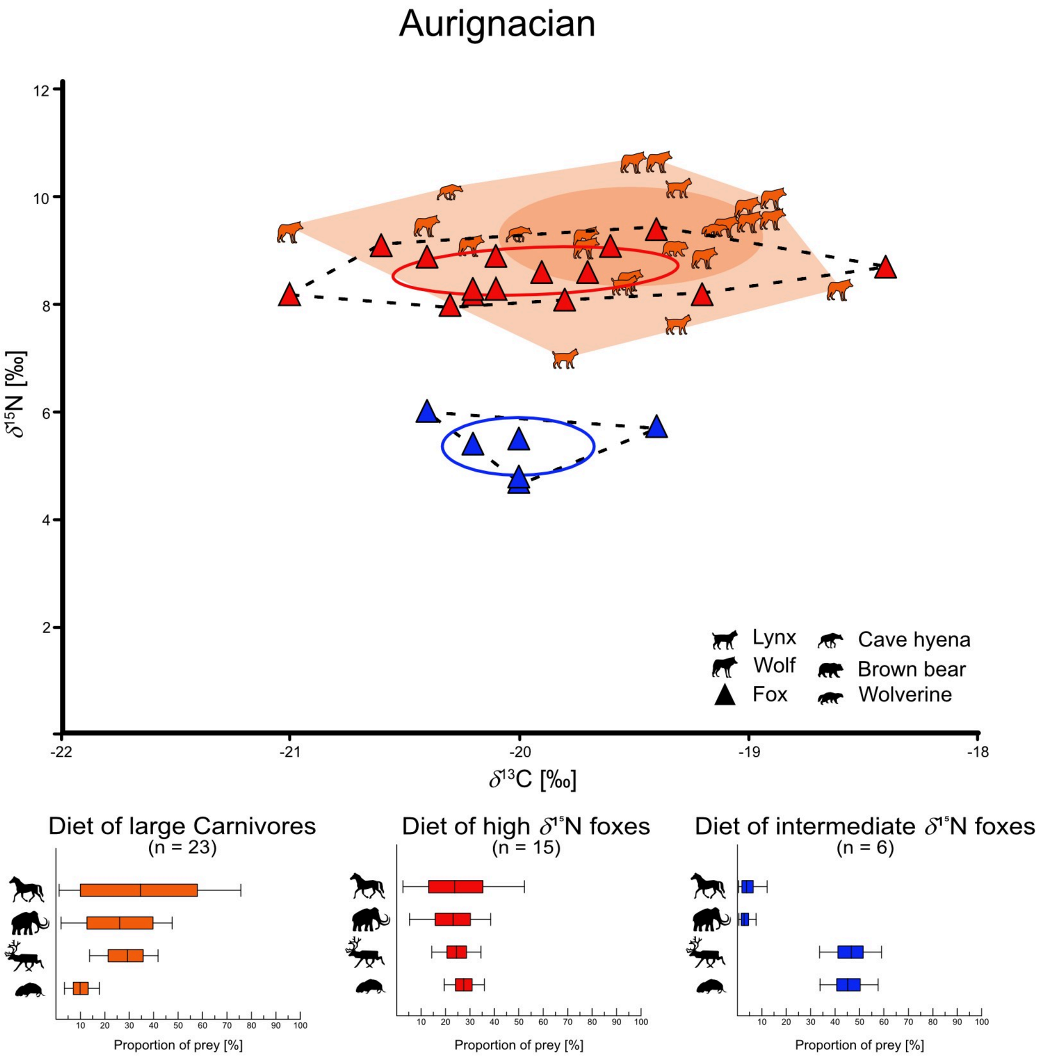

Fig 4. Trophic niches in the Aurignacian. Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Aurignacian with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (outline of the niches). The solid lines in the fox niches and the dark collard ellipses in the carnivore group show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. In the lower part of the figure is the reconstructed diet given. Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.

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chain 1, nine unequal variables in chain 2 and three unequal variables in chain 3 out of 127. Therefore, the calculated model is usable for the dietary reconstruction.

We reconstructed the percentages of the four different prey sources for each fox niche as well as for the large carnivore groups as a whole and separated per period (Table 4, Figs 3–5). The dietary preferences of individuals varied strongly between the niches. Large carnivores of all periods preferred "horse" (34.6 ± 25%), "reindeer" (29.7 ± 9.7%) and "mammoth" (24.7 ± 14.3%). High δ^{15}N foxes included all sources of analyzed prey in their diet in a similar proportion ("Rodents" = 29.2 ± 5.7%, "reindeer" = 25.1 ± 6.6%, "horse" = 24.1 ± 14.5% and "mammoth" = 21.5 ± 9.5%). However, intermediate δ^{15}N foxes were more specialized on "rodents" (46.6 ± 8.5%) and "reindeer" (45.9 ± 8.9%), while low δ^{15}N foxes fed primary on "rodents" (79.6 ± 9.8%).

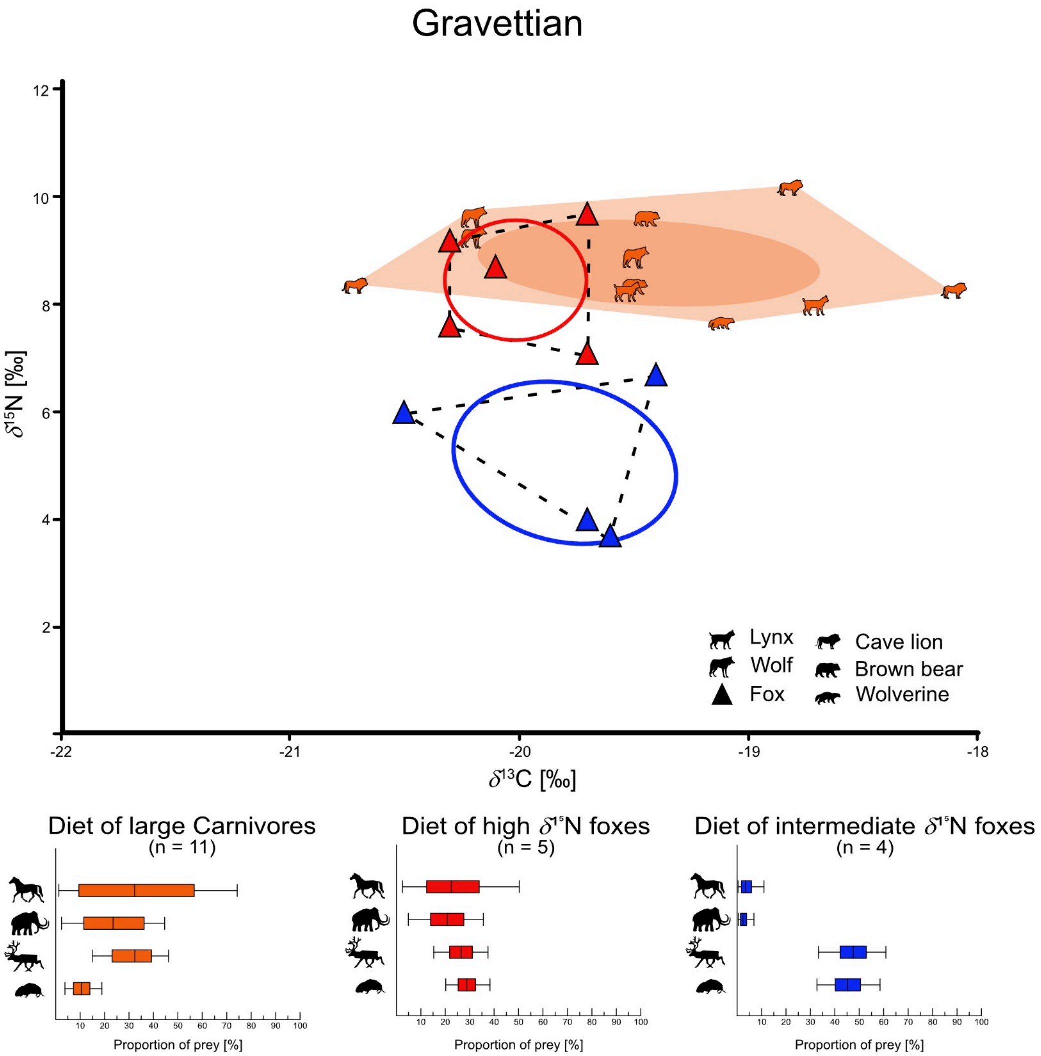

Fig 5. Trophic niches in the Aurignacian. Calculated trophic niches of foxes (Triangles) and large carnivores (shapes) from the Gravettian with SIBER. Dashed lines in the fox niches as well as light collard area in the large carnivore group show the convex hull (outline of the niches). The solid lines in the fox niches and the dark collard ellipses in the carnivore group show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. In the lower part of the figure is the reconstructed diet given. Diet proportions calculated with MixSIAR of each fox niche and the large carnivore group. Solid lines show the 5 to 95% confidence interval, full boxes show the 25 to 75% confidence interval and vertical black line shows the median value.

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Discussion

For the three periods studied (Middle Palaeolithic, Aurignacian and Gravettian), we have sampled both large predators and foxes. Considering the large overlap of the high δ^{15}N fox niches with the large carnivores in all periods together with the dietary reconstructions, we conclude that they consumed a similar diet, consisting of large mammals. However, the high δ^{15}N foxes' diet was complemented by rodents. Intermediate δ^{15}N foxes, primarily fed on reindeer and rodents, while low δ^{15}N foxes fed almost exclusively on rodents.

The Late Pleistocene pre-LGM is a long period of time and covers several tens of thousands of years, so the question naturally arises as to whether the changes in the niches may also be due to environmental factors. Studies on the trophic niches of mammoths and horses have

Table 3. Calculated niche overlap between large carnivores and high δ^{15}N foxes, based on SIBER.

	Middle Palaeolithic		
	Large Carnivores	High δ^{15}N foxes	Overlap Area
TA [‰^{2}]	2.08	0.46	
SEA [‰^{2}]	1.41	0.38	
SEAc [‰^{2}]	1.69	0.47	0.23
%overlap	13.8%	49.6%	
	Aurignacian		
	Large Carnivores	High δ^{15}N foxes	Overlap Area
TA [‰^{2}]	5.19	2.27	
SEA [‰^{2}]	1.57	0.83	
SEAc [‰^{2}]	1.65	0.89	0.35
%overlap	21.1%	39.0%	
	Gravettian		
	Large Carnivores	High δ15N foxes	Overlap Area
TA [‰^{2}]	4.20	1.26	
SEA [‰^{2}]	1.87	1.04	
SEAc [‰^{2}]	2.08	1.38	0.57
%overlap	27.2%	41.0%	

TA = Total Area (= convex hull), SEA = Standard Ellipse Area, SEAc = Standard Ellipse Area corrected to small sample size.

https://doi.org/10.1371/journal.pone.0235692.t003

shown that environmental changes in the Swabian Jura played only a minor role within the early Upper Palaeolithic isospace[68, 79]. This is shown by the newly analyzed rodent isotope data as well, which are quite similar during the Aurignacian and Gravettian (δ^{13}C: Aurignacian (n = 10) = -21.5 ± 0.7‰; Gravettian (n = 4) = -21.1 ± 0.6‰; t-test, $p = 0.35$; δ^{15}N: Aurignacian (n = 10) = +5.25 ± 1.2‰; Gravettian (n = 4) = +4.05 ± 1.4‰; t-test, $p = 0.19$). More difficult to explain is the long period of the Middle Palaeolithic, resulting in a higher variability of rodent isotopes (n = 28; δ^{13}C: -22.6 ± 1.1‰; δ^{15}N: +4.8 ± 2.6‰). However, the high δ^{15}N fox niche and the large carnivore group of the Middle Palaeolithic overlap to a high degree with the Aurignacian niches (niche overlap about 55 to 60%), suggesting similar conditions for the feeding possibilities of these predators across the Middle and Upper Palaeolithic. Therefore, in the following, we will ignore potential natural environmental conditions that could affect the isospace and focus on trophic behavioral reconstructions.

Trophic behavior of foxes

Opportunistic small predators, such as red and Arctic foxes, are very adaptable in their diet and can therefore easily change their trophic behavior [8, 9, 11, 12, 14, 43–46, 48–50, 85, 86]. The same individuals that have hunted rodents alone for years can quickly adapt to scavenging and maintain this as a new trophic behavior as long as it is effective. Different trophic behaviors can also be seen in the dietary and niche reconstructions of the analyzed foxes from the Middle Palaeolithic and early Upper Palaeolithic layers of the Swabian Jura.

The majority of the sampled foxes fall into the high δ^{15}N fox niche and show a strong overlap with the respective large carnivore groups. The high core niche (SEAc) overlap on the foxes' side (39.0–49.6%, Table 3), as well as the similarity in the calculated diet of both groups (Figs 3–5, Table 4) leads to the conclusion that the high δ^{15}N foxes were commensal to large carnivores. This behavior can also be observed in modern red and Arctic foxes [8, 9, 11–13, 43,

Table 4. Reconstructed dietary proportions for the different fox niches and large carnivore groups.

		n	**Dietary source**	**Mean ± SD**	**2.5%**	**5%**	**25%**	**50%**	**75%**	**95%**	**97.5%**
Large Carnivores		**41**	Horse	**34.6 ± 25%**	0.6%	1.4%	10.0%	**33.3%**	56.9%	74.3%	78.5%
			Mammoth	**24.7 ± 14.3%**	1.0%	2.5%	12.2%	**24.5%**	37.5%	46.3%	48.2%
			Reindeer	**29.7 ± 9.7%**	11.7%	14.2%	22.0%	**30.4%**	37.2%	44.1%	46.7%
			Rodents	**11 ± 4.8%**	2.8%	3.7%	7.6%	**10.7%**	14.1%	19.3%	21.5%
	Middle Pal.	**7**	Horse	**34.5 ± 24.8%**	0.6%	1.4%	10.0%	**33.6%**	56.4%	74.3%	78.3%
			Mammoth	**24.4 ± 14.1%**	1.1%	2.5%	12.3%	**24.4%**	36.8%	45.8%	47.9%
			Reindeer	**28.9 ± 9.4%**	11.0%	13.2%	21.4%	**29.6%**	36.3%	42.9%	45.0%
			Rodents	**12.2 ± 5.5%**	3.0%	4.0%	8.1%	**11.8%**	15.6%	22.0%	24.1%
	Aurignacian	**23**	Horse	**35.2 ± 25.5%**	0.5%	1.3%	10.0%	**34.6%**	57.9%	75.7%	80.1%
			Mammoth	**26 ± 15%**	0.9%	2.1%	12.7%	**26.1%**	39.7%	47.6%	49.5%
			Reindeer	**28.6 ± 9%**	11.1%	13.8%	21.4%	**29.3%**	35.7%	41.8%	43.6%
			Rodents	**10.2 ± 4.3%**	2.7%	3.5%	7.1%	**9.9%**	13.2%	17.8%	19.1%
	Gravettian	**11**	Horse	**34.2 ± 25.1%**	0.5%	1.3%	9.5%	**32.3%**	56.7%	74.3%	77.6%
			Mammoth	**23.6 ± 13.8%**	1.0%	2.4%	11.5%	**23.5%**	36.2%	44.6%	46.4%
			Reindeer	**31.3 ± 10.1%**	12.1%	15.0%	23.1%	**32.4%**	39.2%	46.2%	47.9%
			Rodents	**10.9 ± 4.7%**	2.8%	3.8%	7.3%	**10.5%**	14.0%	18.9%	20.5%
		n	**Prey source**	**Mean ± SD**	**2.5%**	**5%**	**25%**	**50%**	**75%**	**95%**	**97.5%**
High δ^{15}N foxes		**26**	Horse	**24.1 ± 14.5%**	1.3%	2.7%	12.7%	**23.0%**	34.2%	50.2%	55.4%
			Mammoth	**21.5 ± 9.5%**	3.1%	5.1%	14.9%	**21.6%**	28.4%	36.7%	38.7%
			Reindeer	**25.1 ± 6.6%**	12.5%	14.3%	20.7%	**24.9%**	29.5%	35.7%	37.8%
			Rodents	**29.2 ± 5.7%**	18.6%	20.6%	25.4%	**29.0%**	32.8%	39.0%	41.0%
	Middle Pal.	**6**	Horse	**23.8 ± 14.5%**	1.2%	2.6%	12.5%	**22.3%**	33.7%	49.4%	54.1%
			Mammoth	**21 ± 9.4%**	2.6%	4.9%	14.2%	**21.1%**	27.7%	36.4%	38.2%
			Reindeer	**23.9 ± 6.3%**	11.5%	13.5%	19.7%	**23.9%**	28.2%	33.9%	35.7%
			Rodents	**31.4 ± 6.4%**	20.5%	21.8%	26.9%	**30.9%**	35.0%	42.7%	46.0%
	Aurignacian	**15**	Horse	**25.1 ± 15.3%**	1.3%	2.6%	13.1%	**23.8%**	35.3%	52.3%	57.8%
			Mammoth	**22.8 ± 9.9%**	3.0%	5.3%	15.8%	**23.1%**	30.2%	38.5%	40.7%
			Reindeer	**24.5 ± 6%**	12.7%	14.4%	20.6%	**24.5%**	28.6%	34.5%	36.1%
			Rodents	**27.6 ± 5%**	18.1%	19.5%	24.1%	**27.5%**	30.9%	35.9%	37.6%
	Gravettian	**5**	Horse	**23.9 ± 14.8%**	1.2%	2.5%	12.4%	**22.5%**	33.9%	50.3%	55.3%
			Mammoth	**20.7 ± 9.3%**	2.6%	4.9%	14.0%	**20.9%**	27.6%	35.6%	37.8%
			Reindeer	**26.5 ± 6.8%**	13.2%	15.3%	21.8%	**26.5%**	31.1%	37.5%	39.7%
			Rodents	**28.9 ± 5.5%**	18.4%	20.2%	25.3%	**28.8%**	32.4%	38.3%	40.4%
		n	**Prey source**	**Mean ± SD**	**2.5%**	**5%**	**25%**	**50%**	**75%**	**95%**	**97.5%**
Intermediate $\delta 1^{5}$N foxes		**10**	Horse	**4.4 ± 3.6%**	0.2%	0.5%	1.8%	**3.5%**	6.2%	11.2%	13.4%
			Mammoth	**3.1 ± 2.2%**	0.4%	0.5%	1.5%	**2.6%**	4.1%	7.4%	8.6%
			Reindeer	**45.9 ± 8.9%**	27.9%	31.3%	40.1%	**46.1%**	51.7%	60.1%	62.7%
			Rodents	**46.6 ± 8.5%**	30.9%	33.5%	41.2%	**46.4%**	52.0%	60.5%	64.4%
	Aurignacian	**6**	Horse	**4.7 ± 3.7%**	0.2%	0.5%	1.9%	**3.8%**	6.5%	12.2%	14.1%
			Mammoth	**3.3 ± 2.3%**	0.4%	0.6%	1.6%	**2.8%**	4.6%	7.7%	9.0%
			Reindeer	**46.5 ± 7.8%**	31.2%	33.7%	41.2%	**46.6%**	51.5%	59.0%	61.9%
			Rodents	**45.5 ± 7.3%**	31.3%	33.9%	40.7%	**45.2%**	50.3%	57.6%	60.1%
	Gravettian	**4**	Horse	**4.3 ± 3.4%**	0.2%	0.4%	1.8%	**3.5%**	5.9%	11.0%	13.1%
			Mammoth	**2.9 ± 2.1%**	0.3%	0.5%	1.4%	**2.4%**	3.9%	6.9%	8.1%
			Reindeer	**47.5 ± 8.4%**	30.6%	33.3%	42.2%	**47.6%**	52.9%	60.9%	63.4%
			Rodents	**45.3 ± 7.9%**	30.0%	32.7%	40.2%	**45.2%**	50.5%	58.5%	60.9%
		n	**Prey source**	**Mean ± SD**	**2.5%**	**5%**	**25%**	**50%**	**75%**	**95%**	**97.5%**

(*Continued*)

Table 4. (Continued)

Low δ^{15}N foxes		**2**	Horse	**6.2 ± 5.8%**	0.3%	0.5%	2.1%	**4.5%**	8.5%	17.8%	21.3%
			Mammoth	**4.8 ± 4.1%**	0.4%	0.6%	1.9%	**3.8%**	6.5%	12.8%	15.4%
			Reindeer	**9.4 ± 7.5%**	0.9%	1.3%	3.8%	**7.2%**	13.1%	24.6%	28.5%
			Rodents	**79.6 ± 9.8%**	57.7%	61.9%	73.8%	**80.8%**	87.0%	93.0%	94.2%
	Middle Pal.	**2**	Horse	**6.2 ± 5.8%**	0.3%	0.5%	2.1%	**4.5%**	8.5%	17.8%	21.3%
			Mammoth	**4.8 ± 4.1%**	0.4%	0.6%	1.9%	**3.8%**	6.5%	12.8%	15.4%
			Reindeer	**9.4 ± 7.5%**	0.9%	1.3%	3.8%	**7.2%**	13.1%	24.6%	28.5%
			Rodents	**79.6 ± 9.8%**	57.7%	61.9%	73.8%	**80.8%**	87.0%	93.0%	94.2%

https://doi.org/10.1371/journal.pone.0235692.t004

44, 46–50, 86, 87] and is also suggested by morphological studies in Late Pleistocene red and Arctic foxes from Belgium [15, 16]. The dimensions of the lower carnassial indicated a higher carnivorous specialization in comparison with modern specimens, especially in Late Pleistocene Arctic foxes, whereas it was not so pronounced in Late Pleistocene red foxes [15]. However, the isotope values of our studied red and Arctic foxes did not show any significant difference (S1 Text), which is why we could not conclude that the two species had different diets.

With a predicted average diet of 79.6 ± 9.8% on rodents, the two foxes from the low δ^{15}N fox niche are most likely to be what we would expect from foxes: rodent hunters. Indeed, rodents are also the main component of the diet of most modern foxes. This is especially true for red foxes [8, 9, 11–13, 44, 48–50, 86], but also for Arctic foxes [43, 47, 85]. Interestingly, only two of 38 sampled foxes were found with a rodent-dominated diet.

The intermediate δ^{15}N foxes have an increased proportion of reindeer and rodents in their calculated diet (Figs 4 and 5, Table 4). A commensalism to (already sampled) large predators can be excluded, since none of the individuals has similar isotopic values, which should be the case with similar nutrition and thus commensalism [67]. However, as foxes are not able to hunt reindeer, they must have had the opportunity to feed regularly and over several years on reindeer carcasses to get the δ^{15}N values that we observed in these foxes [53, 61, 62]. Since none of the other studied predators had developed a similar feeding strategy, it appears to be an exclusive trophic niche for these foxes.

In order to explain the trophic behavior of the intermediate δ^{15}N foxes, we now look at the archaeological context of the sites. This group of foxes occurs exclusively in the early Upper Palaeolithic of the Swabian Jura, the Aurignacian and Gravettian periods. The zooarchaeological record indicates that reindeer and horse were among the most important game species for Middle and early Upper Palaeolithic hunter-gatherers [20, 24, 34, 38, 40–42, 70]. In addition, during the Aurignacian and Gravettian, a large number of mammoth remains were found, which were further processed [34, 42, 88]. Mammoths were not brought to the cave as a whole, but were butchered at the kill sites, while reindeer were brought to the site in their entirety and butchered there [42]. This behavior of Palaeolithic humans opened up two different feeding opportunities for foxes and other predators. On the one hand they had the possibility to scavenge from a high δ^{15}N protein resource at the human (mammoth) kill sites, on the other hand they could scavenge from reindeer carcasses near the camp sites, i.e., the cave sites (for a more detailed explanation of the archaeological interpretation, see S3 Text: Archaeological interpretation). The dietary reconstructions of the Aurignacian fox niches show that these resources were effectively used, each from one niche. Moreover, cut marks on, for instance, two mandibles from Vogelherd Cave [70] show that foxes were exploited for meat and fur, both mandibles were sampled in this study as well and fall into the high δ^{15}N fox niche (PLC-16) and the intermediate δ^{15}N fox niche (PLC-13), respectively. This demonstrates that there was a direct interaction of humans with foxes from both niches.

Seasonality, targeted fox hunting and natural death in caves

There are different approaches to explain how and when foxes came into the sites. Three of them we would like to discuss in more detail in this section and compare them with our obtained results.

The first hypothesis is that Neanderthals and anatomically modern humans occupied the caves only during certain times or seasons [20, 34, 38, 70, 89]. Due to this discontinuous occupation behavior, many caves were alternately inhabited by humans and cave bears [35–37]. The foxes could therefore only have been hunted irregularly by humans. However, indicators of seasonal occupation can be strongly influenced by taphonomic processes [90]. This is especially true when the time depth is several thousand years. For the Middle Palaeolithic as well as for the early Upper Palaeolithic there are only very few clear indications of seasonal occupation and, more importantly, there is no evidence that completely excludes a longer occupation (see more details in chapter "Archaeological interpretation" in S3 Text). Better indicators of human occupation are the thickness of the archaeological horizons and the lithic artefact density, as described by Conard [23], for example. Both factors pointed to a stronger occupation during the early Upper Palaeolithic, and only a weak occupation during the Middle Palaeolithic.

When considering the results from the present study in this context, we have to keep in mind that seasonal or one-time events cannot be documented with isotope analysis from bone collagen [53, 61, 62]. The carbon and nitrogen isotopic values rather integrate a larger time period over several years and show the average nutrition of the last years of the specimen's life. Conversely, this also means that these specimens must have had access to the calculated diet for several years before they died. This is possible for members of high and low δ^{15}N fox niches, which reflect natural trophic behavior. However, the intermediate δ^{15}N foxes from the early Upper Palaeolithic do not show any known trophic behavior, as they had a very restricted diet based on reindeer and rodents. If humans were responsible for this restriction in the prey spectrum, it would mean that they must have done so for several years and not just seasonally.

Next hypothesis, we would like to discuss, is the targeted hunting of foxes. The number of fox remains in the Aurignacian increases abruptly and continues to rise in the Gravettian [17, 20]. For the first time, perforated fox teeth appear in the Aurignacian, and Münzel [38] described fox teeth as the second most important raw material for ornaments after ivory. The importance of the fox seems to have grown in the early Upper Palaeolithic, but does this also mean that foxes were targeted hunted? Baumann [17] discussed several possibilities of Palaeolithic fox hunting and concluded that they must have been hunted with baited traps. This hunting method is not likely to select foxes for certain trophic niches, furthermore, it is more likely that this method will also catch foxes with low δ^{15}N values. However, if the traps were set up only near the occupied caves or at human kill sites, this could explain the selection for certain fox niches. Setting traps in the vicinity also has the advantage that they can be controlled more quickly and more regularly, which increases the success rate of fox hunting and reduces the risk of the trapped fox being consumed by another predator before the hunter collected its catch.

Finally, we would like to examine the hypothesis of a natural death of foxes in the caves. As already mentioned, the archaeological periods each contains several thousand years. During this time, the cave sites were not permanently occupied, although probably for longer than just a few seasons. Nevertheless, there is always the chance that foxes died in the caves without human intervention. Especially for foxes from the two "natural" trophic niches in the Middle Palaeolithic we consider this scenario. In the early Upper Palaeolithic, the low δ^{15}N fox niche is missing and therefore we have an intermediate δ^{15}N fox niche each in Aurignacian and Gravettian, which cannot be naturally evolved. Although, we have direct evidence for fox exploitation in both niches, it can never be excluded that foxes also died naturally in the caves.

As we have shown, none of the presented hypotheses alone can sufficiently explain the observed trophic fox niches. Although each hypothesis can address certain aspects, it is not possible to include all observed results. Therefore, we now turn to the question whether foxes could indicate human population density in the past.

Could foxes indicate human population density in the past?

While the two trophic behaviors of the low and high δ^{15}N foxes represented natural feeding strategies not associated with humans, we hypothesize that the intermediate δ^{15}N foxes had adapted to humans. As the main diet of foxes in both niches was rodents and reindeer, each almost 50%, a commensalism to large predators can be excluded, since none of the individuals show similar isotopic values.

However, there are three arguments that suggest a possible commensalism to humans.

1. Reindeer was also one of the main prey of humans during the early Upper Palaeolithic of the Swabian Jura [20, 24, 34, 38, 41, 42, 70, 91]. Niven [42] explained that the Aurignacian hunters of Vogelherd Cave carried reindeer in their entirety to the site and exploited them there. This process certainly caused some food waste dominated by reindeer remains that would not be present without the influence of humans and could have benefited the foxes living there.
2. The absence of large predators with similar isotopic values indicates that the resources that intermediate δ^{15}N foxes consumed, was probably not accessible for large predators, although people hunted large predators, such as cave lions or wolves. It is likely that Palaeolithic humans tolerated foxes because they were harmless and thus the dietary resource was more continuously available to them over a significant period of time, resulting in their isotope values in bone collagen.
3. The exclusive occurrence of these foxes' trophic behavior in the early Upper Palaeolithic. Despite the high number of fox bones sampled, no intermediate δ^{15}N foxes were found in the Middle Palaeolithic. We assume that the intermediate δ^{15}N fox niche may be related to the population density of humans living in the region and their influence on the Pleistocene ecosystem (see more details in chapter "Archaeological interpretation" in S3 Text). The higher population density of humans probably also led to more frequent visits to the caves, and the food supply from food waste resulting from the butchering of reindeer was more constant over longer times. These circumstances provided for the first time a trophic niche for foxes that lived commensal to humans. Such synanthropic behavior has already been demonstrated in the Swiss Magdalenian site Kesslerloch [67] and is not unusual even in modern foxes [13, 14, 45, 92].

The hypothesis that certain trophic behavior of foxes can only be explained by the regular presence of humans could be applied to other Upper Palaeolithic sites as well (see Table 5 and S4 Text for more detailed information) and graphically implemented in Fig 6.

Table 5. Commensal foxes in other archaeological sites.

Site or region	Time range	Associated period	With human associated prey near camp sites	Foxes commensal to	References
Swabian Jura (Germany)	100 to 42 kyr cal BP	MP	Reindeer and horse	Large carnivores	This study
Swabian Jura (Germany)	42 to 34 kyr cal BP	Aurignacian	Reindeer and horse	Large carnivores and humans	This study
Swabian Jura (Germany)	34 to 30 kyr cal BP	Gravettian	Reindeer and horse	Large carnivores and humans	This study
Předmostí I (Czech Rep.)	32 to 28.6 kyr cal BP	Gravettian	Reindeer	Large carnivores	Bocherens [54]
Buran-Kaya-III (Crimea)	37 to 33 kyr cal BP	early UP	Saiga antelopes	Humans	Péan [93]
Swabian Jura (Germany)	16.7 to 14 kyr cal BP	Magdalenian	Reindeer and horse	Large carnivores	Baumann [67]
Kesslerloch (Switzerland)	16.7 to 14 kyr cal BP	Magdalenian	Reindeer and horse	Humans	Baumann [67]

MP = Middle Palaeolithic, UP = Upper Palaeolithic. More detailed information in S4 Text.

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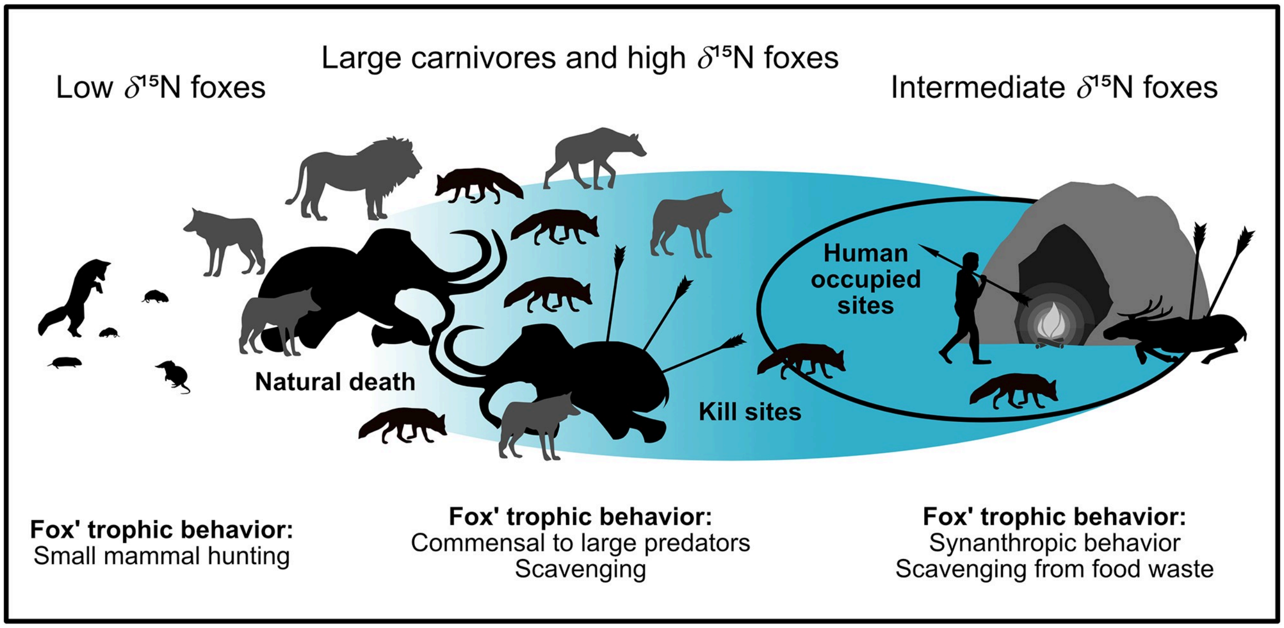

Fig 6. Summary figure for the commensal fox hypothesis. The blue area marks the impact of humans on dietary resources. For low δ^{15}N foxes, humans had no influence, while for intermediate δ^{15}N foxes they had a very strong influence (restricted diet). High δ^{15}N foxes may be influenced (e.g. by scavenging at kill sites) or may be of natural origin (e.g. by scavenging from megafauna that died naturally).

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Conclusion

In this study we have shown how the trophic behavior of Pleistocene foxes changed from the Middle Palaeolithic to the early Upper Palaeolithic in the Swabian Jura. The majority of the sampled foxes exhibited high δ^{15}N values, indicating commensal behavior to large carnivores, and were present in all periods studied. More interesting, however, has been the group of intermediate δ^{15}N foxes, which had consumed a highly restricted diet on reindeer for several years before their death and only appeared in the early Upper Palaeolithic. These specimens may have fed on human food remains. The third group of foxes has low δ^{15}N values and fed almost exclusively on rodents. However, this trophic niche could only be found in the Middle Palaeolithic of the Swabian Jura, which was sparsely populated by Neanderthals.

This leads us to our second goal in this study. We wanted to test to what extent foxes can be used as indicators of human population density and the resulting influence on the Pleistocene ecosystem. With this study we were able to show that the influence of humans on the trophic behavior of small opportunistic predators, such as foxes, is quite recognizable in the Pleistocene. The commensal behavior of foxes to large carnivores, as well as the independent hunting of rodents, are natural trophic behaviors and also recognizable in modern foxes [8, 9, 11, 12, 14, 43–46, 48–50, 85, 86]. The two niches in the Aurignacian and Gravettian, respectively, which show a strongly restricted diet on reindeer and rodents, did not natural occurred and can be attributed to human influence, since reindeer was also a main prey of Paleolithic hunters and was often found in the zooarchaeological record [20, 24, 34, 38, 41, 42, 70, 91]. Even if our data only refer to a small region (Swabian Jura: Ach and Lone Valleys), we assume that our hypothesis can also be applied to other regions. Our results and conclusions agree with the human impacts on the Pleistocene ecosystem already determined by studies on mammoths (see also chapter "Possible impact of prehistoric people on Pleistocene ecosystems" in S5 Text).

For a better understanding of trophic niches and the interaction of foxes and humans during the Palaeolithic, besides further isotope analyses of such strongly human-influenced sites, it is also important to integrate sites that are not directly connected to humans or have only very low/irregular human occupation. This will help to gain a better understanding of the foxes' natural trophic niches and thus to better evaluate human influence. In the Swabian Jura, for example, these would be the two cave sites Fetzershaldenhöhle (Lone Valley; [94]) and Kogelstein (Ach Valley, [95]), which are distinguished as hyena dens, as well as Bärenhöhle (near Sonnenbühl-Erpfingen; [96]) and Schafstall (near Veringenstadt; [97–99]).

We expect that further methods, such as isotopic studies on individual amino acids, will lead to a more detailed dietary reconstruction and, based on this, to a differentiated consideration of trophic niches. This will then also lead to better interpretations of the human influence on Pleistocene foxes' niches. Further studies on strontium may also be useful, as this could provide information on the geographical position and movement patterns of foxes. Last but not least, with this study we have provided an impulse to pay a little more attention to small opportunistic predators as they may be the key to understanding human-made changes in Europe's Pleistocene ecosystems.

Supporting information

S1 Text. Statistical test for isotopic variance of both fox species
(PDF)

S2 Text. Intra-individual variability
(PDF)

S3 Text. Archaeological interpretation
(PDF)

S4 Text. Applying the hypothesis to other archaeological sites
(PDF)

S5 Text. Possible impact of prehistoric people on Pleistocene ecosystems
(PDF)

S1 Fig. Calculated trophic niches of foxes from the Middle Palaeolithic. Dashed lines show the convex hull (outline of the niches), while the collard ellipses show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. BS = Bockstein, HF = Hohle Fels, HS = Hohlenstein-Stadel.
(TIFF)

S2 Fig. Calculated trophic niches of foxes from the Aurignacian. Dashed lines show the convex hull (outline of the niches), while the collard ellipses show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. Red area = high δ15N foxes, blue area = intermediate δ15N foxes, BS = Bockstein, GK = Geißenklösterle, HF = Hohle Fels, HS = Hohlenstein-Stadel, Si = Sirgenstein, VH = Vogelherd.
(TIFF)

S3 Fig. Calculated trophic niches of foxes from the Gravettian. Dashed lines show the convex hull (outline of the niches), while the collard ellipses show the calculated Standard Ellipse Area (SEA) and reflect the core niches, based on Bayesian statistics. Red area = high δ15N foxes, blue area = intermediate δ15N foxes, BS = Bockstein, GK = Geißenklösterle, Si = Sirgenstein.
(TIFF)

S4 Fig. Intra-individual variation in the Aurignacian samples. Black symbols show the potential affected samples from Vogelherd (VH), grey symbols show the potential affected samples from Hohlenstein-Stadel (HS) and white symbols show the potential affected samples from Sirgenstein (Si). Solid lines indicated most likely samples originated from one individual, according to the isotopic values and the limits. Dotted lines indicates a more unlikely origin from one specimen.
(TIFF)

S5 Fig. Intra-individual variation in the Aurignacian samples. Black symbols show the potential affected samples from Geißenklösterle (GK) and white symbols show the potential affected samples from Sirgenstein (Si). Solid lines indicated most likely samples originated from one individual, according to the isotopic values and the limits. Dotted lines indicates a more unlikely origin from one specimen.
(TIFF)

S1 Table. Additional isotopic data. Isotopic values from carnivores and herbivores from Swabian Jura sites, taken from literature.
(XLSX)

S2 Table. Prey groups List of the included prey taxa, sorted into prey groups.
(XLSX)

S3 Table. Fox niches List of the included carnivore taxa, sorted into fox niches and large carnivore groups.
(XLSX)

S4 Table. Niche parameters. Niche parameters of all niches (n>3) calculated with SIBER. TA = Total Area (= convex hull), SEA = Standard Ellipse Area, SEAc = Standard Ellipse Area corrected to small sample size.
(XLSX)

S5 Table. List of probably affected samples. AH = archaeological horizon, MNI = Minimum Number of Individuals. Bold names show the samples that are most likely to come from an individual, based on the isotope values that are below the limit.
(XLSX)

S6 Table. Isotopic differences. Differences in the isotopic values of the archaeological, zooarchaeological and genetic ambiguous samples. Values below the limits are marked in red,

values above 1 show a clear difference and are marked in blue. Values between both limits are marked yellow.
(XLSX)

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S1 Text:

Intra-individual variability

In order to investigate intra-individual variability, we examine each site separately. First we consider the archaeological assignment and then the morphological and palaeogenetical assignments to exclude multiple sampling of one individual. For the remaining ambiguous samples an intra-individual variation is only assumed for carbon isotopic values in a range of 0.6‰ and nitrogen isotopic values in a range of 0.7‰, according to DeNiro and Schoeniger (1). The results are additionally summarized in Tables S5. Table S6 shows the differences in carbon and nitrogen values of unsafe individuals. Values below the limits given by DeNiro and Schoeniger (1) are marked in red and indicate the same individual. Values above 1 show a clear difference and are marked in blue. It is very likely that there are two individuals, even if the second value is below the limit. Values between both limits are marked yellow.

Bockstein is a cave site complex from which we analyzed specimens from Bocksteinschmiede (BS; n = 5), Westloch (n = 1) and Bockstein-Törle (BT; n = 3). All samples came from different archaeological layers, except PLC-80 and PLC-84, which both came from BS III, but from different geological layers (GH 21 and GH 22, respectively). Due to the spatial and temporal distribution of the specimens, we do not assume multiple sampling of single individuals, and consequently strict inter-individual variability in the analyzed Bockstein samples.

In **Geißenklösterle**, two sets of samples each come from the same archaeological layer. There are two left fox tibiae from AH I (VLP-4 and VLP-5), which certainly belong to two different individuals. Furthermore, two lynx bones, one rib (PLC-18) and one mandible (PLC-19) from AH Ir were sampled, which could come from one individual. The range of isotope values suggests that both samples could belong to the same specimen.

In **Hohle Fels**, two sets of two wolf samples each originated from the same archaeological layers: JK 2180 (humerus) and JK2184 (metacarpal IV) came from AH IV and a genetic analysis (mtDNA), as well as direct dating could only be done with JK 2180 (publication in preparation; personal communication with Saskia Pfrengle), therefore, we cannot exclude that both samples could come from the same individual. However, the differences between the isotopic values make belonging to one individual quite unlikely (see Table S5). The two Gravettian samples JK 2174 (scapula) and JK 2183 (calcaneus) were taken from the related AH IIc and IIcf, but were both directly dated. The dates do not overlap, but are actually about 360 years apart (publication in preparation), indicating no intra-individual variability

Hohlenstein is another cave site complex, although we have only analyzed samples from Hohlenstein-Stadel. Most of the samples were found separately in space (find square) and time (Hieb), however, four samples show the same locality and time sequence. These are the two right wolf mandibles PLC-24 and PLC-25, and the red fox samples PLC-26 (mandible) and PLC-27 (humerus) from find square 19 and Hieb 2. While the wolf samples originate certainly from two different individuals, the fox samples may originate from the same specimen. An analysis of the mtDNA of both samples showed a strong relationship and does not exclude the possibility that it is one individual (personal communication with Yumeko Tarusawa). Since the stable isotope data are very comparable, we also assume that this could be corresponding to intra-individual variability.

The spatial position of the samples from **Sirgenstein** is unfortunately impossible to evaluate, since the cave was completely excavated by R.R. Schmidt in 1906 during a one-year excavation campaign and no find squares were recorded [2]. Consequently, it is also very difficult to exclude that only different individuals have been sampled. In our study, this applies to red foxes, as we can only assume that we deal with at least four different individuals out of nine samples. PLC-66 to PLC-69 from the Aurignacian layer AH IV include a right and a left mandible, a left humerus and a left tibia. A study on mtDNA of PLC-67 and PLC-68 showed that these two samples (left mandible and humerus) are two individuals, the other two samples could not be analyzed genetically (personal communication with Yumeko Tarusawa). If we apply the genetic conclusion to the isospace, it is most likely that only PLC-66 and PLC-67 belong to the same individual. From the analyzed samples from layer AH I we can only assume that the two right mandibles PLC-43 and PLC-72 belong to two different individuals, and the two right humeri PLC-71 and PLC-73 are not the same individual. If we consider their position in the isospace, then PLC-43 and PLC-73 are very close to each other, which could indicate that they belong to the same individual. For the last three samples, PLC-71, PLC-72 and PLC-75, it is very unlikely that they originate from the same specimen due to the isotopic values.

Vogelherd Cave was excavated in a single action as well, namely in spring 1931 by G. Riek [3, 4]. Again, spatial localization of the samples is impossible, having sampled several bones of single individuals cannot be excluded. With the wolves, this refers mainly to four samples from AH IV: one radius (PLC-2), one tibia (PLC-45), one left and one right ulna (PLC-46 and PLC-47 respectively). Since no genetic studies or direct dating of these bones have been performed, it cannot be excluded that this is one single individual. However, the ranges of their isotopic values suggest an origination from two individuals (Table S5 and S6). The two Middle Paleolithic wolf samples from AH VIII, an astragalus (PLC-48) and a tibia (PLC-49) might belong to the same individual, but show large differences in their isotopic values. Therefore, it is more likely that they belong to separate individuals. Similarly, the two sampled Arctic foxes from AH IV, PLC-1 (tibia) and PLC-16 (mandible) are most likely single specimens, due to their isotopic values. Among the six red fox samples from AH IV, we can only be certain of four individuals, which were partially genetically determined. The mtDNA study suggests that PLC-9 (femur), PLC-11 (radius), and PLC-14 (right mandible) are not related and do not represent one individual. Furthermore, the three right mandibles (PLC-13 to PLC-15) are not from the same fox. Same applies to the two right tibiae, PLC-9 and PLC-10. Considering their position in the isospace, we could identify at least four individual red foxes: PLC-11 and PLC-15 could originate from one individual, PLC-9 and PLC-13 from a second and PLC-14 and PLC-10 represents the third and fourth individual.

In summary, we cannot exclude an impact of unrecognized same individual sampling among some analyzed bones on the inter-individual variability in our samples (S4 and S5 Figs). This concerns especially wolf and fox samples from the old excavations in Sirgenstein and Vogelherd. Although the samples from Aurignacian are the most affected (two cases in wolves and four cases in foxes), there is no mixing of the samples beyond the trophic niches (S4 Fig). This means that the calculations of trophic niches, as we identified in our study, are still correct.

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S2 Text:

Statistical test for isotopic variance of both fox species

To determine the extent to which the trophic niches of the two fox species overlap, it would be possible to use SIBER, similar to the trophic overlap of the large carnivores and high δ^{15}N foxes. However, we have been able to sample far fewer Arctic foxes (n = 11) than red foxes (n = 28). Divided over the three periods studied, the numerical differences are even greater (see Table 1). Therefore, we applied a Welch ANOVA test on δ^{13}C and δ^{15}N separated by the three periods by using JMP 14.2.0. This type of ANOVA tests for equality of mean values as well, but does not require the same sample size. The statistical test shows significant differences if the *p*-values is below 0.05.

Since we only have one Arctic fox in the Middle Palaeolithic, a statistical statement was not possible. However, this Arctic fox falls into the same niche as a red fox (low δ^{15}N foxes). In the Aurignacian, statistical analysis showed no differences between the δ^{13}C (F = 0.75, *p* = 0.40) and δ^{15}N values (F = 3.36, *p* = 0.09) of red and Arctic fox. Similarly, in the Gravettian, no difference was found between the δ^{13}C (F = 3.89, *p* = 0.10) and δ^{15}N values (F = 2.17, *p* = 0.19) of both species.

S3 Text:

Archaeological interpretation

Foxes from three sites were sampled for the Middle Palaeolithic: Bockstein and Hohlenstein-Stadel in the Lone Valley, and Hohle Fels in the Ach Valley (S1 Figure, Tab. 1). Conard (1) showed that the Swabian Jura was sparsely populated by Neanderthals in the Middle Palaeolithic, as suggested by the low density of lithic artefacts and burnt bones. Bones found from fetal horses and very young mammoths indicate that the caves were occupied primarily in winter and spring [2]. The main prey of the Neanderthals was a little different between both valleys. While in the Lone Valley horse was a common game species [3-5], in the Ach Valley mainly reindeer was hunted [2, 6, 7].

We will now compare these insights with the isotope data obtained from the foxes. During the Middle Palaeolithic of the Swabian Jura we found two different trophic niches of foxes. All of the high δ^{15}N foxes come from the Lone Valley. However, the two low δ^{15}N foxes come from both valleys. Since the population density of the Neanderthals in this region was low and the caves were only visited at certain times of the year, it is unlikely that the foxes were hunted by the Neanderthals. In addition, there is only one fox bone (phalanx from Bockstein, Krönneck (4)) with cut marks indicating that a fox was exploited by Neanderthals. In general, the use of small game such as hares, fish and birds was very limited during this period in both valleys [6]. Both trophic niches of the investigated foxes (high δ^{15}N foxes = commensal to large predators; low δ^{15}N foxes = rodent hunters) belong to the usual dietary spectrum of these small opportunistic predators.

For the Aurignacian, we have sampled foxes from three Lone Valley sites (Bockstein, Hohlestein-Stadel, Vogelherd) and three Ach Valley sites (Geißenklösterle, Hohle Fels, Sirgenstein; Fig. S2, Tab. 1). Compared to the Middle Palaeolithic, the human population density in the Aurignacian was about 10 to 15 times higher, as determined by Conard (1) based on artefact densities. The zooarchaeological record indicates that, as in the Middle Palaeolithic, reindeer and horse were among the most important game species of the Palaeolithic hunters [2-4, 6-10]. In addition, there are also a large number of mammoth remains found. In both valleys, these remains were bones (e.g., ribs) and ivory, which were further processed [2, 9, 11]. In contrast to the small herbivores, mammoths were not brought to the cave as a whole, but were butchered at the kill sites. Smaller herbivores, such as reindeer, were brought to the site in their entirety and butchered there [9]. There has been so far little research on seasonality in the Aurignacian, as well as in the Middle Palaeolithic. Difficulties in the interpretation of the seasonality are mainly due to the taphonomic processes in the layers, which additionally reduce the use of the few seasonality indicators [12]. Nevertheless, there are some studies for the Aurignacian. For the Ach Valley, this information is based on the evaluation of Geißenklösterle and Hohle Fels. On one hand the studies show a clear human occupation of the caves in winter and spring, based on cut marks on cave bear bones, the presence of fetal horse bones, and thick layers of burnt bones [2, 7]. On the other hand, a year-round occupation of the region could not be excluded, because of the increased evidence of the use of fish and birds, which were probably caught from spring to autumn (personal communication from Susanne Münzel; [6]). In the Lone Valley, Vogelherd and Hohlenstein-Stadel were the best investigated sites. For Vogelherd, Niven (8) assumed that the cave was occupied from late summer to late autumn due to reindeer migration, while for neighboring Hohlenstein-Stadel, Gamble (13) assumed that the cave was occupied in winter, spring and autumn. In contrast to the Middle Palaeolithic occupation of the Swabian Jura, it seems that during the Aurignacian, humans with a higher population density were present for longer times of the year.

In this context, we will now evaluate the trophic data obtained from the analyzed foxes. We have identified two trophic niches for the Aurignacian of the Swabian Jura. The high δ^{15}N foxes are the numerically strongest niche in the Aurignacian, as well as the intermediate δ^{15}N fox niche. Sites of both valleys are present in both niches, so that there is no regional division. From the zooarchaeological record we know that fox remains were significantly more abundant in the Aurignacian than in the preceding Middle Palaeolithic [6, 14] and perforated canines were used as pendants [3, 7, 15-22]. The use of foxes was obviously more important for people in the Aurignacian than in the Middle Palaeolithic. Furthermore, the cut marks found on mandibles [8] and long bones [6, 7, 18] show that foxes were butchered both for their fur and their meat. Both mandibles from the Aurignacian layer AH IV of Vogelherd [8] were sampled for this study (Arctic fox, Lab ID: PLC-16 and red fox, Lab ID: PLC-13). However, the niche and dietary reconstructions indicate that both specimens had different feeding strategies: one specimen (PLC-16) falls into the niches of high δ^{15}N foxes, while the other specimen (PLC-13) falls into the niche of intermediate δ^{15}N foxes. With this we have a clear proof that foxes from both trophic niches were exploited by humans. If we now compare the prey spectrum of humans, based on faunal evidence, and the average diet of the last years of life of foxes in the two niches, based on their stable carbon and nitrogen isotopes, we find some interesting overlap. With reference to the studies of Niven (9), we can try to locate the Aurignacian trophic niches in the environment. The high δ^{15}N foxes, as well as the large predators, show a high proportion of mammoth and other herbivores in their calculated diet (Fig. 4, Tab. 4). Mammoths could have died naturally in certain places [23, 24], or could have been hunted by humans [11, 25-27]. In both cases, scavenging carnivores would have easy access to their carcasses. Since the isotope signature in bone collagen reflects the average diet for several years [28-30], the δ^{15}N values obtained from the sampled animals cannot be explained by one-time events or seasonality. Therefore, it could be possible that large carnivores and foxes regularly visited the kill sites of Paleolithic hunters after they butchered their prey and took the necessary body parts with them. If one of the predators came too close to humans, they were also killed and (perhaps only partially) taken to the sites.

Besides rodents the main diet of the intermediate δ^{15}N foxes was reindeer. It is obvious that this diet was quite restricted, as it can be assumed that if a fox has the option to feed on carrion, it will not be choosy which carrion it is. The foxes from this trophic niche originate from three different sites in both valleys, thus excluding the possibility that this diet was a unique phenomenon. One explanation is that their diet came from the direct vicinity near the caves, as humans had only brought certain animals, such as reindeer, as complete bodies to the cave and processed them there [9]. In addition, foxes that live permanently close to humans are easier to hunt than those foxes that avoid humans.

Looking at the Gravettian period, we have included Geißenklösterle and Sirgenstein from the Ach Valley and Bockstein from the Lone Valley (Fig. S3, Tab. 1). The archaeological data, primarily based on lithic artefacts, show that the Gravettian is so far mainly traceable in the Ach Valley [31]. Radiocarbon dating of bones from Bockstein [31-33] and a worked 3rd incisor of a brown bear from Vogelherd [8, 34], however, suggests that at least sporadic settlement of the Lone Valley must have taken place at this time. The population density in the Gravettian of the Swabian Jura has not yet been investigated in detail. The most recent data were provided by Maier and Zimmermann (35), although their study provides only a generalized, broad overview of human population density in the Gravettian of Europe. They found that there was a strong decrease after the Aurignacian, although population densities could vary widely locally. However, the extent to which the sites investigated in our study were occupied by humans cannot yet be fully determined. Most of the Gravettian foxes included in our study come from the AH I layer of Sirgenstein [10]. The results of the Sirgenstein faunal analysis show strong similarities with those found in Geißenklösterle and Hohle Fels and differ little from the Aurignacian [6, 7, 10]. Reindeer, horse and mammoth were identified as main prey, and small prey species such as hares, fish and birds became more numerous. We also see similarities to the Aurignacian in the distribution of the isotope analyzed foxes. Although the number of foxes found and analyzed is not as high as in the previous period, both share the same trophic niches: in the high δ^{15}N foxes all the sites we analyzed are represented, whereas in the intermediate δ^{15}N niche only foxes from Sirgenstein can be found. An indication that foxes were exploited by humans is found in two bones with cut marks from Hohle Fels [6] and further fox tooth pendants from Geißenklösterle and Hohle Fels [7, 15, 16, 18-22]. The conclusions we drew above for the Aurignacian can also be applied to the Gravettian. At least for Sirgenstein one strongly human-influenced trophic fox niche (intermediate δ^{15}N foxes) can be assumed. The high δ^{15}N foxes may also have fed without human influence, resulting in a commensalism to large predators (similar to the interpretation for the Middle Palaeolithic), although regular visits of human kill sites would be possible.

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S4 Text:

Applying the hypothesis to other archaeological sites

To apply our hypothesis to other sites, two important requirements must be given. Firstly, foxes must be present in the zooarchaeological record and secondly, isotope data of herbivores and carnivores (from the region, at best even from the site), including foxes, must be available.

An important site where these data are available is the Czech open air site Předmostí I. Archaeological studies showed that this site was inhabited for a long time in the Gravettian [1]. Mammoth remains are the most common, which also often show cut marks [2]. However, the second most common species are wolves and arctic foxes. Reindeer and horse are far less common. Předmostí I is therefore also interpreted as a seasonal mammoth hunting site [1]. The high number of predators alone indicates a time slot that was free of humans, so that these animals could scavenge. Bocherens (3) published the stable carbon and nitrogen isotope values of among others large herbivores, wolves and also six arctic foxes from this site. The δ^{15}N values of these foxes are generally lower than other carnivores, although they also cluster together with individual wolves, wolverines and brown bears. Similar to the groups of the high δ^{15}N foxes from the Swabian Jura, the Předmostí I foxes seem to behave commensal to the local large carnivores. A special aspect of this site is the group of reindeer-consuming canids, which are considered as palaeo-dogs and were probably fed by humans [3-6]. The diet of the arctic foxes, on the other hand, indicates unrestricted scavenging. A direct synanthropic commensalism, as we suggested for the Swabian Jura early Upper Palaeolithic, is not visible in Předmostí I. This can be explained by the seasonal human occupation of the site and the resulting low continuity of such a trophic niche, but also by the occurrence of palaeo-dogs, which probably kept other predators, including foxes, away from humans.

Another site that matches the mentioned requirements is Buran-Kaya-III, a rock shelter located on the southern Crimea. The zooarchaeological record shows that especially in the layers 6-1 and 6-2 (both dated to 37,100 - 33,100 cal BP, [7]) many saiga antelopes (*Saiga tatarica*) were killed and butchered by early Upper Palaeolithic hunters [8, 9]. Based on this, Buran-Kaya-III was interpreted as a seasonal hunting camp, used only by humans during the annual migration of the saiga antelopes [8, 9]. Besides saiga antelopes, bones of foxes, at least one wolf and humans were also found and investigated in an isotope study [10]. Drucker (10) sampled among others five foxes (both red and arctic foxes) from both layers. The main difference was observed in the δ^{13}C values between the foxes from layer 6-1 and 6-2. In addition to bulk collagen, the two amino acids phenylalanine and glutamic acid were also analysed. It was shown that most of the foxes had been feeding on saiga antelope. Humans, on the other hand, had mammoth in their diet in addition to saiga antelopes. However, this diet did not apply to two foxes. They are also lower in their δ^{15}N values and fed on smaller prey such as hares [10]. If we now consider that it takes several years to generate δ^{15}N levels in bone collagen, most foxes should also have had several years of regular access to saiga antelope as a food resource. Similar to the reindeer in the Swabian Jura, the saiga antelope is a food resource for foxes, which at that time and in this site could mainly have been obtained by humans [8-10]. The adaptation of the foxes' trophic behavior to human food remains in Buran-Kaya-III also shows the influence of humans on the Pleistocene ecosystem in Eastern Europe.

If we take a look at the Magdalenian of the pre-Alpine region of Germany and Switzerland (about 16,300 to 14,000 cal BP [11]), we see that three different niches have also been identified, namely “fox niche”, “wolf niche” and “dog niche” [12]. At that time the Swabian Jura was not densely populated by humans, which is also reflected in the low density of finds at the archaeological sites [11, 13-18]. Due to the differences in isospace before and after the LGM, these periods are not directly comparable [19]. However, it is possible to compare the composition of the trophic niches and their dietary reconstructions. One fox from Vogelherd was sampled for the Magdalenian, which fell into the "wolf niche", the equivalent of the high δ^{15}N foxes in the pre-LGM. As in the Middle Palaeolithic and the early Upper Palaeolithic, there was a niche with foxes, which were commensal to large predators. Into the Magdalenian "fox niche" there fell both a fox from the Geißenklösterle and a fox from Hohle Fels. This trophic niche would correspond to the low δ^{15}N foxes, as they fed mainly on small prey as well. These two niches do not seem to have been substantially influenced by humans in the Magdalenian either [12]. But this is different with the "dog niche", which contains a fox in addition to all dogs. This niche, however, only existed in the Swiss site Kesslerloch. In contrast to the Swabian Jura, the Magdalenian was more present in the Kesslerloch and humans seemed to have occupied this region more intensively [20].

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S5 Text:

Possible impact of prehistoric people on Pleistocene ecosystems

As we could show in this study, the trophic behavior of foxes and a possible human impact on the Pleistocene environments could be documented. However, foxes are not the only animals that can make this possible impact visible. Studies on mammoths and horses also show a change in trophic niches [1, 2]. It is hypothesized that due to hunting pressure on mammoths in the Gravettian of the Swabian Jura their natural dietary niche (plants with high δ^{15}N values [3]) could not be completely occupied by these animals. As a consequence, direct competition by horses increased [1]. Zooarchaeological studies showed that early Upper Palaeolithic humans in this region hunted mammoth as their main prey [4-9], besides reindeer as already mentioned. The hunting took place probably in spring, as bones with cut marks of mammoth calves were also found [7, 9, 10]. Assuming that the reproduction rate of mammoths was low, hunting calves over a longer period of time would lead to a dramatic population decrease, which in turn would give the horses the chance to occupy the mammoths' trophic niche [1]. Besides modern humans, Neanderthals have also hunted mammoths [2, 11, 12] and may have caused population changes in these animals. However, this assumption could not be confirmed until now. Niche changes of mammoths and the associated ecological stress have so far only been proven in the early Upper Palaeolithic corresponding to modern humans [1, 2]. One important factor may be the population density of Neanderthals compared to that of modern humans [13]. We can assume with our study the regular presence of mammoth carcasses in the Middle Palaeolithic environment of the Swabian Jura by dietary reconstruction of high δ^{15}N foxes and large carnivores. However, this did not seem to have a significant impact on the trophic niche of mammoths, or on the occupation of the mammoth trophic niche by another herbivorous species, such as horse. In contrast, from the early Upper Palaeolithic onwards, modern humans changed the occupation of trophic niches in the ecosystem, so that horses also benefited from food resources that had previously been used exclusively by mammoths [1, 2]. Finally, with the appearance of the new intermediate δ^{15}N niches of foxes, we see another indication of changes in the Pleistocene ecosystem that may have been caused by humans, where foxes directly benefit from anthropogenic subsidies left around human camps.

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Tab S1

Lab ID	Reference	Period	Location	Taxon	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
TUB-83	Bocherens et al. 2011	Middle Paleolithic	Hohle Fels	*Ursus arctos*	-19.4	8.1
HST-12	Bocherens et al. 2011	Aurignacian	Geißenklösterle	*Crocuta crocuta*	-20.0	9.4
HST-16	Bocherens et al. 2011	Aurignacian	Hohlenstein Stadel	*Crocuta crocuta*	-20.3	10.2
EQ-GK 331	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.6	6.1
EQ-GK 319	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-21.4	4.2
EQ-GK 321	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.1	8.5
EQ-GK 322	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.8	6.3
EQ-GK 323	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.7	6.1
EQ-GK 325	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.8	7.1
EQ-GK 326	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-21.0	6.1
EQ-GK 327	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.9	5.9
EQ-GK 329	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-20.8	6.9
EQ-GK 330	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Equus* sp.	-21.6	6.9
P-21810	Drucker et al. 2015	Aurignacian	Geißenklösterle	*Equus* sp.	-20.8	8.9
P-22980	Drucker et al. 2015	Aurignacian	Geißenklösterle	*Equus* sp.	-20.9	6.3
P-22978	Drucker et al. 2015	Aurignacian	Geißenklösterle	*Equus* sp.	-20.2	7.9
HF-7	Münzel et al. 2014	Aurignacian	Hohle Fels	*Equus* sp.	-20.7	6.3
HF-8	Münzel et al. 2014	Aurignacian	Hohle Fels	*Equus* sp.	-20.9	6.2
HF-9	Münzel et al. 2014	Aurignacian	Hohle Fels	*Equus* sp.	-20.5	6.9
HF-6	Münzel et al. 2014	Aurignacian	Hohle Fels	*Equus* sp.	-20.5	6.8
HF-10	Münzel et al. 2014	Aurignacian	Hohle Fels	*Equus* sp.	-20.5	6.5
P-22976	Drucker et al. 2015	Aurignacian	Geißenklösterle	*Mammuthus primigenius*	-21.5	8.0
JK2769	Münzel et al. 2014	Aurignacian	Geißenklösterle	*Mammuthus primigenius*	-21.1	8.9
JK2764	Münzel et al. 2014	Aurignacian	Geißenklösterle	*Mammuthus primigenius*	-21.1	8.0
JK2778	Münzel et al. 2014	Aurignacian	Geißenklösterle	*Mammuthus primigenius*	-20.8	10.0
JK2771	Münzel et al. 2014	Aurignacian	Geißenklösterle	*Mammuthus primigenius*	-21.2	8.8
JK2766	Münzel et al. 2014	Aurignacian	Hohle Fels	*Mammuthus primigenius*	-21.7	8.4
RA-GK 303	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-18.9	2.4
RA-GK 308	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-18.7	3.4
RA-GK 309	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.1	3.9
RA-GK 311	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-18.6	3.4
RA-GK 312	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.0	2.6
RA-GK 299	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.2	3.8
RA-GK 300	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-18.6	3.8
RA-GK 302	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.1	4.6
RA-GK 304	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.5	4.4
RA-GK 306	Bocherens et al. 2011	Aurignacian	Geissenklösterle	*Rangifer tarandus*	-19.4	4.7
KIA-35462	Münzel et al. 2014	Aurignacian	Hohle Fels	*Rangifer tarandus*	-19.5	4.8
TUB-14	Bocherens et al. 2011	Aurignacian	Geißenklösterle	*Ursus arctos*	-19.3	9.1
EQ-GK 314	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Equus* sp.	-20.7	8.7
EQ-GK 316	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Equus* sp.	-20.6	7.3
EQ-GK 317	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Equus* sp.	-20.7	5.5
EQ-GK 318	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Equus* sp.	-21.8	3.4
GK15	Drucker et al. 2015	Gravettian	Geißenklösterle	*Equus* sp.	-20.4	7.1
GK14	Drucker et al. 2015	Gravettian	Geißenklösterle	*Equus* sp.	-20.6	6.3
JK2781	Drucker et al. 2015	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-21.0	8.9
P-22981	Drucker et al. 2015	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-21.3	8.1
JK2774	Münzel et al. 2014	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-21.1	9.1
JK2777	Münzel et al. 2014	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-21.0	9.0
JK2779	Münzel et al. 2014	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-20.9	8.3
JK2780	Münzel et al. 2014	Gravettian	Geißenklösterle	*Mammuthus primigenius*	-20.9	8.7
TUB-73	Bocherens et al. 2011	Gravettian	Hohle Fels	*Panthera spelaea*	-18.8	10.2
TUB-74	Bocherens et al. 2011	Gravettian	Hohle Fels	*Panthera spelaea*	-20.7	8.4
TUB-75	Bocherens et al. 2011	Gravettian	Hohle Fels	*Panthera spelaea*	-18.1	8.2
RA-GK 294	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Rangifer tarandus*	-18.9	4.3
RA-GK 295	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Rangifer tarandus*	-19.3	3.7
RA-GK 296	Bocherens et al. 2011	Gravettian	Geissenklösterle	*Rangifer tarandus*	-19.0	4.2
P-21815	Drucker et al. 2015	Gravettian	Geißenklösterle	*Rangifer tarandus*	-18.9	4.6
TUB-84	Bocherens et al. 2011	Gravettian	Hohle Fels	*Ursus arctos*	-19.4	9.6
TUB-8	Bocherens et al. 2011	Gravettian	Geißenklösterle	*Ursus arctos*	-19.5	8.3

Tab S2

Lab ID	**Prey group**	**Taxon**	**$\delta^{13}C_{coll}$ [‰]**	**$\delta^{15}N_{coll}$ [‰]**
SJM-7	Horse	*Dicrostonyx torquatus*	-21.2	5.5
SJM-8	Horse	*Dicrostonyx torquatus*	-21.0	6.7
SJM-9	Horse	*Dicrostonyx torquatus*	-21.2	7.1
SJM-54	Horse	*Dicrostonyx torquatus*	-21.2	6.4
SJM-55	Horse	*Dicrostonyx torquatus*	-20.3	7.1
SJM-56	Horse	*Dicrostonyx torquatus*	-20.9	5.2
SJM-51	Horse	*Dicrostonyx torquatus*	-21.3	6.1
SJM-48	Horse	*Dicrostonyx torquatus*	-21.1	5.6
P-22980	Horse	*Equus* sp.	-20.9	6.3
P-22978	Horse	*Equus* sp.	-20.2	7.9
HF-7	Horse	*Equus* sp.	-20.7	6.3
HF-8	Horse	*Equus* sp.	-20.9	6.2
HF-9	Horse	*Equus* sp.	-20.5	6.9
HF-6	Horse	*Equus* sp.	-20.5	6.8
HF-10	Horse	*Equus* sp.	-20.5	6.5
EQ-GK 331	Horse	*Equus* sp.	-20.6	6.1
EQ-GK 321	Horse	*Equus* sp.	-20.1	8.5
EQ-GK 322	Horse	*Equus* sp.	-20.8	6.3
EQ-GK 323	Horse	*Equus* sp.	-20.7	6.1
EQ-GK 325	Horse	*Equus* sp.	-20.8	7.1
EQ-GK 326	Horse	*Equus* sp.	-21.0	6.1
EQ-GK 327	Horse	*Equus* sp.	-20.9	5.9
EQ-GK 329	Horse	*Equus* sp.	-20.8	6.9
EQ-GK 316	Horse	*Equus* sp.	-20.6	7.3
EQ-GK 317	Horse	*Equus* sp.	-20.7	5.5
GK15	Horse	*Equus* sp.	-20.4	7.1
GK14	Horse	*Equus* sp.	-20.6	6.3
SJM-3	Horse	*Lemmus lemmus*	-20.7	6.5
SJM-57	Horse	*Lemmus lemmus*	-21.4	5.2
SJM-60	Horse	*Lemmus lemmus*	-20.9	5.6
SJM-47	Horse	*Lemmus lemmus*	-21.3	6.1
P-21810	Mammoth	*Equus* sp.	-20.8	8.9
EQ-GK 314	Mammoth	*Equus* sp.	-20.7	8.7
JK2769	Mammoth	*Mammuthus primigenius*	-21.1	8.9
JK2764	Mammoth	*Mammuthus primigenius*	-21.1	8.0
P-22976	Mammoth	*Mammuthus primigenius*	-21.5	8.0
JK2778	Mammoth	*Mammuthus primigenius*	-20.8	10.0
JK2771	Mammoth	*Mammuthus primigenius*	-21.2	8.8
JK2766	Mammoth	*Mammuthus primigenius*	-21.7	8.4
JK2781	Mammoth	*Mammuthus primigenius*	-21.0	8.9
JK2774	Mammoth	*Mammuthus primigenius*	-21.1	9.1
JK2777	Mammoth	*Mammuthus primigenius*	-21.0	9.0
JK2779	Mammoth	*Mammuthus primigenius*	-20.9	8.3
JK2780	Mammoth	*Mammuthus primigenius*	-20.9	8.7
P-22981	Mammoth	*Mammuthus primigenius*	-21.3	8.1
SJM-52	Reindeer	*Dicrostonyx torquatus*	-20.2	3.5
VLP-12	Reindeer	*Lepus* sp.	-20.4	2.8
VLP-13	Reindeer	*Lepus* sp.	-20.2	3.5
KIA-35462	Reindeer	*Rangifer tarandus*	-19.5	4.8
RA-GK 303	Reindeer	*Rangifer tarandus*	-18.9	2.4
RA-GK 308	Reindeer	*Rangifer tarandus*	-18.7	3.4
RA-GK 309	Reindeer	*Rangifer tarandus*	-19.1	3.9
RA-GK 311	Reindeer	*Rangifer tarandus*	-18.6	3.4
RA-GK 312	Reindeer	*Rangifer tarandus*	-19.0	2.6
RA-GK 299	Reindeer	*Rangifer tarandus*	-19.2	3.8
RA-GK 300	Reindeer	*Rangifer tarandus*	-18.6	3.8
RA-GK 302	Reindeer	*Rangifer tarandus*	-19.1	4.6
RA-GK 304	Reindeer	*Rangifer tarandus*	-19.5	4.4
RA-GK 306	Reindeer	*Rangifer tarandus*	-19.4	4.7
RA-GK 294	Reindeer	*Rangifer tarandus*	-18.9	4.3
RA-GK 295	Reindeer	*Rangifer tarandus*	-19.3	3.7
RA-GK 296	Reindeer	*Rangifer tarandus*	-19.0	4.2
P-21815	Reindeer	*Rangifer tarandus*	-18.9	4.6
SJM-11	Rodents	*Dicrostonyx torquatus*	-25.1	-1.5
SJM-50	Rodents	*Dicrostonyx torquatus*	-21.1	3.6
EQ-GK 330	Rodents	*Equus* sp.	-21.6	6.9
EQ-GK 319	Rodents	*Equus* sp.	-21.4	4.2
EQ-GK 318	Rodents	*Equus* sp.	-21.8	3.4
SJM-12	Rodents	*Lemmus lemmus*	-23.1	1.0
SJM-14	Rodents	*Lemmus lemmus*	-24.9	-0.6
SJM-15	Rodents	*Lemmus lemmus*	-24.6	1.0
SJM-16	Rodents	*Lemmus lemmus*	-24.5	0.6
SJM-17	Rodents	*Lemmus lemmus*	-22.9	2.5
SJM-18	Rodents	*Lemmus lemmus*	-23.5	2.5
SJM-5	Rodents	*Lemmus lemmus*	-21.9	7.3
SJM-6	Rodents	*Lemmus lemmus*	-21.8	6.8
SJM-1	Rodents	*Lemmus lemmus*	-21.8	5.9
SJM-4	Rodents	*Lemmus lemmus*	-22.0	5.8
SJM-13	Rodents	*Lemmus lemmus*	-23.2	5.2
SJM-2	Rodents	*Lemmus lemmus*	-22.2	4.8
SJM-58	Rodents	*Lemmus lemmus*	-22.8	6.6
SJM-59	Rodents	*Lemmus lemmus*	-21.6	3.9
SJM-61	Rodents	*Lemmus lemmus*	-21.7	4.2
SJM-10	Rodents	*Microtus arvalis/agrestis*	-22.4	7.3
SJM-29	Rodents	*Microtus arvalis/agrestis*	-22.5	7.9
SJM-31	Rodents	*Microtus arvalis/agrestis*	-22.6	6.7
SJM-32	Rodents	*Microtus arvalis/agrestis*	-23.0	7.4
SJM-33	Rodents	*Microtus arvalis/agrestis*	-23.1	5.4
SJM-34	Rodents	*Microtus arvalis/agrestis*	-22.0	5.7
SJM-36	Rodents	*Microtus arvalis/agrestis*	-22.2	5.9
SJM-37	Rodents	*Microtus arvalis/agrestis*	-21.8	5.7
SJM-38	Rodents	*Microtus arvalis/agrestis*	-23.0	6.2
SJM-30	Rodents	*Microtus arvalis/agrestis*	-22.1	4.5
SJM-35	Rodents	*Microtus arvalis/agrestis*	-22.7	4.4
SJM-53	Rodents	*Microtus arvalis/agrestis*	-21.7	3.0
SJM-49	Rodents	*Microtus arvalis/agrestis*	-22.4	2.3
SJM-62	Rodents	*Microtus arvalis/agrestis*	-22.1	3.8
SJM-63	Rodents	*Microtus arvalis/agrestis*	-21.8	4.5

Tab S3

Lab ID	**Period**	**Niche/Group**	**Taxon**	$\delta^{13}C_{coll}$ **[‰]**	$\delta^{15}N_{coll}$ **[‰]**
PLC-1	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-18.4	8.7
PLC-16	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-19.4	9.4
PLC-28	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-19.7	8.6
PLC-55	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-20.1	8.9
VLP-1	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-20.6	9.1
VLP-3	Aurignacian	High δ^{15}N foxes	Vulpes lagopus	-19.9	8.6
PLC-15	Aurignacian	High δ^{15}N foxes	Vulpes sp.	-20.4	8.9
PLC-10	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-19.2	8.2
PLC-11	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-19.6	9.1
PLC-8	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-20.1	8.3
PLC-26	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-19.8	8.1
PLC-27	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-20.2	8.2
PLC-66	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-20.3	8.0
PLC-67	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-21.0	8.2
PLC-85	Aurignacian	High δ^{15}N foxes	Vulpes vulpes	-20.2	8.3
PLC-42	Gravettian	High δ^{15}N foxes	Vulpes lagopus	-20.3	7.6
PLC-77	Gravettian	High δ^{15}N foxes	Vulpes lagopus	-20.1	8.7
PLC-75	Gravettian	High δ^{15}N foxes	Vulpes vulpes	-20.3	9.2
VLP-4	Gravettian	High δ^{15}N foxes	Vulpes vulpes	-19.7	7.1
VLP-5	Gravettian	High δ^{15}N foxes	Vulpes vulpes	-19.7	9.7
PLC-80	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-19.7	10.0
PLC-82	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-20.2	7.8
PLC-83	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-20.4	8.2
PLC-84	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-20.1	9.0
PLC-39	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-20.3	8.4
PLC-40	Middle Paleolithic	High δ^{15}N foxes	*Vulpes vulpes*	-19.9	8.6
PLC-24	Aurignacian	Large Carnivores	Canis lupus	-19.1	9.5
PLC-25	Aurignacian	Large Carnivores	Canis lupus	-19.0	9.6
PLC-29	Aurignacian	Large Carnivores	Canis lupus	-19.4	10.7
PLC-30	Aurignacian	Large Carnivores	Canis lupus	-19.7	9.2
PLC-31	Aurignacian	Large Carnivores	Canis lupus	-19.0	9.8
PLC-32	Aurignacian	Large Carnivores	Canis lupus	-19.5	8.5
PLC-44	Aurignacian	Large Carnivores	Canis lupus	-18.9	9.6
PLC-46	Aurignacian	Large Carnivores	Canis lupus	-19.7	9.3
PLC-47	Aurignacian	Large Carnivores	Canis lupus	-19.2	8.9
PLC-78	Aurignacian	Large Carnivores	Canis lupus	-19.5	8.5
JK2175	Aurignacian	Large Carnivores	Canis lupus	-19.5	10.7
JK2180	Aurignacian	Large Carnivores	Canis lupus	-18.6	8.3
JK2184	Aurignacian	Large Carnivores	Canis lupus	-18.9	10.0
PLC-2	Aurignacian	Large Carnivores	Canis lupus	-20.2	9.1
PLC-3	Aurignacian	Large Carnivores	Canis lupus	-21.0	9.4
PLC-45	Aurignacian	Large Carnivores	Canis lupus	-20.4	9.5
HST-12	Aurignacian	Large Carnivores	Crocuta crocuta	-20.0	9.4
HST-16	Aurignacian	Large Carnivores	Crocuta crocuta	-20.3	10.2
PLC-62	Aurignacian	Large Carnivores	Gulo gulo	-19.1	9.4
PLC-17	Aurignacian	Large Carnivores	Lynx lynx	-19.3	7.7
PLC-23	Aurignacian	Large Carnivores	Lynx lynx	-19.3	10.2
PLC-63	Aurignacian	Large Carnivores	Lynx lynx	-19.8	7.0
TUB-14	Aurignacian	Large Carnivores	Ursus arctos	-19.3	9.1
JK2174	Gravettian	Large Carnivores	Canis lupus	-20.2	9.7
JK2183	Gravettian	Large Carnivores	Canis lupus	-20.2	9.3
JK2178	Gravettian	Large Carnivores	Canis lupus	-19.5	8.9
PLC-70	Gravettian	Large Carnivores	Gulo gulo	-19.1	7.6
PLC-18	Gravettian	Large Carnivores	Lynx lynx	-19.5	8.4
PLC-19	Gravettian	Large Carnivores	Lynx lynx	-18.7	8.0
TUB-73	Gravettian	Large Carnivores	Panthera spelaea	-18.8	10.2
TUB-74	Gravettian	Large Carnivores	Panthera spelaea	-20.7	8.4
TUB-75	Gravettian	Large Carnivores	Panthera spelaea	-18.1	8.2
TUB-84	Gravettian	Large Carnivores	Ursus arctos	-19.4	9.6
TUB-8	Gravettian	Large Carnivores	Ursus arctos	-19.5	8.3
PLC-79	Middle Paleolithic	Large Carnivores	*Canis lupus*	-20.1	10.6
PLC-35	Middle Paleolithic	Large Carnivores	*Canis lupus*	-20.0	7.7
PLC-37	Middle Paleolithic	Large Carnivores	*Canis lupus*	-20.1	8.5
PLC-38	Middle Paleolithic	Large Carnivores	*Canis lupus*	-19.4	10.0
PLC-48	Middle Paleolithic	Large Carnivores	*Canis lupus*	-19.2	8.3
PLC-49	Middle Paleolithic	Large Carnivores	*Canis lupus*	-19.7	7.3
TUB-83	Middle Paleolithic	Large Carnivores	*Ursus arctos*	-19.4	8.1
PLC-76	Middle Paleolithic	Low δ^{15}N foxes	*Vulpes lagopus*	-21.4	1.0
VLP-10	Middle Paleolithic	Low δ^{15}N foxes	*Vulpes vulpes*	-21.1	3.0
PLC-22	Aurignacian	Intermediate δ^{15}N foxes	Vulpes lagopus	-20.2	5.4
PLC-9	Aurignacian	Intermediate δ^{15}N foxes	Vulpes vulpes	-19.4	5.7
PLC-13	Aurignacian	Intermediate δ^{15}N foxes	Vulpes vulpes	-20.0	4.7
PLC-14	Aurignacian	Intermediate δ^{15}N foxes	Vulpes vulpes	-20.0	5.5
PLC-68	Aurignacian	Intermediate δ^{15}N foxes	Vulpes vulpes	-20.4	6.0
PLC-69	Aurignacian	Intermediate δ^{15}N foxes	Vulpes vulpes	-20.0	4.8
PLC-71	Gravettian	Intermediate δ^{15}N foxes	Vulpes vulpes	-20.5	6.0
PLC-43	Gravettian	Intermediate δ^{15}N foxes	Vulpes vulpes	-19.7	4.0
PLC-73	Gravettian	Intermediate δ^{15}N foxes	Vulpes vulpes	-19.6	3.7
PLC-72	Gravettian	Intermediate δ^{15}N foxes	Vulpes vulpes	-19.4	6.7

Tab S4

Large Carnivores

	Middle Pal.	Aurignacian	Gravettian
TA [‰²]	2.08	5.19	4.20
SEA [‰²]	1.41	1.57	1.87
SEAc [‰²]	1.69	1.65	2.08

High δ^{15}N foxes

	Middle Pal.	Aurignacian	Gravettian
TA [‰²]	0.46	2.27	1.26
SEA [‰²]	0.38	0.83	1.04
SEAc [‰²]	0.47	0.89	1.38

Intermediate δ^{15}N foxes

	Aurignacian	Gravettian
TA [‰²]	0.59	1.58
SEA [‰²]	0.53	2.20
SEAc [‰²]	0.67	3.31

Tab S5

Site	Lab ID	Excav. No	AH	Period	Taxon	Element	Name in S4 and S5 Figs	MNI
Geißenklösterle	PLC-18	GK 9/3	AH Ir	Gravettian	Lynx	Rib	S5 Fig: GK lynx	1
	PLC-19	GK 121/93	AH Ir	Gravettian	Lynx	Mandible		
Hohlenstein-Stadel	**PLC-26**	**HS 19/2-9298**	Hieb 2	Aurignacian	Red fox	Mandible	**S4 Fig: HS fox**	1
	PLC-27	**HS 19/2-9359**	Hieb 2	Aurignacian	Red fox	Humerus		
Sirgenstein	PLC-66	Si 3360	AH IV	Aurignacian	Red fox	Mandible (R)	S4 Fig: Si fox	1
	PLC-67	Si 3361	AH IV	Aurignacian	Red fox	Mandible (L)		
	PLC-43	**Si 773**	AH I	Gravettian	Red fox	Mandible (R)	**S5 Fig: Si fox**	1
	PLC-73	**Si 2214**	AH I	Gravettian	Red fox	Humerus (R)		
Vogelherd	**PLC-2**	**Vg IV 9059**	AH IV	Aurignacian	Wolf	Radius	**S4 Fig: VH wolf 1**	2
	PLC-45	**Vg IV 10685**	AH IV	Aurignacian	Wolf	Tibia		
	PLC-46	**Vg IV 1732**	AH IV	Aurignacian	Wolf	Ulna (L)	**S4 Fig: VH wolf 2**	
	PLC-47	**Vg IV 7214**	AH IV	Aurignacian	Wolf	Ulna (R)		
	PLC-11	Vg IV 7259	AH IV	Aurignacian	Red fox	Radius	S4 Fig: VH fox 1	2
	PLC-10	Vg IV 7245	AH IV	Aurignacian	Red fox	Tibia		
	PLC-15	Vg IV 12782	AH IV	Aurignacian	Fox	Mandible (R)		
	PLC-9	Vg IV 3551	AH IV	Aurignacian	Red fox	Femur	S4 Fig: VH fox 2	1
	PLC-13	Vg IV 12776	AH IV	Aurignacian	Red fox	Mandible (R)		

Tab S6

Lab ID	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]	Lab ID	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]	Differences in $\delta^{13}C$	Differences in $\delta^{15}N$	MNI	Taxon	Site
PLC-18	-19.5	8.4	PLC-19	-18.7	8.0	0.8‰	0.4‰	1	Lynx	Geißenklösterle
JK 2180	-18.6	8.3	JK 2184	-18.9	10.0	0.3‰	1.7‰	2	Wolf	Hohle Fels
PLC-26	-19.8	8.1	PLC-27	-20.2	8.2	0.4‰	0.1‰	1	Red fox	Hohlenstein-Stadel
PLC-66	-20.3	8.1	PLC-67	-21.0	8.2	0.7‰	0.1‰	1	Red fox	Sirgenstein
PLC-68	-20.4	6.0	PLC-69	-20.0	4.8	0.4‰	1.2‰	2	Red fox	Sirgenstein
PLC-43	-19.7	4.0	PLC-73	-19.6	3.7	0.1‰	0.3‰	1	Red fox	Sirgenstein
PLC-71	-20.5	6.0	PLC-72	-19.4	6.7	1.1‰	0.7‰	2	Red fox	Sirgenstein
PLC-71	-20.5	6.0	PLC-75	-20.3	9.2	0.2‰	3.2‰	2	Red fox	Sirgenstein
PLC-72	-19.4	6.7	PLC-75	-20.3	9.2	0.9‰	2.5‰	2	Red fox	Sirgenstein
PLC-2	-20.2	9.1	PLC-45	-20.4	9.5	0.2‰	0.4‰	1	Wolf	Vogelherd
PLC-2	-20.2	9.1	PLC-46	-19.7	9.3	0.6‰	0.2‰	1	Wolf	Vogelherd
PLC-2	-20.2	9.1	PLC-47	-19.2	8.9	1‰	0.2‰	2	Wolf	Vogelherd
PLC-45	-20.4	9.5	PLC-46	-19.7	9.3	0.8‰	0.2‰	1	Wolf	Vogelherd
PLC-45	-20.4	9.5	PLC-47	-19.2	8.9	1.2‰	0.7‰	2	Wolf	Vogelherd
PLC-46	-19.7	9.3	PLC-47	-19.2	8.9	0.5‰	0.5‰	1	Wolf	Vogelherd
PLC-48	-19.2	8.3	PLC-49	-19.7	7.3	0.5‰	1‰	2	Wolf	Vogelherd
PLC-1	-18.4	8.7	PLC-16	-19.4	9.4	1.1‰	0.8‰	2	Arctic fox	Vogelherd
PLC-10	-19.2	8.2	PLC-11	-19.6	9.1	0.5‰	0.9‰	1	Red fox	Vogelherd
PLC-10	-19.2	8.2	PLC-15	-20.4	8.9	1.2‰	0.8‰	2	Red fox	Vogelherd
PLC-11	-19.6	9.1	PLC-15	-20.4	8.9	0.8‰	0.2‰	1	Red fox	Vogelherd
PLC-9	-19.4	5.7	PLC-13	-20.0	4.7	0.6‰	0.9‰	1	Red fox	Vogelherd

Figure S1

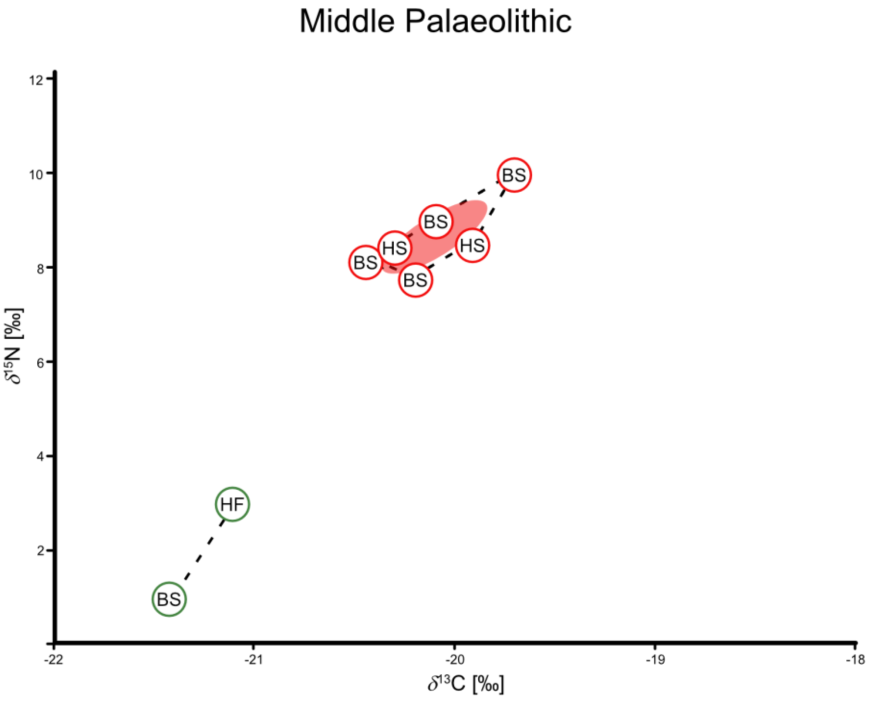


Figure S2

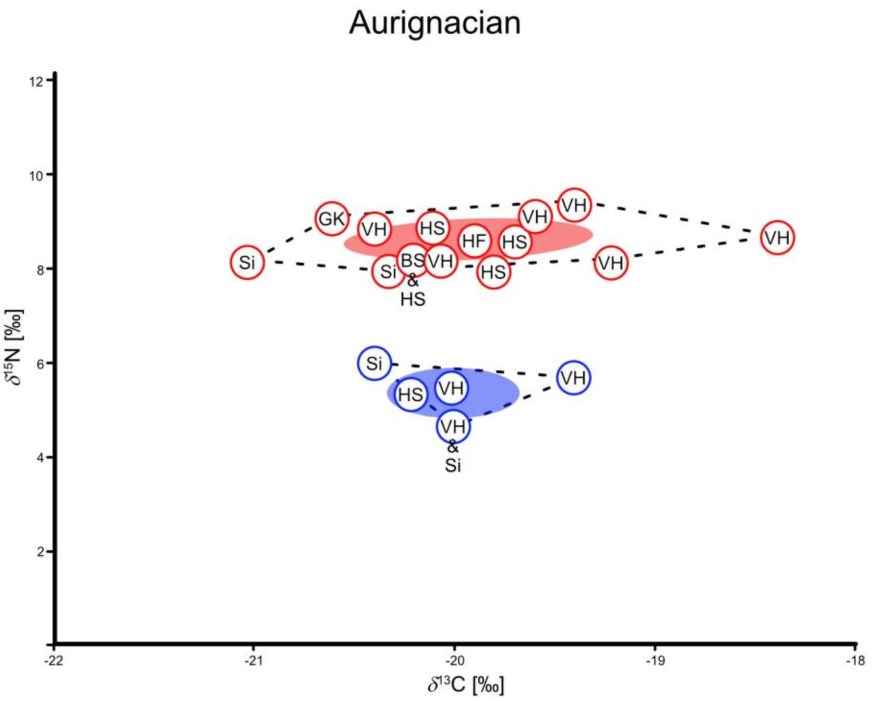


Figure S3

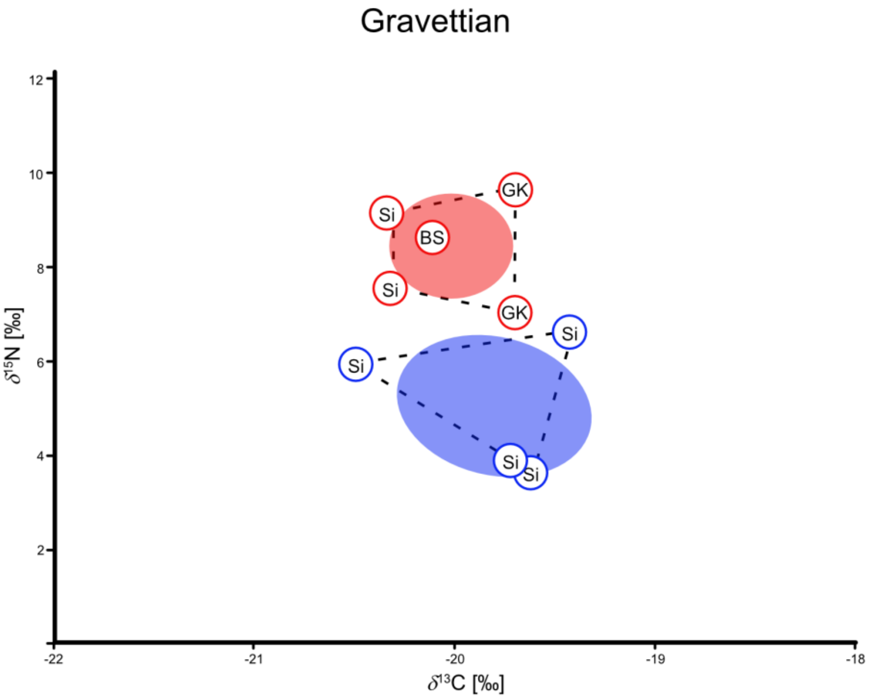


Figure S4

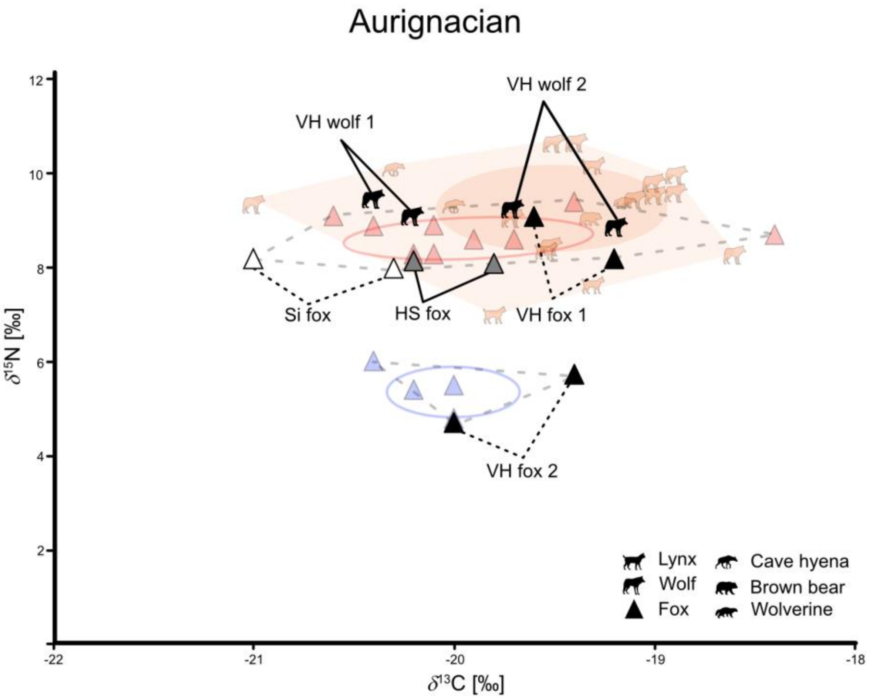
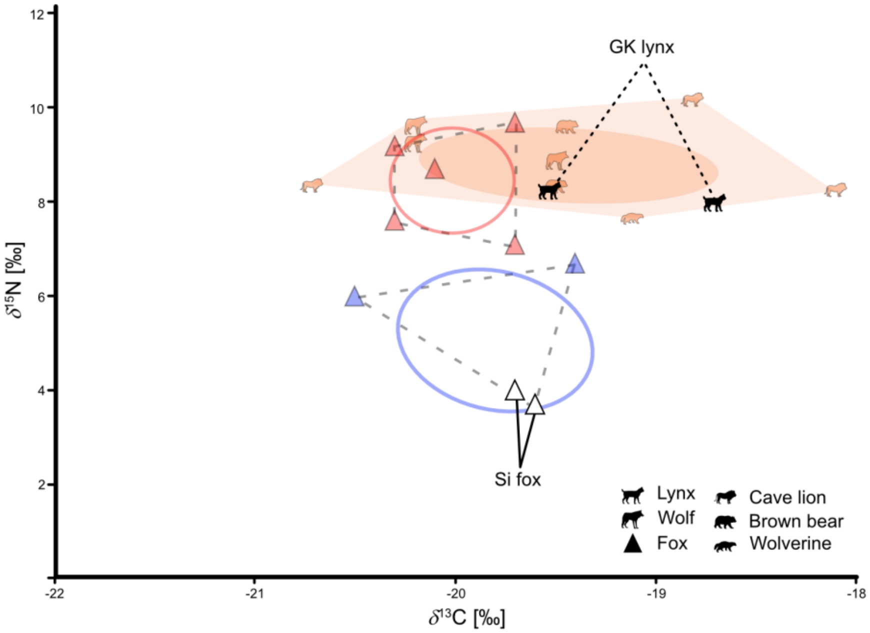


Figure S5


GK lynx
Si fox
Lynx
Wolf
Fox
Cave lion
Brown bear
Wolverine
δ15N [‰]
δ13C [‰]
12
10
8
6
4
2
-22
-21
-20
-19
-18

Appendix 3

Dietary niche partitioning among Magdalenian canids
in southwestern Germany and Switzerland.

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Dietary niche partitioning among Magdalenian canids in southwestern Germany and Switzerland

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ABSTRACT

Fox (*Vulpes vulpes* and *Vulpes lagopus*), wolf (*Canis lupus*) and dog (*Canis lupus familiaris*) remains are commonly found in the faunal assemblages of Magdalenian sites in Central Europe. However, little is known about their ecology in terms of food preference and niche partitioning. We hypothesize that domestication leads to a new trophic niche for dogs and even for commensal animals, such as foxes, compared to their wild counterparts (i.e. wolves and wild non-commensal foxes). To test our hypothesis, we used stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$) of bone collagen extracted from canid bones from several Magdalenian sites in southwestern Germany and Switzerland (between 17,000 and 13,000 years ago). We then ran Bayesian statistic systems (SIBER, mixSIAR) to reconstruct the trophic niches and diets of Magdalenian canids. We conclude that a significant niche partitioning of canids is reflected in their carbon and nitrogen isotopic composition. Furthermore, we were able to distinguish between the niche of dogs and individual commensal foxes on the one hand, and wolves on the other hand. We suggest that while wolves had permanent, unrestricted access to all types of dietary resources coming from a diversity of prey species, the diet of dogs was controlled by humans. Most of the foxes built their own niche with a diet primarily comprised of small mammals. However, some red foxes showed commensal relationships in their reconstructed diet to dogs and wolves.

1. Introduction

1.1. Magdalenian canids

During the Magdalenian in southwestern Germany and Switzerland (17,000–13,000 cal BP (Gaudzinski and Street, 2003; Hahn, 1995; Housley et al., 1997; Kind, 2003; Napierala, 2008; Taller et al., 2014)), four canids were present on the landscape. Red fox (*Vulpes vulpes*) and arctic fox (*Vulpes lagopus*) are small, solitary, opportunistic predators, which tend to live commensal to larger predators and humans in modern times (Pulliaines, 1993; Wandeler and Lüps, 1993). European wolves (*Canis lupus*) are larger predators, which organize in packs to hunt larger prey (Peters, 1993). In the archaeological sites of southwestern Germany and Switzerland, we find remains of these three canid taxa in many layers before and after the Last Glacial Maximum (LGM) (Boger et al., 2014; Krönneck, 2012; Napierala, 2008; Napierala et al., 2014; Niven, 2007). However, starting in the Magdalenian, after the LGM, we find a fourth canid taxon in this region: the dog, *Canis lupus familiaris*, whose diet likely reflected its relationship with humans (Camarós et al., 2016; Germonpré et al., 2018; Napierala and Uerpmann, 2012; Thalmann et al., 2013; Wayne et al., 2006).

Several studies have established that dog domestication started independently in different areas of eastern Asia, Central Asia, the Middle East, and Europe around 40,000 to 30,000 years ago (Crockford and Kuzmin, 2012; Germonpré et al., 2009, 2012, 2013, 2015, 2016, 2018; Larson et al., 2012; Morey and Jeger, 2017;

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Ovodov et al., 2011; Perri, 2016; Thalmann and Perri, 2018; Thalmann et al., 2013; Vilà et al., 1997; Wayne et al., 2006). After the LGM, dog remains are often found in European archaeological sites (Janssens et al., 2018; Napierala and Uerpmann, 2012; Thalmann and Perri, 2018; Thalmann et al., 2013; Wayne et al., 2006). During the Magdalenian these animals became increasingly important for humans.

Why and how they were domesticated is a very active field of research with little consensus (Germonpré et al., 2013, 2018; Larson et al., 2012; Morey, 2014; Morey and Jeger, 2015, 2017; Perri, 2016). In this discussion, two hypotheses have prevailed. First is that wolves self-domesticated. This scenario is based on an ecological association between humans and wolves and the fact that both were specialized on the same spectrum of prey (Germonpré et al., 2018; Morey and Jeger, 2015; Russell, 2002; Vigne, 2015). Several researchers suggested that in the Paleolithic, wolves were attracted to human food waste (e.g. prey animals that were left behind after butchering) and scavenged from these resources. Only wolves that were less anxious and aggressive were tolerated by humans and became commensal, resulting in their domestication after some generations (Coppinger and Coppinger, 2001; Germonpré et al., 2018; Larson and Burger, 2013; Larson et al., 2012; MacHugh et al., 2017; O'Connor, 1997; Zeder, 2012a, b). However, there is substantial criticism of this hypothesis. Studies on modern hunter-gatherer societies showed that they leave little food waste, and in addition, have multiple strategies for protecting their uneaten food (Fair, 1997; Germonpré et al., 2018; Lavrillier, 2011; Tanner, 1979). Furthermore, Lupo (2017) established that dogs that subsist entirely on human refuse display poor health and have reduced life spans. The other main criticism of the self-domestication hypothesis is that habituated wolves are dangerous. If wolves associate humans with food, they can also attack and kill people, especial children (Behdarvand and Kaboli, 2015; Bisi et al., 2007; Linnell and Boitani, 2011; Linnell et al., 2002, 2003; McNay, 2002; McNay and Mooney, 2005; Rajpurohit, 1999). Germonpré et al. (2018) suggested that Paleolithic people did everything possible to avoid these dangerous outcomes. The second prevailing hypothesis for wolf domestication is that Paleolithic foragers were intentionally keeping pets (Germonpré et al., 2018; Russell, 2002, 2011). Ethnographic studies show that the keeping of young carnivores as pets is common in modern hunter-gatherer societies in northern latitudes (Drucker, 1951; Proko'yeva, 1964; Russell, 2002, 2011; Sokolova, 2000). In both hypotheses, there is selection for tameness and reduced fear, which could be driving factors in domestication (Belyaev et al., 1985; Germonpré et al., 2018; Kukekova et al., 2011; Morey and Jeger, 2015, 2017; Trut et al., 2004, 2009; Trut, 1999).

Although these questions are still under debate, we do know that dogs are the oldest domestic animals, and human control over their diet, reproduction, and health started quite early in the history of human-canid relationship (Germonpré et al., 2018). However, there is a difference in the feeding pattern between both domestication scenarios: in the self-domestication model, wolf food resources are human refuse, while in the pet-keeping model, canids are actively fed by humans (Germonpré et al., 2018). In the first case, the diet of the canids would resemble those of the human, while in the second case their food intake diet could differ significantly both from those of the human and/or their wild counterparts. Interestingly, evidence for the control of canid diets was showed through morphological study and stable isotope analyses in an archaeological site of Central Europe as early as the Gravettian, ca. 29,500–31,500 cal BP (Bocherens et al., 2015; Germonpré et al., 2018).

Current research indicates that, unlike wolves, arctic and red foxes were not domesticated in the European Paleolithic, though their domestication was possible, as indicated by the Russian farm-fox experiment (Belyaev et al., 1985; Dugatkin, 2018; Gogoleva et al., 2011; Kukekova et al., 2011; Trut et al., 2004, 2009; Trut, 1999). The earliest evidence of close human-fox interactions comes from the Natufian period in Jordan (ca. 14,500–11,600 years ago), where a human was buried with a fox (Maher et al., 2011). Excavators identified the burial as a secondary inhumation, and recovered pieces of ochre from on top of both human and fox bones, which they hypothesize highlights the relationship between the two individuals (Maher et al., 2011). A possible case of fox domestication was found in two Early to Middle Bronze Age sites (Can Roqueta and Minferri, ca. 4000 years ago) in the Iberian Peninsula (Grandal-d'Anglade et al., 2019). Excavators recovered burials with humans and both foxes and dogs. In addition to a morphological analysis of the humans and canids, Grandal-d'Anglade et al. (2019) reconstructed their diets, based on their carbon and nitrogen isotopic values. Whereas the diets of men were dominated by meat, the diets of dogs, foxes, women, and children were primarily comprised of cereals. This indicates that humans controlled the food of dogs and foxes and both taxa were likely domesticated. It is also interesting that most dogs showed pathologies that came from carrying loads, while only one older fox had a similar pathology. The other foxes preserved no similar evidence of behavior-related pathologies (Grandal-d'Anglade et al., 2019).

Today, foxes show another type of relationship with humans; they are synanthropic commensals, which means that they benefit from human lifestyles without positively or negatively affecting people (Hulme-Beaman et al., 2016). Red foxes, for example, often live commensal to humans and benefit from their food waste (Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Panek and Budny, 2017; Sidorovich et al., 2006; Soe et al., 2017; Wandeler and Lüps, 1993). Arctic foxes also use human food waste as a dietary resource (Pulliaines, 1993). As in the case of domestic animals, where humans take control over an animal's diet, commensal animals change their trophic niche in comparison to their non-commensal conspecifics. Several ecological studies have investigated this matter (Kays and Feranec, 2011; Merkle et al., 2011; Murray et al., 2015; Newsome et al., 2010, 2015; Warsen et al., 2014).

However, since paleoecological studies, like the current one, are based on fossil remains, it is not possible to use the methods applied by ecologists to study living animals. Alternatively, with the carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic composition of bone collagen, we can build trophic niches and reconstruct the diets of fossil canids (Ambrose, 1990; Bearhop et al., 2004; Bocherens and Drucker, 2013; Jackson et al., 2011; Layman et al., 2007; Warsen et al., 2014).

1.2. Principles of isotopic dietary tracking

For a better understanding of trophic relationships between members of a fossil community, we need reliable tracers of predator-prey relationships and we cannot rely exclusively on modern analogues. During the past three decades, carbon and nitrogen isotopic abundances measured in fossil bone collagen of different species from Pleistocene sites have provided such information (e.g. Bocherens (2015); Bocherens et al. (1997); Bocherens et al. (1991) Fox-Dobbs et al. (2008)). Isotopes from collagen, which comprises the organic fraction of bone, can provide information about the environment and the diet of an individual. Therefore, if collagen is preserved in archaeological bones, it is possible to reconstruct the paleoenvironment and the structure of the trophic system.

The studies of Ambrose and Norr (1993) and Tieszen and Fagre (1993) have shown that the δ^{13}C values in bone collagen are linked to the protein fraction of the diet. If all biochemical fractions (e.g. lipids, proteins and carbohydrates) come from an isotopically homogenous source, the $\delta^{13}C$ values in bone collagen are 5‰ higher than in the diet. This is generally the case for herbivores. For predators, the $\delta^{13}C$ values in bone collagen are 1‰ higher on average than in the collagen of their prey (Bocherens, 2003, 2015; Bocherens and Drucker, 2013). In contrast to $\delta^{13}C$, $\delta^{15}N$ values in the collagen increase 3–5‰, depending on the average diet. Therefore, these values are linked to the trophic level (Bocherens and Drucker, 2003; Krajcarz et al., 2018).

1.3. Principles of trophic niche modeling

In ecological studies, niches are complex systems with multiple variables that define a species' role in the ecological system (Araujo et al., 2011; Pocheville, 2015). One important model is the trophic niche, which has been used in several ecological and paleoecological studies (Araujo et al., 2011; Bassi et al., 2012; Hulme-Beaman et al., 2016; Kidawa and Kowalczyk, 2011; Morey and Jeger, 2017; Soe et al., 2017; Wikenros et al., 2017). This model defines the niches of species or even individuals by their position in the food web (Araujo et al., 2011; Bearhop et al., 2004; Higashi et al., 1992; Pocheville, 2015). In particular, studies that focus on dietary reconstructions using stable isotopes make use of this model (Bearhop et al., 2004; Bocherens, 2015; Bocherens et al., 1994, 1997, 2011, 2015; Bocherens and Drucker, 2003; Germonpré et al., 2009; Immel et al., 2015; Krajcarz et al., 2018; Wißing et al., 2016). Throughout this study, we use the term "niche" for a trophic niche.

Foxes and wolves are generalist predator/scavengers that occupy broad niches. If we build species-related niches for each individual, all the niches will strongly overlap, because individual food preferences can be very broad. This phenomenon has been recognized in other studies as well (Bocherens, 2015; Bocherens et al., 2011, 2015; Wißing et al., 2016). However, individuals in such broad niches can specialize under certain circumstances, and eventually build new, more specific, niches (Araujo et al., 2011; Sheppard et al., 2018; Svanbäck and Persson, 2004). We see something similar in modern carnivores that were influenced by human behavior (Poessel et al., 2017; Prange et al., 2004; Roth, 2003; Warsen et al., 2014; Yirga et al., 2012) or in invasive species (Dammhahn et al., 2017; Jackson and Britton, 2014). If individuals feed from the same sources, they occupy the same trophic niche and are competitors.

1.4. Aims and hypothesis

Stable isotope-based dietary reconstructions and the resulting trophic niche constructions can help to shed new light on these interactions between humans and canids. In this study, we focus on the analysis of $\delta^{13}C$ and $\delta^{15}N$ values from bone collagen, extracted from Magdalenian canids. We hypothesize that the niche partitioning of dogs, wolves and foxes is recognizable in the isospace. If this is the case, we should find the different taxa occupying niches with different diets. Additionally, we aim to determine whether commensal foxes are detectable through stable isotope analysis. We hypothesize that foxes might plot in the niches of dogs if they are commensal to humans or in the niche of wolves if they are commensal to large canids.

Though it is an important topic, within this study we will not discuss variability in the isotopic structure of living wild populations of the included species or the role of life history or body parts that we sampled. For our purposes, we only focus on the variability of the species and their niches in the Magdalenian environment based on published and newly analyzed isotopic data.

2. Material & methods

2.1. Study sites

This study examines faunal material from five archaeological sites in southwest Germany and Switzerland (Fig. 1). Three of these sites are located in the Swabian Jura: Geißenklösterle, Hohle Fels, and Vogelherd. Geißenklösterle Cave is part of a limestone massif located 60 m above the floor of the Ach Valley. It was first excavated in 1973 by Eberhard Wagner (Hahn, 1988) and final excavations at the site were undertaken from 2001 to 2002 by Nicholas Conard (Conard and Malina, 2003). Hohle Fels Cave is one of the largest caves in southwestern Germany. Theodor Hartmann and Oscar Fraas conducted the first excavations at the site between 1870 and 1871. Hohle Fels has a long history of excavation that includes work by Robert Rudolf Schmidt, Gustav Riek and Joachim Hahn. Since 1997, Nicholas Conard has been leading the annual excavations at Hohle Fels (Conard and Uerpmann, 1998; Conard et al., 1999; Conard and Malina, 2015; Conard and Wolf, 2014). Vogelherd Cave, located in the nearby Lone Valley, was discovered and completely excavated by Gustav Riek in 1931 over the course of three months (Riek, 1932, 1934). From 2005 to 2012 Nicholas Conard supervised a re-excavation of the backfill (Conard et al., 2008, 2010, 2013; Conard and Zeidi, 2011, 2012).

Following the Danube upriver, we find the two other sites of this study. The cave of Gnirshöhle is located in the Hegau region of Germany. From 1977 to 1979 Gerd Albrecht led excavations at the site (Albrecht, 2002; Albrecht et al., 1977). Finally, Kesslerloch Cave is located in Switzerland, near the German border and was excavated by Konrad Merk between 1873 and 1903 (Heierli, 1907; Merk, 1875; Nüesch, 1904).

2.2. Material

In this study, we used a database of 106 carbon and nitrogen stable isotopic values from Magdalenian herbivores and carnivores (Tables 1–4). Twelve of the values are unpublished and have been measured on bone collagen from the Magdalenian layers of Hohle Fels, Geißenklösterle, Gnirshöhle, Kesslerloch and Vogelherd (Table 1). The $\delta^{13}C$ and $\delta^{15}N$ values of herbivores were all taken from the literature (except for one newly analyzed hare sample). Forty-one of them came from the Magdalenian layers of Hohle Fels, Geißenklösterle and Kesslerloch (Table 3) as well as three additional canid carbon and nitrogen stable isotopic values (Table 2). Since Magdalenian sites in Central Europe were ecologically similar to those in Southwestern Germany and Northern Switzerland (Bocherens et al., 2011), we included 49 published $\delta^{13}C$ and $\delta^{15}N$ values from bone collagen of large and small herbivores and one $\delta^{13}C$ and $\delta^{15}N$ value from one canid from other parts of Central Europe to form a comprehensive isotopic dataset (Tables 2 and 4). For the purposes of the current study, we viewed the data from multiple sites over a large area and over a couple thousands of years as directly comparable and do not consider issues related to spatial or chronological, individual and intra and inter-population variability. In an ideal situation the record would help us to do so, but the current level of resolution does not allow this. The newly analyzed samples include red fox (*Vulpes vulpes*, n = 3), arctic fox (*Vulpes lagopus*, n = 1), hare (*Lepus* sp.; brown or arctic hare, n = 1), as well as specimens belonging to the genus *Canis* (wolf, *Canis lupus*, or dog, *Canis lupus familiaris*, n = 7). The fox species identifications of the samples from Hohle Fels, Geißenklösterle, Gnirshöhle and Vogelherd were based on metric and morphological comparisons with recent skeletons from several German zoological and zooarchaeological collections: Museum für Naturkunde (Berlin), Staatliches Museum für Naturkunde Stuttgart,

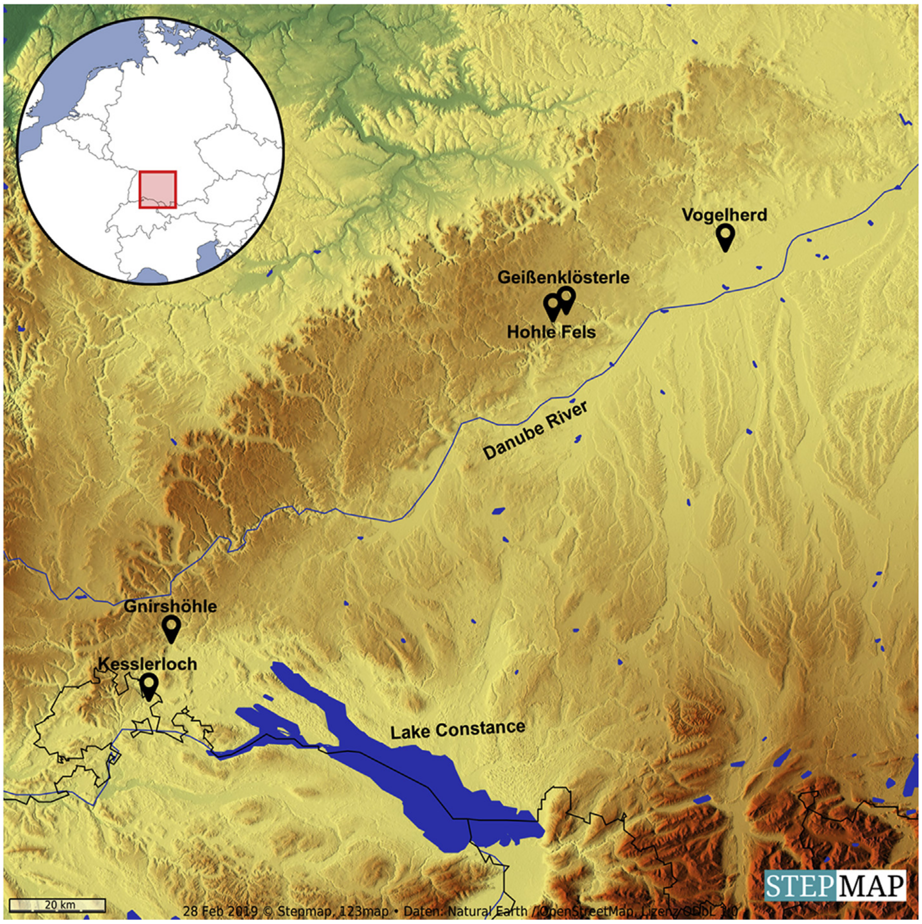

Fig. 1. Location map of studied sites.

Table 1
List of newly analyzed isotopic values reported in this study. GH = Geological horizon, AH = Archaeological horizon.

Lab ID	Location	Excav. No	GH	AH	Taxon	Skeleton element	N_{bone} [%]	yield [mg/g]	C_{coll} [%]	N_{coll} [%]	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	δ^{15}Ncoll [‰]
JK2177	Hohle Fels	HF 59/912	3AD	IIAD	*Canis lupus*	Tibia	3.3	148.3	41.5	14.6	3.3	−19.0	8.9
PLC-21	Gnirshöhle	Gn2 P/22-171			*Vulpes vulpes*	Femur	1.7	65.9	40.1	14.0	3.3	−20.6	4.5
PLC-12	Vogelherd	Vg III 17185		III	*Vulpes vulpes*	Ulna	3.0	147.5	42.6	14.8	3.3	−19.7	8.2
VLP-6	Geißenklösterle	GK 78/17	GH 2	AH Io	*Vulpes vulpes*	Tibia	2.5	53.2	43.2	14.8	3.4	−20.6	5.1
VLP-8	Hohle Fels	HF 56/211	GH 0c	AH 0	*Vulpes lagopus*	Tibia	3.1	111.4	43.6	15.3	3.3	−20.6	5.3
VLP-15	Geißenklösterle	GK 76/76	GH 2b	AHIo	*Lepus* sp.	Tibia	2.9	116.4	43.5	15.2	3.3	−20.8	1.9
JK2176	Hohle Fels	HF 55/1250.1	-3B	-IIB	*Canis lupus*	Metacarpus II	3.7	169.4	41.6	14.7	3.3	−19.6	8.6
JK2179	Hohle Fels	HF 55/1250.2	-3B	-IIB	*Canis lupus*	Carpus	3.8	173.5	39.9	14.2	3.3	−19.5	9.1
JK2181	Hohle Fels	HF 100/530	3B	IIB	*Canis lupus*	Cranium	3.3	147.1	40.9	14.6	3.3	−19.4	7.4
KLS-44	Kesslerloch	M001:189			*Canis l. familiaris*	Palatinum	1.8	73.0	38.9	13.8	3.3	−19.2	5.9
M 58	Kesslerloch	M001:58			*Canis lupus*	Mandibula			29.0	9.8	3.5	−20.1	7.1
M 62	Kesslerloch	M001:62			*Canis lupus*	Maxilla			45.4	15.7	3.4	−20.0	7.9

Table 2
Isotopic values of Magdalenian canids from Kesslerloch and Schussenquelle, taken from Bocherens et al. (2011).

Lab ID	Location	Taxon	Reference	C/Ncoll	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
KSL-13	Kesslerloch	*Canis lupus*	Bocherens et al. (2011)	3.4	−19.0	5.7
KSL-14	Kesslerloch	*Canis lupus*	Bocherens et al. (2011)	3.4	−19.1	6.4
SCH-11	Schussenquelle	*Canis lupus*	Bocherens et al. (2011)	4.2	−20.3	5.8
KSL-17	Kesslerloch	*Vulpes vulpes*	Bocherens et al. (2011)	3.3	−19.6	4.7

Zentralmagazin für Naturwissenschaftliche Sammlungen (Halle) and the zoological and zooarchaeological collections at the University of Tübingen, in addition to published metric data (Degerbøl, 1933; Germonpré and Sablin, 2004; Street and Turner, 2013).

All of the canid samples (i.e. the seven newly analyzed ones as well as the three from Bocherens et al. (2011)) were previously part of morphometric, isotopic, or genetic studies (Bocherens et al., 2011; Napierala, 2008; Napierala and Uerpmann, 2012; Thalmann

Table 3
Isotopic values of Magdalenian herbivores from the sites Hohle Fels, Geißenklösterle and Kesselerloch, taken from the literature.

Lab ID	Location	Taxon	Reference	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
KSL-10	Kesslerloch	*Bison* sp.	Bocherens et al. (2011)	3.4	−19.8	2.2
KSL-11	Kesslerloch	*Bison* sp.	Bocherens et al. (2011)	3.3	−20.0	2.4
KSL-12	Kesslerloch	*Bison* sp.	Bocherens et al. (2011)	3.2	−20.3	2.3
KSL-45	Kesslerloch	*Cervus elaphus*	Bocherens et al. (2011)	3.4	−20.2	2.0
KSL-7	Kesslerloch	*Coeolodonta antiquitatis*	Bocherens et al. (2011)	3.3	−19.9	2.1
KSL-1	Kesslerloch	*Equus ferus*	Bocherens et al. (2011)	3.4	−20.6	1.3
KSL-2	Kesslerloch	*Equus ferus*	Bocherens et al. (2011)	3.4	−20.4	1.6
KSL-3	Kesslerloch	*Equus ferus*	Bocherens et al. (2011)	3.4	−20.2	2.3
KSL-4	Kesslerloch	*Equus ferus*	Bocherens et al. (2011)	3.4	−20.3	0.6
KSL-5	Kesslerloch	*Equus ferus*	Bocherens et al. (2011)	3.4	−20.0	1.7
KSL-19	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.1	−20.8	0.9
KSL-20	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.2	−20.2	0.7
KSL-22	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.3	−20.8	0.5
KSL-23	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.0	−21.4	0.2
KSL-24	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.0	−20.6	0.3
KSL-25	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.3	−20.4	2.3
KSL-26	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.0	−19.7	1.3
KSL-27	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.4	−20.2	0.4
KSL-28	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.3	−20.4	0.6
KSL-29	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.1	−20.5	1.1
KSL-30	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.1	−20.2	0.5
KSL-31	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.0	−20.1	1.9
KSL-32	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.1	−20.4	1.0
KSL-33	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.0	−20.3	1.6
KSL-34	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	2.9	−20.2	0.9
KSL-35	Kesslerloch	*Lepus timidus*	Bocherens et al. (2011)	3.3	−20.9	1.5
KSL-6	Kesslerloch	*Mammuthus primigenius*	Bocherens et al. (2011)	3.3	−21.3	5.0
KSL-47	Kesslerloch	*Mammuthus primigenius*	Bocherens et al. (2011)	3.2	−20.5	6.4
HF-15	Hohle Fels	*Megaloceros giganteus*	Immel et al. (2015)	3.3	−20.1	2.9
OxA-6254	Geißenklösterle	*Rangifer tarandus*	Stevens and Hedges (2004)	3.0	−19.4	0.1
GSK-1	Geißenklösterle	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−19.6	2.0
HFL-1	Hohle Fels	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−19.4	1.0
RA-KSL-620	Kesslerloch	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.1	2.4
RA-KSL-628	Kesslerloch	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.9	2.6
RA-KSL-632	Kesslerloch	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.8	2.7
RA-KSL-633	Kesslerloch	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−20.3	2.9
RA-KSL-635	Kesslerloch	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.9	2.8
KSL-37	Kesslerloch	*Spermophilus major*	Bocherens et al. (2011)	3.5	−20.9	1.7
KSL-38	Kesslerloch	*Spermophilus major*	Bocherens et al. (2011)	3.3	−20.3	2.0
KSL-39	Kesslerloch	*Spermophilus major*	Bocherens et al. (2011)	3.3	−21.0	2.5
KSL-40	Kesslerloch	*Spermophilus major*	Bocherens et al. (2011)	3.4	−20.8	2.2

et al., 2013). To interpret the trophic niches of dog and wolf, it is necessary to distinguish between them and we present in the following paragraphs the different specimens and the features that allow us to categorize them as dog or wolf. From Kesslerloch, a maxilla fragment (Excavation-No.: M001/189; Lab ID: KSL-44) was morphologically and metrically studied by Napierala (2008) and Napierala and Uerpmann (2012). In both studies, it was identified as a dog. The main argument for this identification was the morphology of the protocone in the fourth upper premolar (P^4). Unlike wolves, which have a protocone that is oriented towards the mesial side of the tooth, the protocone of M001/189 is set farther back distally. Another argument that Napierala and Uerpmann (2012) used to support M001/189 being assigned to dog, was that the carnassial is shorter than all other measured wolf specimens; M001/189 is outside the range of any known European wolf populations (Napierala, 2008; Napierala and Uerpmann, 2012). Another maxilla fragment in our study (Excavation-No.: M001/62, Lab ID: M 62) was assigned to wolf by Napierala (2008) based on the metrics of the upper P^4 and M^1. Additionally, Thalmann et al. (2013) analyzed the mitochondrial DNA (mtDNA) of M001/62 and also determined that it is a wolf based on its position in the reconstructed maximum likelihood tree. M001/58 (Lab ID: M 58) is a mandible fragment and was genetically identified as wolf by Thalmann et al. (2013). Further, morphological and metrical traits of the first lower molar (M_1) of this specimen are similar to other wolves (Napierala, 2008). We included HE24/43 (Lab ID: KSL-13) and HE24/58 (Lab ID: KSL-14) in this study as well, data from both came from Bocherens et al. (2011). Both samples are postcranial elements (HE24/43 is a radius and HE24/58 is a third metatarsal) and were treated as wolves. However, Napierala (2008), who reanalyzed the old excavation materials from Kesslerloch, did not include these two samples in the list of measurable elements. Therefore, it is not certain that these specimens are indeed wolf.

From Hohle Fels, we included the isotopic data of four samples, all of which are part of a genetic study (Feuerborn, unpublished data). The specimens HF 59/912 (Lab ID: JK2177, tibia), HF 55/1250 (Lab ID: JK2176, metacarpal II) and HF 55/1250 (Lab ID: JK2179, carpal bone) were morphologically and metrically identified by Susanne Münzel as wolf. The genetic analysis of Feuerborn confirmed that these individuals are wolves. HF 100/530 (Lab ID: JK2181, maxilla) was morphometrically analyzed by Camarós et al. (2016) and dated to the Gravettian because of the archaeological layer. New, unpublished radiocarbon data, however, date the specimen to the Magdalenian (personal communication with Verena Schünemann). The maxilla was found to be more wolf-like based on the metrical traits of the teeth but more dog-like in morphological features. For example, the P^4 protocone is located farther back distally and orientated differently than in wolves. However, the first upper molar (M^1) shows some wolf characteristics. Camarós et al. (2016) interpreted it as a mixture of

Table 4
Isotopic values of Magdalenian herbivores from different sites of western Central Europe, taken from the literature.

Lab ID	Location	Taxon	Reference	C/N_{coll}	$\delta^{13}C_{coll}$ [‰]	$\delta^{15}N_{coll}$ [‰]
SCH-6	Schussenquelle	*Alces alces*	Bocherens et al. (2011)	3.4	−20.2	3.0
SCH-7	Schussenquelle	*Alces alces*	Bocherens et al. (2011)	3.4	−19.8	2.9
BVN-9(2)	Bavans	*Cervus elaphus*	Bocherens et al. (2011)	3.2	−20.8	2.1
RCD500	Rochedane	*Cervus elaphus*	Drucker et al., 2011a	3.2	−19.9	0.8
RCD10900	Rochedane	*Cervus elaphus*	Drucker et al., 2011a	3.0	−20.4	2.0
RCD11000	Rochedane	*Cervus elaphus*	Drucker et al., 2011a	3.2	−20.6	2.4
ARL-1	Grotte de Chaze II	*Coeolodonta antiquitatis*	Bocherens et al. (2011)	3.1	−20.3	5.3
CHM-2	Champréveyres	*Equus ferus*	Bocherens et al. (2011)	3.0	−19.8	1.6
CHM-4	Champréveyres	*Equus ferus*	Bocherens et al. (2011)	3.0	−20.1	1.5
MRZ-1	Monruz	*Equus ferus*	Bocherens et al. (2011)	3.1	−20.4	1.3
MRZ-2	Monruz	*Equus ferus*	Bocherens et al. (2011)	3.2	−20.6	2.1
ZUG-1	Risch-Rotkreuz	*Mammuthus primigenius*	Drucker et al. (2018)	3.3	−21.1	6.2
HST-28	Hohlenstein Stadel	*Megaloceros giganteus*	Immel et al. (2015)	3.4	−20.7	2.2
TUB-57	Buttentalhöhle	*Rangifer tarandus*	Bocherens et al. (2011)	3.3	−19.7	1.7
FLS-7	Fellställe	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.8	2.1
FLS-8	Fellställe	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.3	2.2
FLS-9	Fellställe	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−20.2	2.1
FRT 1	Grotte de la Baume Noire	*Rangifer tarandus*	Bocherens et al. (2011)	3.3	−19.5	3.7
BLS 1	Grotte du Chaumois-Boivin	*Rangifer tarandus*	Bocherens et al. (2011)	3.3	−19.5	2.4
ARL 6	Grotte Grappin	*Rangifer tarandus*	Bocherens et al. (2011)	3.1	−19.1	2.8
RA-PTF 363	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.8	2.4
RA-PTF 364	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.6	2.1
RA-PTF 365	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.9	2.3
RA-PTF 366	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.2	−20.0	1.2
RA-PTF 367	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.2	−19.9	1.2
RA-PTF 368	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.4	2.4
RA-PTF 369	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−20.2	2.6
RA-PTF 370	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.1	2.3
RA-PTF 371	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.5	−19.7	2.1
RA-PTF 373	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.7	2.5
RA-PTF 374	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.7	1.4
RA-PTF 375	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−20.0	3.3
RA-PTF 376	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.7	2.4
RA-PTF 377	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.9	2.0
RA-PTF 379	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.5	−19.5	2.6
RA-PTF 380	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.6	−19.6	2.4
RA-PTF 381	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.6	−19.3	2.3
RA-PTF 382	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.1	1.9
RA-PTF 383	Petersfels	*Rangifer tarandus*	Drucker et al., 2011b	3.6	−19.4	2.9
RAN-10	Ranchot	*Rangifer tarandus*	Bocherens et al. (2011)	3.0	−19.1	3.9
RCD100	Rochedane (D1)	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−19.3	1.7
RCD200	Rochedane (D1)	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−19.7	2.7
RCD400	Rochedane (D1)	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−19.5	1.3
RCD10800	Rochedane (D1)	*Rangifer tarandus*	Bocherens et al. (2011)	3.2	−20.3	2.1
SCH-1	Schussenquelle	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−19.8	2.5
SCH-2	Schussenquelle	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.7	2.8
SCH-3	Schussenquelle	*Rangifer tarandus*	Drucker et al., 2011b	3.4	−20.1	1.8
SCH-4	Schussenquelle	*Rangifer tarandus*	Drucker et al., 2011b	3.3	−19.4	1.9
SCH-5	Schussenquelle	*Rangifer tarandus*	Drucker et al., 2011b	3.5	−19.5	2.2

morphological features of wolf and dog. The results from Feuerborn were not entirely clear, however, she tended more towards wolf rather than dog.

Finally, we included one sample from Schussenquelle, for which isotopic data were taken from Bocherens et al. (2011). This femur fragment (Excavation-No.: 4829.4, lab ID: SCH-11) was identified as wolf by Schuler (1994) based on morphological traits.

2.3. Isotopic analysis

For the isotopic analysis, we cut small samples (0.3–0.7 g) from the bones using a Saeshin Forte 200 alpha micro-circular saw. After successive cleaning in Millipore water and acetone, we ground the samples to powder manually (grain size less than 0.7 mm). To evaluate how much collagen was still present in the samples, we performed a CNS elemental analysis of the bone samples following Bocherens et al. (2005a). For most samples, this analysis was performed at the Laboratory for Soil Science and Geoecology (University of Tübingen) using a Vario EL III elemental analyzer. However, for JK and PLC samples ($n = 7$), elemental measurements were done at the Hydrogeochemisty department (University of Tübingen) using the Vario EL elemental analyzer. Sulfanilic acid from Merck was used as the international standard in both laboratories.

Collagen extraction followed the protocol of Bocherens et al. (1997) and was performed in the laboratory of the Biogeology working group (University of Tübingen). Depending on the percentage of nitrogen in the bone powder ($\%N_{bone}$) of each sample, as measured by the CNS analysis, we used 120 mg (4.0–4.5$\%N_{bone}$) to 450 mg (0.4–1.0$\%N_{bone}$) of bone powder for the extraction. The collagen extraction process included a step of soaking the bone powder in 0.125 M NaOH between the demineralization and solubilization steps to achieve the elimination of lipids and humic acids. After this, the samples were freeze-dried.

The isotopic measurements of collagen for the VLP, KSL and M samples ($n = 6$) were performed at the Geochemical department of the University of Tübingen, using an elemental analyzer NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. While the isotopic measurements for JK and PLC samples (n = 7) were undertaken at the Laboratory of Chronology (Finnish Museum of Natural History), using an NC 2500 elemental analyzer coupled to a Thermo Delta V Plus isotope ratio mass spectrometer.

The isotopic ratios are expressed using the δ (delta) value as follows:

$$\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{reference} - 1] \times 1000\ (‰)$$
$$\delta^{15}N = [(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{reference} - 1] \times 1000\ (‰)$$

We used the international references V-PDB for $\delta^{13}C$ values and atmospheric nitrogen (AIR) for $\delta^{15}N$ values. The samples measured in Tübingen were calibrated to $\delta^{13}C$ values of USGS-24 ($\delta^{13}C = -16.0‰$) and to $\delta^{15}N$ values of IAEA-305A ($\delta^{15}N = 39.8‰$). Reproducibility was ±0.1‰ for $\delta^{13}C$ measurements and ±0.2‰ for $\delta^{15}N$ measurements, based on multiple analyses of purified collagen from modern bones. For the samples analyzed in Helsinki, the international reference materials USGS-40 ($\delta^{13}C = -26.8‰$, $\delta^{15}N = -4.7‰$) and USGS-41 ($\delta^{13}C = +36.1‰$, $\delta^{15}N = +46.7‰$) were used for calibration. Based on multiple measurements of matrix matched in-house reference materials, the reproducibility was ±0.19‰ for $\delta^{13}C$, ±0.24‰ for $\delta^{15}N$ values. The reproducibility error for the amounts of C and N was lower than 4% in both laboratories. According to DeNiro (1985) and Ambrose (1990), we only used collagen samples with an atomic carbon-to-nitrogen-ratio (C/N_{coll}) between 2.9 and 3.6 and a percentage of nitrogen higher than 5% for palaeoecological interpretations.

2.4. Niche modeling and diet reconstruction

To reconstruct the niches of the Magdalenian canids in this study, we first applied a multivariate cluster analysis to the $\delta^{13}C$ and $\delta^{15}N$ isotopic values in JMP 14. As a result, we obtained three different clusters that were not dependent on species determination; instead, they depended exclusively on the individual trophic source that is reflected by carbon and nitrogen isotopes. We then used SIBER (Stable Isotope Bayesian Ellipses in R) to calibrate the niches out of the clusters (Jackson et al., 2011). With this R package, it was possible to reconstruct the complete niches (= convex hull, Layman et al. (2007)) and the core niches (= standard ellipse area, Jackson et al. (2011)) of the canid communities. The complete niche includes all individuals of a niche, but is quite sensitive to sample size. In contrast, the core niche depicts the center of a niche that is calculated by using most likelihood estimation and Bayesian statistics (Jackson et al., 2011). It is more reliable for analyzing small sample sizes.

For dietary reconstructions, it was necessary to combine single prey species into larger groups with clearer isotopic differences (e.g. minimum and maximum values of $\delta^{13}C$ and $\delta^{15}N$). If we would use every species as its own group, the overlapping zone among species would be too large and the statistics program MixSIAR (see below) could not work effectively. Therefore, we built three source groups, all of which are herbivores, taken from literature (Tables 3 and 4): “Megaherbivores,” “Ungulates,” and “Small mammals.” The “Megaherbivore” group includes only mammoth (*Mammuthus primigenius*, n = 3) isotopic values. The “Ungulates” group includes isotopic values from elk (*Alces alces*, n = 2), bison (*Bison* sp., n = 3), red deer (*Cervus elaphus*, n = 5), woolly rhinoceros (*Coeolodonta antiquitatis*, n = 2), horse (*Equus ferus*, n = 10), giant deer (*Megaloceros giganteus*, n = 2) and reindeer (*Rangifer tarandus*, n = 44). Finally, the “Small mammals” group includes isotopic values from ground squirrel (*Spermophilus major*, n = 4), hare (*Lepus* sp., n = 17), including the newly analyzed hare sample from this study.

To reconstruct the proportions of different prey group in the protein fraction of the Magdalenian canid diet, we used MixSIAR (Bayesian Mixing Models in R, Stock and Semmens (2016)). The calculations of this package are based on a Bayesian statistical approach. This Bayesian approach is quite robust for small sample sizes ($n < 20$) (Inger et al., 2010). Initially, such R packages (SIAR, MixSIAR) were designed for ecologists who work with recent ecosystems and food chains but the model has been subsequently successfully applied to archaeological contexts (e.g. Bocherens et al. (2015); Wißing et al. (2019); Wißing et al. (2016)). MixSIAR allowed us to reconstruct the most likely diet of the carnivores based on the nitrogen and carbonate isotopes from their bone collagen relative to isotope values from prey species. In order to use MixSIAR, it was essential to establish distinct prey sources as well as comparative TEF (Trophic Enrichment Factor) values. TEF values reflect the enrichment of nitrogen and carbon in collagen. The stable isotope composition of a predator differs from the composition of its prey in a predictable manner. The TEFs correspond to the difference between the stable isotope ratios of the consumer (predator collagen) and its diet (prey collagen) and are the result of the discrimination of stable isotopes due to the behavior and physiology of the consumer (Bocherens et al., 2015; Dionne et al., 2016; Krajcarz et al., 2018). For this study, we used TEF values ($\Delta 13C = 1.1 \pm 1.1‰$; $\Delta^{15}N = 3.2 \pm 1.8‰$) from a study on modern fox by Krajcarz et al. (2018). To get a robust statistical analysis, we set the MCMC (Markov Chain Monte Carlo, see Stock and Semmens (2016)) chain length to 1,000,000 with a burn-in of 500,000 in 3 chains. We verified the model convergence with Gelman-Rubin and Geweke tests. The Gelman-Rubin test shows model convergence if the values are near 1. In most analyses, values below 1.1 are acceptable (Gelman et al., 2014). Additionally, the Geweke test compares the mean of the first part of each chain with the mean of the second part, using a two-sided z-test. If both means are the same, the model is convergent (Stock and Semmens, 2016).

3. Results

3.1. Elemental and isotopic analysis

The $\%N_{bone}$ values measured on the 12 samples we analyzed in this study confirmed the favorable conditions of preservation (1.7–3.8%), establishing quantitatively that collagen is preserved in the samples. Moreover, the atomic C/N_{coll} ratios of all analyzed extracts (3.3–3.5) determined that the preservation of collagen was appropriate for the interpretation of the isotopic analysis (Table 1).

Among the isotopic values, we found a clear difference between foxes (red and arctic fox), wolves and dogs. Both fox species had $\delta^{13}C$ values of −20.6‰ and their $\delta^{15}N$ values ranged from +4.5 to +5.3‰. The only exception was PLC-12, with higher values in both isotopes ($\delta^{13}C = -19.7‰$ and $\delta^{15}N = +8.2‰$). This fox fell within the range of the wolves ($\delta^{13}C = -20.1$ to −19.0‰ and $\delta^{15}N = +7.1$ to +9.1‰). The $\delta^{13}C$ and $\delta^{15}N$ values of the analyzed dog fragments were −19.2‰ and 5.9‰, respectively.

3.2. Niche modeling and diet reconstruction

Using the isotopic values of the herbivores, we calculated three main niches of potential prey: megaherbivores, ungulates and small mammals (Fig. 2). While the groups of ungulates and small mammals overlap in their complete niches (= convex hull, Layman et al. (2007)), the core niches (= standard ellipse area, Jackson et al. (2011)) do not overlap. Therefore, we used these prey sources for dietary reconstructions by MixSIAR. For canids we calculated three niches as well (Fig. 3). Six wolves (from Kesslerloch and Hohle Fels) and one red fox (from Vogelherd) matched the first niche (Niche A), which shows a range of $\delta^{13}C$ values from −20.1 to −19.0‰ and a range of $\delta^{15}N$ value from +7.1 to +9.1‰. The second niche (Niche B)

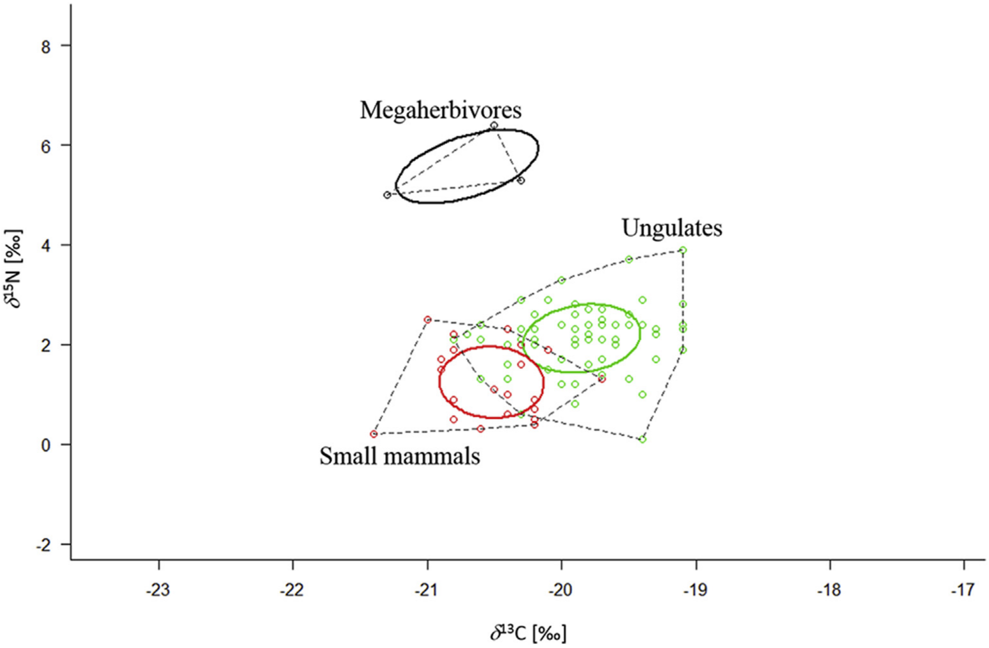

Fig. 2. Diet sources calculated with SIBER. Megaherbivores includes only mammoth (n = 3). Ungulates (n = 68) includes elk, bison, red deer, woolly rhinoceros, horse, giant deer and reindeer. Small mammal (n = 21) includes hare and ground squirrel. Dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of one group (Layman et al., 2007). Solid line shows the Bayesian based Standard Ellipse Area (SEA), which reflects the core niche (Jackson et al., 2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

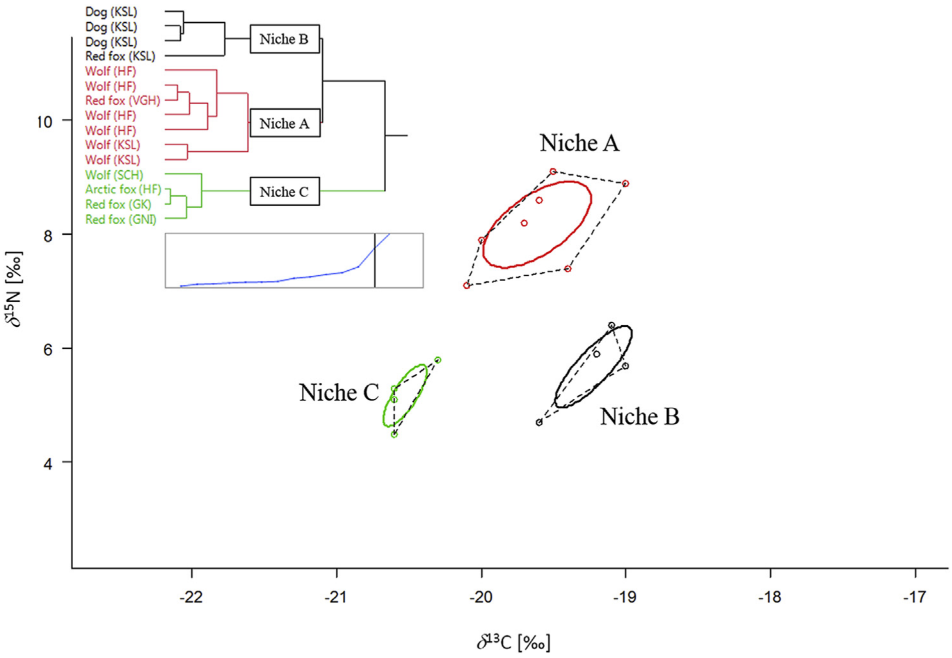

Fig. 3. Canid niches calculated with SIBER and cluster analysis. Cluster analysis shows three different niches, regarding δ^{13}C andδ^{15}N values. Niche A includes six wolves and one red fox. Niche B includes four potential dogs and one red fox. Niche C includes one wolf, one arctic fox and two red foxes. Dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of one niche (Layman et al., 2007). Solid line shows the Bayesian based Standard Ellipse Area (SEA), which reflects the core niche (Jackson et al., 2011). Abbreviations of the archaeological sites: GK = Geißenklösterle, GNI = Gnirshöhle, HF = Hohle Fels, KSL = Kesslerloch, SCH = Schussenquelle, VGH = Vogelherd. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

includes three probable dogs (from Kesslerloch) and one red fox (from Kesslerloch). The isotopic values of this niche range from −19.6 to −19.0‰ in δ^{13}C and from +4.7 to +6.1‰ in δ^{15}N. Finally, the third niche (Niche C) includes one wolf (from Schussenquelle), one arctic fox (from Hohle Fels) and two red foxes (from Geißenklösterle and Gnirshöhle). This niche has δ^{13}C values between −20.6 and −20.3‰ and δ^{15}N values from +4.5 to +5.8‰.

The MixSIAR calculated model for diet reconstructions showed convergence in both tests. Both diagnostics tested 50 variables of the model. In the Gelman-Rubin test, ten of these variables were higher than 1.01, but no variable was higher than 1.1. Additionally, the Geweke diagnostic revealed only one unequal variable in chain 1, five unequal variables in chain 2 and three unequal variables in chain 3 out of 50. Therefore, the calculated model is useable for the diet reconstruction. We reconstructed the percentages of the three different diet sources for each niche and for each species in the niches (Table 5, Figs. 4–6). The dietary preferences of individuals varied strongly between the niches. Individuals of niche A had a strong preference for megaherbivores. Animals in niche B fed on small mammals as much as on large mammals (ungulates and megaherbivores) and individuals in niche C had a high preference for small mammals.

4. Discussion

Based on our results, we can divide the samples into three predatory niches (see Fig. 7). For the most part, the niches are comprised of members of a specific taxon, which is reflected in the niche names. In all cases, there is at least one sample that does not match the niche name, which we expand upon below.

4.1. Niche A: the "wolf" niche

Niche A is formed by six morphologically and genetically identified wolves and one red fox. Two wolves came from Kesslerloch and four from Hohle Fels. The red fox comes from Vogelherd and will be discussed in section 4.3. Carbon and nitrogen isotopic abundances of sample HF 100/530 (Lab ID: JK2181) from Hohle Fels (which was morphologically ambiguous as dog or wolf (Camarós et al., 2016)), also match this niche. Therefore, we consider that this canid is probably a wolf.

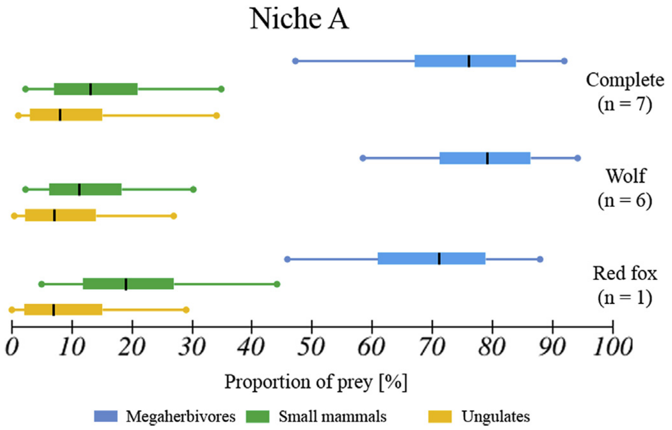

Fig. 4. Diet proportions calculated with MixSIAR of complete niche A and the included species. Colored lines of the box plots show the 5–95% confidence interval, full boxes show the 25–75% confidence interval and the black line shows the median value.

The main protein component of wolf diets were megaherbivores, with a mean percentage of 74 ± 15% for the complete niche and 78 ± 11% for the wolves within this niche (Fig. 4). However, in the faunal assemblage of the Magdalenian layers, mammoths are very rare. The Hohle Fels layers AH 0-IIa contain only 28 specimens that belong to mammoth or mammoth-rhino size class, which corresponds to less than 1% of the faunal remains (Napierala et al., 2014). A similar situation is found in the Kesslerloch faunal material (Napierala, 2008). Moreover, in Geißenklösterle (Münzel,

Table 5
Reconstructed dietary proportions for the different niches, including the diet reconstruction for the individual species in the niches. The probability of each proportion is given with the mean ± SD, 2.5%, 5%, 25%, 50%, 75%, 95% and 97.5%.

Taxon	Number of individuals	Source	Mean ± SD	2.5%	5%	25%	50%	75%	95%	97.5%
Niche A complete	n = 7	Megaherbivores	74 ± 15%	35%	47%	67%	76%	84%	92%	94%
		Small mammals	15 ± 11%	2%	2%	7%	13%	21%	35%	41%
		Ungulates	11 ± 11%	0%	1%	3%	8%	15%	34%	43%
Wolf	n = 6	Megaherbivores	78 ± 11%	54%	58%	71%	79%	86%	94%	96%
		Small mammals	13 ± 9%	1%	2%	6%	11%	18%	30%	34%
		Ungulates	9 ± 9%	0%	0%	2%	7%	14%	27%	32%
Red fox	n = 1	Megaherbivores	69 ± 14%	38%	46%	61%	71%	79%	88%	91%
		Small mammals	21 ± 13%	3%	5%	12%	19%	27%	44%	51%
		Ungulates	10 ± 10%	0%	0%	2%	7%	15%	29%	36%
Niche B complete	n = 4	Megaherbivores	29 ± 11%	10%	13%	21%	27%	34%	49%	57%
		Small mammals	50 ± 16%	14%	21%	40%	51%	62%	75%	80%
		Ungulates	21 ± 16%	1%	2%	9%	18%	31%	51%	57%
Wolf/dog	n = 2	Megaherbivores	27 ± 11%	5%	10%	21%	27%	34%	44%	49%
		Small mammals	47 ± 19%	3%	10%	35%	49%	61%	74%	78%
		Ungulates	26 ± 21%	1%	1%	9%	22%	38%	68%	80%
Dog	n = 1	Megaherbivores	27 ± 11%	6%	11%	21%	27%	34%	45%	49%
		Small mammals	48 ± 18%	7%	15%	37%	49%	61%	75%	80%
		Ungulates	25 ± 20%	1%	1%	9%	21%	36%	61%	73%
Red fox	n = 1	Megaherbivores	22 ± 10%	6%	9%	16%	21%	28%	39%	44%
		Small mammals	61 ± 17%	22%	28%	50%	62%	73%	85%	88%
		Ungulates	17 ± 15%	0%	1%	5%	13%	26%	48%	57%
Niche C complete	n = 4	Megaherbivores	17 ± 14%	2%	3%	7%	13%	21%	42%	57%
		Small mammals	73 ± 19%	15%	30%	67%	78%	86%	94%	96%
		Ungulates	10 ± 13%	0%	1%	2%	5%	12%	36%	50%
Wolf	n = 1	Megaherbivores	20 ± 17%	2%	3%	9%	16%	27%	53%	68%
		Small mammals	70 ± 21%	7%	25%	62%	75%	85%	94%	96%
		Ungulates	10 ± 13%	0%	0%	2%	5%	12%	36%	49%
Arctic fox	n = 1	Megaherbivores	15 ± 15%	0%	1%	6%	12%	20%	41%	60%
		Small mammals	76 ± 20%	9%	31%	69%	80%	89%	97%	98%
		Ungulates	9 ± 14%	0%	0%	2%	5%	11%	33%	49%
Red fox	n = 2	Megaherbivores	12 ± 13%	1%	2%	5%	9%	15%	30%	49%
		Small mammals	81 ± 17%	25%	50%	76%	85%	91%	96%	98%
		Ungulates	7 ± 11%	0%	0%	1%	4%	9%	23%	36%

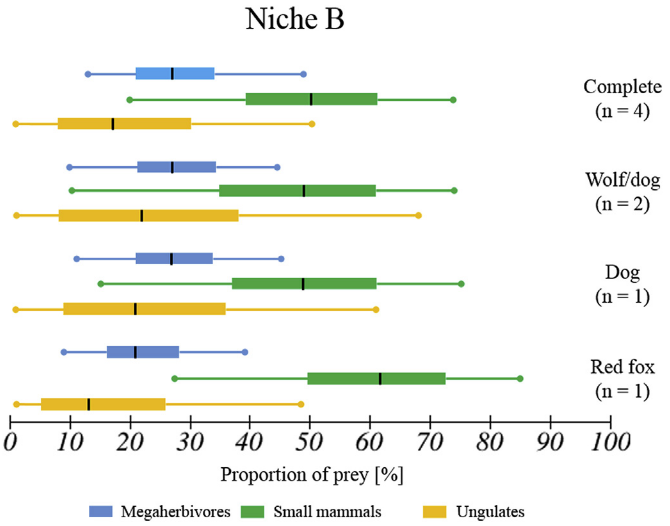

Fig. 5. Diet proportions calculated with MixSIAR of complete niche B and the included species. Colored lines of the box plots show the 5–95% confidence interval, full boxes show the 25–75% confidence interval and the black line shows the median value.

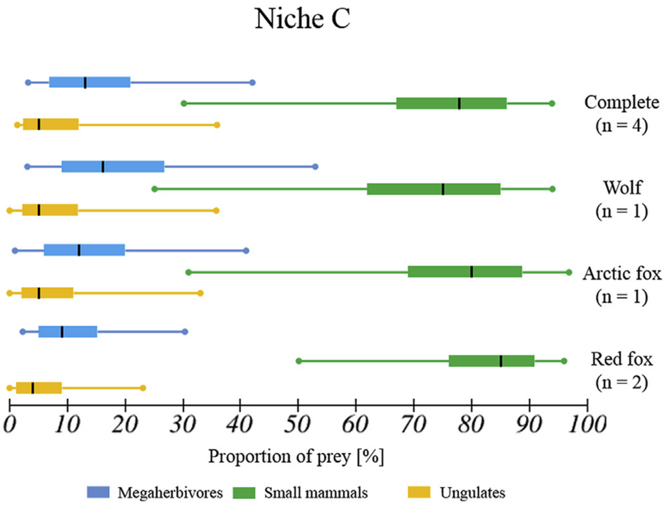

Fig. 6. Diet proportions calculated with MixSIAR of complete niche C and the included species. Colored lines of the box plots show the 5–95% confidence interval, full boxes show the 25–75% confidence interval and the black line shows the median value.

2019) and Gnirshöhle (Münzel, unpublished data), no mammoth remains were found. Vogelherd Cave preserves 39 mammoth specimens in the Magdalenian layers (13 from AH II and 26 from AH III). Proportionally, mammoth comprises 8% and 46% of the assemblages, respectively, but this is because the Magdalenian sample sizes are small. In addition to this, Conard et al. (2003) dated some of the mammoths and found a much older date than expected for the Magdalenian (35,610 ± 511 and 30,832 ± 392 cal BP). Niven (2006) assumed that these dates belong to mixed archaeological layers (Magdalenian and older) or that ancient mammoth bones were collected and brought back to the site by Magdalenian people. It is possible, therefore, that during this phase, the occupants of Vogelherd were consuming even less mammoth than we originally thought.

Since the measured nitrogen values of bone collagen represent on average several years of life of an individual (Bocherens et al., 1997; Bocherens and Drucker, 2003; Krajcarz et al., 2018), the high $\delta^{15}N$ values of the individuals in niche A can only be explained by permanent access to prey with high nitrogen values. In the database of Central European Magdalenian carbon and nitrogen stable isotopic values, only mammoth showed such high values. It cannot be excluded that there were either more mammoths or mammoth carcasses on the landscape during the Magdalenian than indicated based on the zooarchaeological record, or that there was another prey type that had the same high nitrogen levels but has not yet been sampled. For example, it is possible that juvenile herbivores have altered carbon and nitrogen values due to the ingestion of milk from their mothers. This has been shown to be the case in both brown and cave bears (Bocherens et al., 2004; Pérez-Rama et al., 2011).

In contrast to other Magdalenian carnivores (see, e.g. Bocherens et al. (2011) and supplementary data), the “wolf” niche has the highest $\delta^{15}N$ values. Bocherens et al. (2011) and Bocherens (2015) argued that, during the Aurignacian, wolves, hyenas (*Crocuta crocuta spelaea)*, brown bears (*Ursus arctos*) and cave lions (*Panthera leo spelaea*) were in competition. As a result, wolves showed lower $\delta^{15}N$ values because they had less access to prey with high $\delta^{15}N$ values (i.e., mammoth) compared to hyenas. Aurignacian wolves preferred ungulates that include chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*) and giant deer (*Megaloceros giganteus*) as dietary resources (Bocherens, 2015). After the LGM, no hyenas were recognized in Europe and carnivore niches changed (Bocherens, 2015; Varela et al., 2010). Consequently, wolves gained access to different kinds of prey, even those with high $\delta^{15}N$ values, which is reflected in their own high nitrogen values (Bocherens, 2015; Bocherens et al., 2011). However, cave lions were restricted to prey with higher $\delta^{13}C$ values, but lower $\delta^{15}N$ values (i.e., reindeer). The newly analyzed wolf samples fit this model. In contrast to the Aurignacian, the diets of Magdalenian wolves included a mean percentage lower than 11 ± 11% of ungulates (e.g. reindeer, red deer and giant deer). Additionally, we recognized a minor contribution of small mammals (e.g., hares and ground squirrels) in their diet, with a mean percentage lower than 15 ± 11%.

4.2. Niche B: the “dog” niche

Three dog-like canids and one red fox (which will be discussed in section 4.3) occupied Niche B. Interestingly, all members of this niche belong to the site Kesslerloch. However, not all Kesslerloch canids belong to niche B. Two canids with high nitrogen values belong to the “wolf” niche. The “dog” niche includes the highest percentage of ungulates (e.g. horse and reindeer) of all of the three reconstructed niches in this study. Ungulates such as horse and reindeer were also the main prey of Magdalenian hunters in southwestern Germany and Switzerland as reflected by zooarchaeological research (Albrecht et al., 1977; Napierala, 2008; Napierala et al., 2014; Schuler, 1994; Weniger, 1987a, 1987b).

The isotopic values place the two other canids from Kesslerloch (HE24/43 and HE24/58) near the morphological dog M001/189 (Lab ID: KSL-44, Kesslerloch) and the cluster analysis suggests that they shared niche B. Moreover, the reconstructed diet of these two individuals is similar to the diet of the Kesslerloch dog. Therefore, we conclude that both canids fed like dogs and therefore possibly were dogs.

Already in the Gravettian, Germonpré et al. (2009) and Bocherens et al. (2015) recognized different canid trophic niches. While one group of large canids (Gravettian wolves), humans and some scavengers displayed high $\delta^{15}N$ values, another group of canids (possible Gravettian dogs) had lower $\delta^{15}N$ but higher $\delta^{13}C$ values. Bocherens et al. (2015) argued that this was the result of differential access to food sources. Gravettian humans from Předmostí hunted mammoth for multiple reasons, including food and ivory (Bocherens et al., 2015). Gravettian wolves had similar $\delta^{15}N$ values as humans at the site, meaning that their diet was

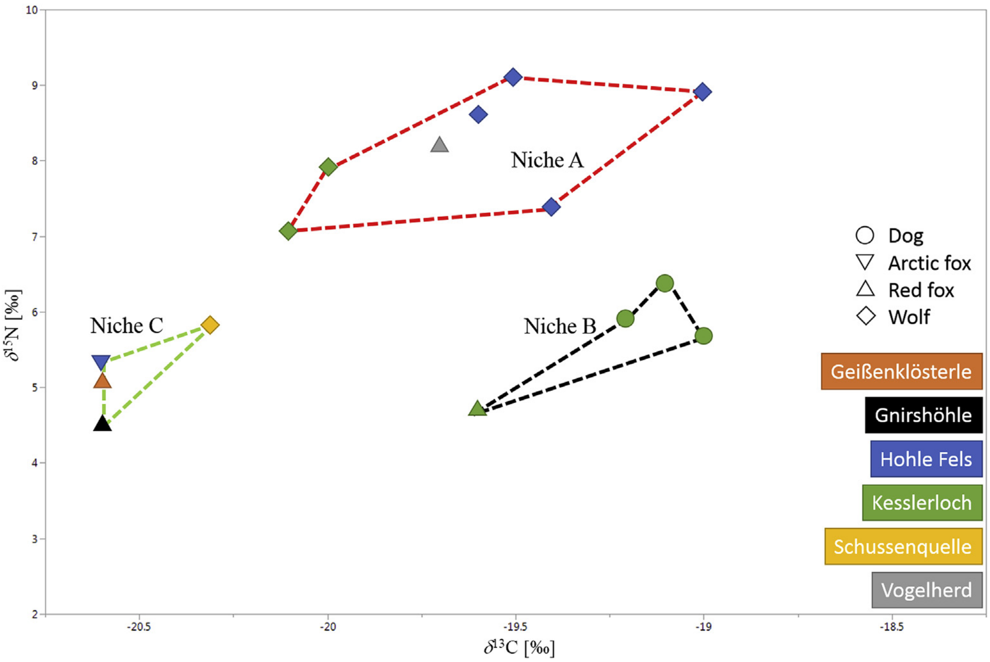

Fig. 7. Calculated niches differed according to the sites. Dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of each niche (Layman et al., 2007).

dominated by mammoth. However, the reconstructed diet of the second canid group (possible Gravettian dogs) was mainly based on reindeer (Bocherens et al., 2015). Gravettian wolves, as well as other predators, scavenged from mammoths hunted by humans, while Gravettian dogs had no access to this source. The diet of the dog group was controlled by humans, who probably fed them with reindeer meat (Bocherens, 2015).

In the Magdalenian of southwestern Germany and Switzerland, we found a similar situation. While canids in niche A include large amounts of mammoth meat in their diet (see 4.1), niche B show lower δ^{15}N value that indicates less mammoth in the diets of these canids (Fig. 5). The mean percentage of megaherbivores in the diet was less than 29 ± 11%. Small mammals (e.g., hares) were included in the diet with a mean percentage of 50 ± 16% and ungulates (e.g., reindeer and red deer) with 21 ± 16%. It seems that members of this niche did not have unrestricted access to all meat sources, as did members of the “wolf” niche.

Therefore we hypothesize, similar to the explanation from Bocherens (2015) for the Gravettian dogs from Předmostí, that the Magdalenian dog diet (niche B) was strongly influenced or even controlled by humans.

4.3. Niche C: the “fox” niche

This niche includes three foxes (two red foxes and one arctic fox) and one wolf. All of the canids came from different sites: one red fox from Geißenklösterle and Gnirshöhle, respectively, an arctic fox from Hohle Fels, and a wolf from Schussenquelle.

Modern red and arctic foxes feed mainly on different species of small mammals, birds (and their eggs), scavenged carcasses, and fruit (Dell’Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; Krajcarz et al., 2018; MacDonnald, 1977; Murdoch et al., 2010; Pulliaines, 1993; Sidorovich et al., 2006; Soe et al., 2017; Wandeler and Lüps, 1993). Ground squirrels (*Spermophilus* sp.), hares (*Lepus* sp.), and Ptarmigan (*Lagopus* sp.) would all have been likely prey of Magdalenian foxes. Ground squirrels and hares both have low carbon and nitrogen isotopic values. There are currently no data available for Magdalenian ptarmigan, though Bocherens et al. (2016) showed that ptarmigans were quite low in nitrogen in the Pre-Dorset context from Umingmak (Banks Island, Canada). Because of this, we only included ground squirrels and hares in this study. The reconstructed diet of the “fox” niche reflects the consumption of hares and ground squirrel resources, representing 73 ± 19% of the diets of the specimens (Fig. 6). Individuals in this niche likely had occasional access to carcasses of large mammals because their diet included a mean percentage of 17 ± 14% megaherbivores and 10 ± 13% ungulates. Several studies on the ecology of modern foxes showed that the percentage of large mammal carcasses in their diet is approximately 20–30% (Dell’Arte et al., 2007; Hartová-Nentvichová et al., 2010; Jędrzejewski and Jędrzejewska, 1992; Kidawa and Kowalczyk, 2011; MacDonnald, 1977; Murdoch et al., 2010; Sidorovich et al., 2006; Soe et al., 2017; Wandeler and Lüps, 1993; Wikenros et al., 2017), which is similar to the upper end of the potential ranges from our model.

Interestingly, one wolf specimen (4829.4 from Schussenquelle) plotted in Niche C. The diet of this individual was dominated by small mammals (70 ± 21%). It is unusual for wolves to consume such a large number of small mammals, as shown by studies on modern wolves in Finland, Slovakia, Russia, Estonia and Italy. All of the individuals in the modern studies consumed less than 20% small prey (hares and small mammals) (Boitani, 1992; Hell, 1982; Peters, 1993; Pulliainen, 1965; Valdmann et al., 1998; Zlatanova et al., 2014), even in hard winters or rodent-rich years (Peters, 1993). Wolves regularly hunting arctic hare and lemmings have been reported only from the High Arctic. In these areas, wolves can subsist on arctic hare in the absence of large ungulates (Dalerum et al., 2017). Another study on modern American grey wolves by Thurber and Peterson (1993) showed that solitary wolves often feed on small mammals. A possible explanation for the Schussenquelle individual plotting in the “fox” niche might be that this wolf was a solitary individual who could only hunt small prey.

4.4. Signs of commensalism and domestication

Two of the analyzed red foxes do not fit into the “fox” niche (niche C) with the other foxes. One individual from Vogelherd (Excavation-No.: Vg III 17185, Lab ID: PLC-12) is included in niche A (the “wolf” niche), and one from Kesslerloch (Lab ID: KSL-17) belongs to niche B (the “dog” niche). The reconstructed diet of the Vogelherd fox has similar dietary proportions as the wolves in its niche, but also a higher percentage of small mammals (21 ± 13%). The latter is probably explained by the known diet of foxes, which is based on rodents (Dell’Arte et al., 2007; Jędrzejewski and Jędrzejewska, 1992; MacDonnald, 1977; Soe et al., 2017; Wandeler and Lüps, 1993). The large percentage of megaherbivores in the diet of this individual can be explained by a similar access to these resources as wolves. Based on this, we hypothesize that this red fox lived commensal to large canids and fed after wolves left the carcasses. This behavior has been observed in modern arctic and red foxes, although it is more common in arctic foxes (Bassi et al., 2012; Pulliaines, 1993; Soe et al., 2017; Wandeler and Lüps, 1993; Wikenros et al., 2017).

It should be noted that the age and sex of an individual could change dietary preferences as well, but not strongly (Kidawa and Kowalczyk, 2011; MacDonnald, 1977). However, seasonality, climate and the associated frequency of small mammals on the landscape, can have a major influence on the dietary preferences of foxes (Dell’Arte et al., 2007; Hartová-Nentvichová et al., 2010; MacDonnald, 1977; Murdoch et al., 2010; Sidorovich et al., 2006; Soe et al., 2017). In periods with fewer small mammals (e.g. in winter), the amount of large mammal carcasses in fox diets has been recorded to be high, while in periods with dramatic vole population increases, fox diets consisted primarily of voles (Kidawa and Kowalczyk, 2011; Sidorovich et al., 2006).

The red fox from Kesslerloch belongs to niche B, which is primarily composed of dog isotopic values. As with the Vogelherd fox, the mean percentage of small mammals in the Kesslerloch fox’s diet is higher than in the other members of its niche (61 ± 17%). However, ungulates were more important in the diet of this fox compared to the other foxes. One hypothesis is that this fox was commensal to humans and scavenged human refuse. Ecologists have documented this behavior among modern foxes (MacDonnald, 1977; Panek and Budny, 2017; Wandeler and Lüps, 1993). The fact that this fox belongs to Kesslerloch as the other canids in niche B, supports our hypothesis. Another possibility is that in Kesslerloch this fox was domesticated or kept in captivity by humans. For example, Proko’yeva (1964) showed that some modern hunter-gatherer societies kept fox kits as pets. They kept them captive, fed them, and killed them for their winter fur. It is therefore conceivable that Magdalenian people also kept young foxes and fed them with the same resources they fed their dogs. A similar situation was discussed by Grandal-d’Anglade et al. (2019) in the case of the two Bronze Age burials from the Iberian Peninsula. The diet of the foxes for which stable isotopes were analyzed matched that of dogs at the site.

In the present study, the Kesslerloch fox matched the “dog” niche, which was mostly comprised of dogs from Kesserloch. However, at Kesserloch we find a higher proportion of small mammals in the fox diet as compared to the dogs. This contrasts with the study of Grandal-d’Anglade et al. (2019), where the niches of buried foxes and dogs were quite similar and the authors argued for both canid groups being domesticated. Rather, the dietary pattern of the Kesserloch fox fits either with a tamed individual, that was occasionally fed by humans, but also moved freely and hunted small prey, or with an individual that scavenged from human refuse.

Based on our study, we can identify ways in which canids can be classified as commensal, domesticated, or as part of their typical hunting niches, based on their isotopic values. First, in cases based on commensalism or self-domestication, we should find diets that reflect the food waste of dominant predators in the ecosystem. In the isospace, this would be reflected with (more or less) similar carbon and nitrogen values as the food owners, be they humans or larger carnivores. The Vogelherd fox shows similar values as the wolves. Therefore, we consider that it was commensal to wolves. However, it is also possible that this fox was commensal to other predators that had high nitrogen values, such as Magdalenian hunters. A human specimen from Brillenhöhle, a cave site near Geißenklösterle, dated to 14,766 ± 307 cal BP, had a δ^{13}C value of −19.2‰ and a δ^{15}N value of 8.5‰ (Benazzi et al., 2011), which falls within the “wolf” niche. It is conceivable, therefore, that the Vogelherd fox could have scavenged from the food waste of Magdalenian hunters, Magdalenian wolves, or both. A synanthropic commensal behavior could also be assumed for the wolves, but is unlikely, as humans try to keep dangerous predators away from their camp and their prey.

The second scenario that we can explore with our study is the pet-keeping hypothesis. If animals were kept as pets, the individuals should show a more restricted, human controlled diet. In our study, we analyzed three dogs. One of these canids was morphologically identified as a dog by Napierala and Uerpmann (2012). The other two canids, while morphologically ambiguous, showed similar isotopic values and fall in the same niche as the dog (niche B, see section 4.2). The diets of these canids were different compared to their wild relatives. While the wolves fed mainly on megaherbivores, dogs fed on ungulates. As we discussed in section 4.2, despite the unusual isotope signature of the Brillenhöhle human, horse and reindeer were the main prey of Magdalenian hunters and therefore, bones of these species are numerous in the zooarchaeological record. If the humans used ungulate remains as dog food it could explain the restricted diet of the dogs. However, there is also a fox in the “dog” niche. It is possible that this particular specimen was tamed; as we know from the Russian fox farm experiment, foxes are easy to genetically manipulate by selection for behavioral tolerance toward humans (Belyaev et al., 1985; Dugatkin, 2018; Gogoleva et al., 2011; Trut et al., 2004, 2009; Trut, 1999). On the other hand, the diet of the Kesserloch fox also contained isotope values consistent with consuming small animals, so it is difficult to determine if it was tamed or simply commensal.

5. Conclusion

Our work has led us to conclude that niche partitioning of canids in the Magdalenian of southwestern Germany and Switzerland is reflected in their isospace. Therefore, this study can provide a baseline for investigating canid-human interactions in other Paleolithic contexts, for instance during the pre-LGM Upper Paleolithic, where the possibility of wolf domestication is heavily debated (e.g., Coppinger and Coppinger (2001); Crockford and Kuzmin (2012); Larson et al. (2012); Lupo (2017); Morey (2014); Morey and Jeger (2015, 2017); Perri (2016); Thalmann and Perri (2018); Vilà et al. (1997); Wayne et al. (2006)).

Our results indicates that we can distinguish between Magdalenian dogs and wolves based on their diets. While wolves had permanent unrestricted access to all types of dietary sources (including high-nitrogen prey), dog diets were controlled by humans.

Most of the red and arctic foxes from different sites fed on small game (e.g., small mammals and birds). However, two red foxes showed a different pattern. One fox from Vogelherd plotted with the wolves and one fox from Kesslerloch with the dogs. Both had a diet with more large mammals as compared to the other foxes. Therefore, we hypothesized a commensal relationship, in one case with wolves and in the other case with humans. If we refer to the pet-keeping hypothesis of domestication, it is also possible that the fox from Kesslerloch was tamed and treated like a dog.

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Appendix A. Supplementary data

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Supplementary information

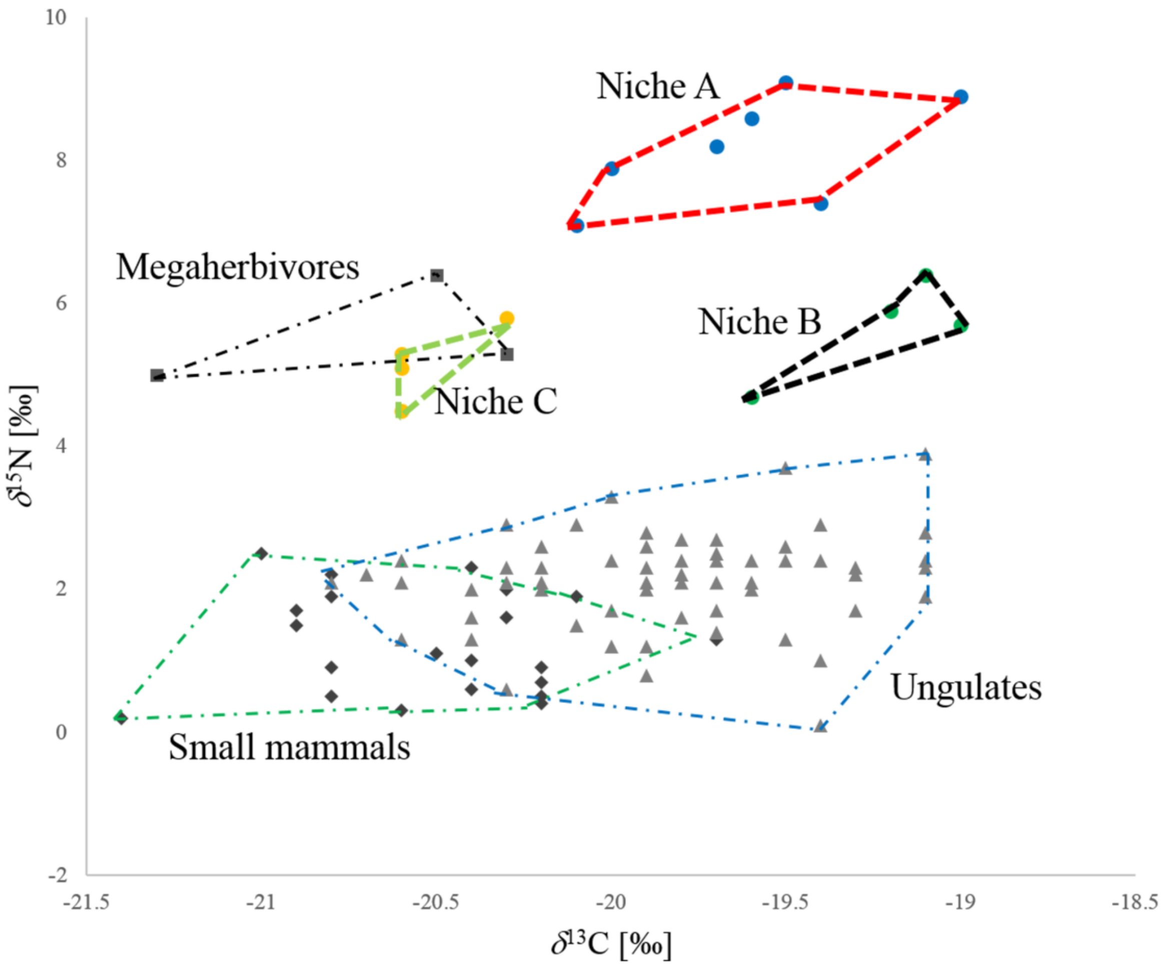

Fig. S 1: Calculated canid niches (niche A, B and C) in combination with herbivore groups in the isospace. The dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of each group (Layman et al., 2007).

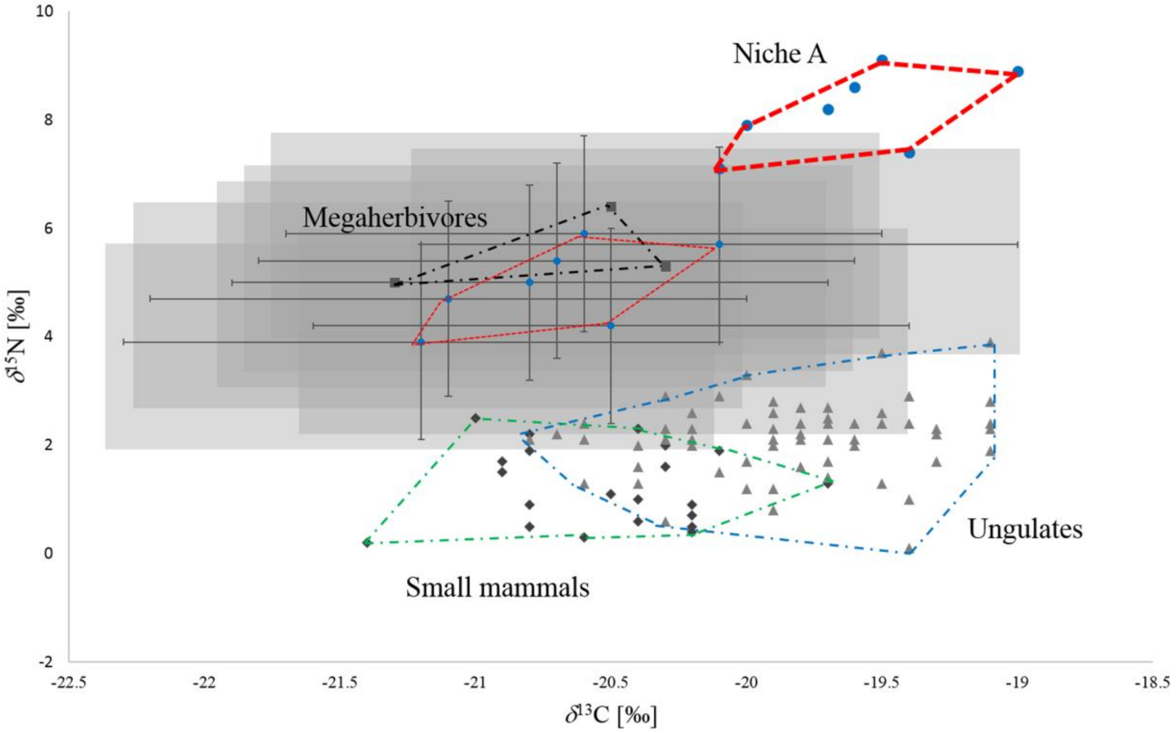

Fig. S 2: Graphical implementation of the calculated diet for niche A. The bold red dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of niche A (Layman et al., 2007). The dashed lines from Ungulates, Small mammals and Megaherbivores show the convex hulls of these groups as well. The thin red dashed line shows the down-calculated convex hull of niche A, while the grey boxes and the error bars show their standard deviation (SD). For this calculation we used the TEF values (δ^{13}C = 1.1 ± 1.1 ‰; δ^{15}N = 3.2 ± 1.8 ‰) from a study on modern foxes by Krajcarz et al. (2018).

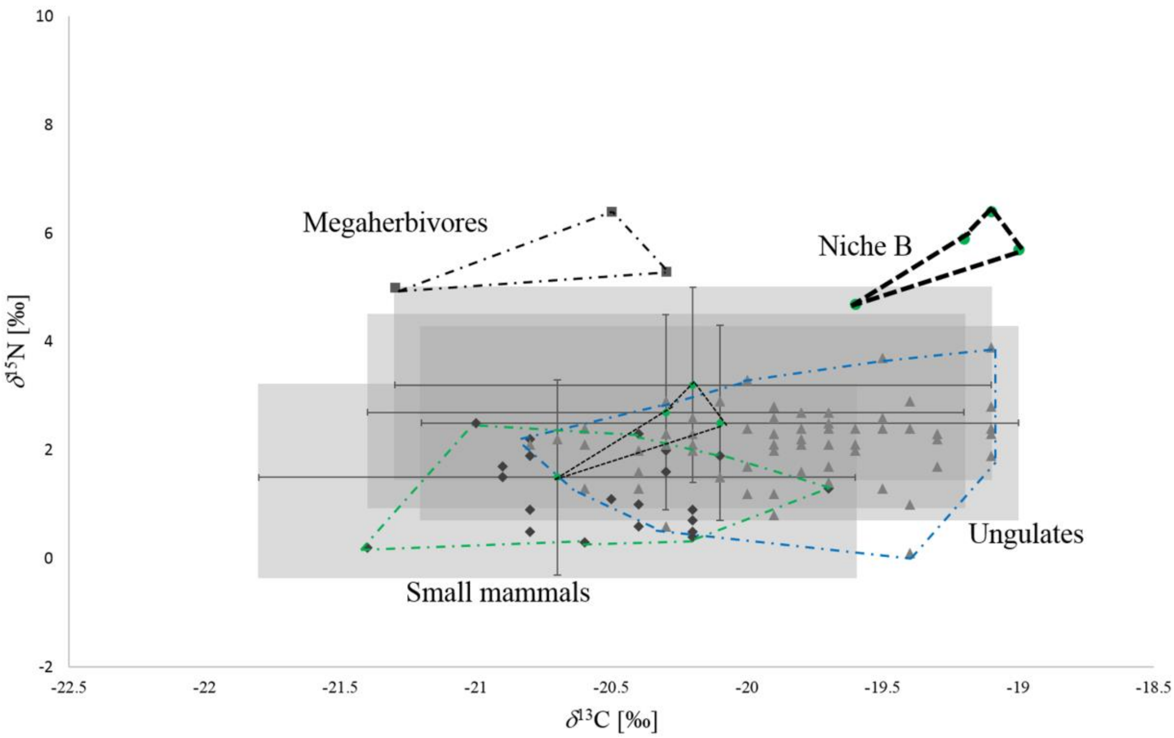

Fig. S 3: Graphical implementation of the calculated diet for niche B. The bold black dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of niche B (Layman et al., 2007). The dashed lines from Ungulates, Small mammals and Megaherbivores show the convex hulls of these groups as well. The thin black dashed line shows the down-calculated convex hull of niche B, while the grey boxes and the error bars show their standard deviation (SD). For this calculation we used the TEF values (δ^{13}C = 1.1 ± 1.1 ‰; δ^{15}N = 3.2 ± 1.8 ‰) from a study on modern foxes by Krajcarz et al. (2018).

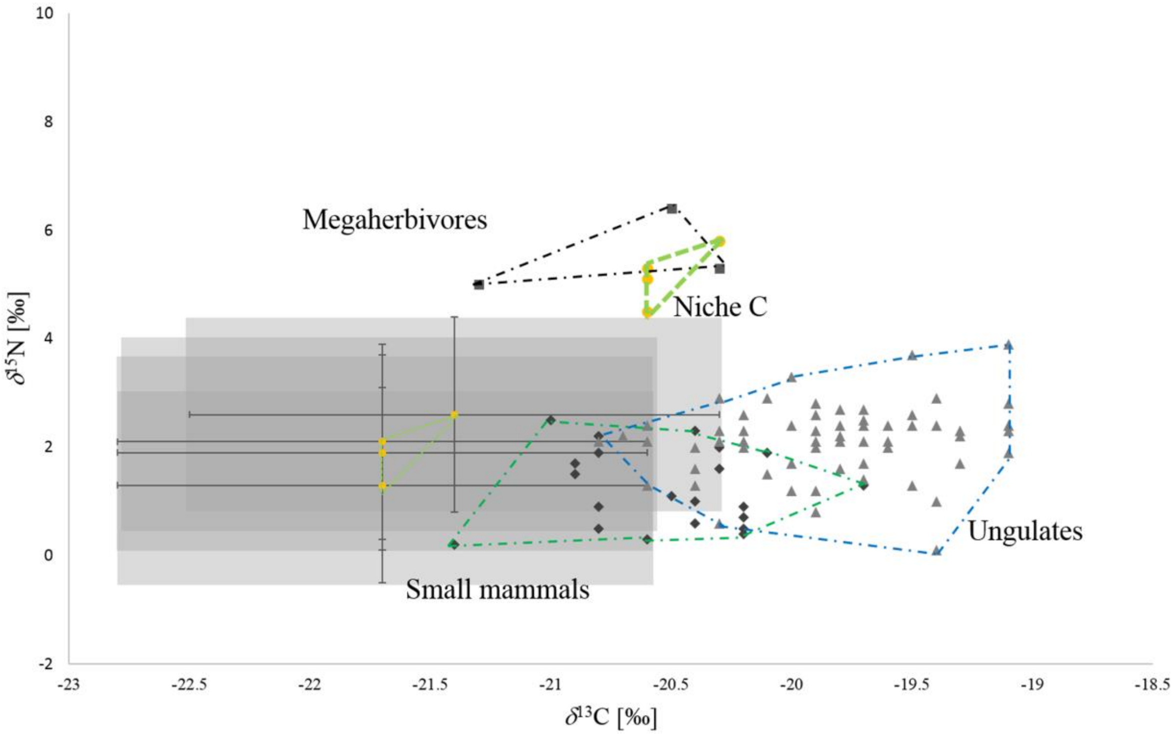

Fig. S 4: Graphical implementation of the calculated diet for niche C. The bold green dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of niche C (Layman et al., 2007). The dashed lines from Ungulates, Small mammals and Megaherbivores show the convex hulls of these groups as well. The thin green dashed line shows the down-calculated convex hull of niche C, while the grey boxes and the error bars show their standard deviation (SD). For this calculation we used the TEF values (δ^{13}C = 1.1 ± 1.1 ‰; δ^{15}N = 3.2 ± 1.8 ‰) from a study on modern fox by Krajcarz et al. (2018).

Other predators in contrast to the canid niches

The isospace plot, according to Layman et al. (2007), in Fig. S 5 shows no overlap of large carnivores with the three niches that were defined earlier based on the isotopic results on canids. Niche A reflects the top (non-human) predators on the Magdalenian landscape; no other published predator's value is higher in nitrogen than these canids. Only one of the published wolverine values (KLS-15, Bocherens et al. (2011)) is equal to the wolf, M 58, analyzed in this study. The other published wolverine (KLS-16, Bocherens et al. (2011)) is located between niche A and niche C, with δ^{15}N values similar to niche C, but lower δ^{13}C values. Cave lion data (KSL-8, KSL-9 and RAN-32lion, Bocherens et al. (2011)) show higher δ^{13}C values than all of the canid niches, but similar δ^{15}N values to niche B. Two of the published brown bears (TUB-56 and TUB-82, Bocherens et al. (2011)), as well as the published lynx (KSL-18, Bocherens et al. (2011)), show δ^{13}C values similar to niche B, but much lower δ^{15}N values. Two other brown bears (SCH-8 and SCH-9, Bocherens et al. (2011)) show the same carbon values as niche C, but much lower nitrogen values. Bocherens et al. (2011) have suggested that these bears fed mostly on plant foods.

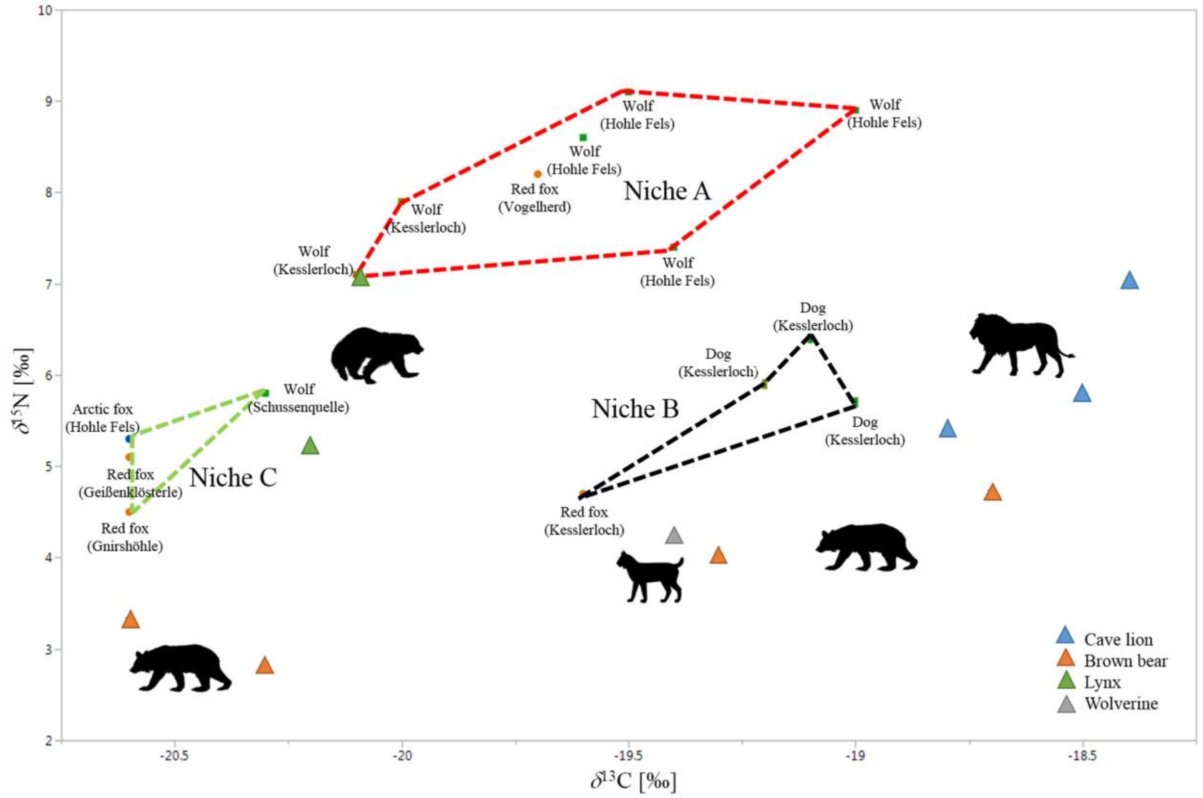

Fig. S 5: Calculated niches in contrast to other Magdalenian predators. The dashed line shows the convex hull, the smallest possible surface that encompasses all individuals of each niche (Layman et al., 2007).

Tab. S 1: Isotopic values of other Magdalenian carnivores taken from Bocherens et al. (2011).

Lab ID	**Location**	**Taxon**	**Reference**	**C/N$_{coll}$**	**$\delta^{13}C_{coll}$ [‰]**	**$\delta^{15}N_{coll}$ [‰]**
KSL-15	Kesslerloch	*Gulo gulo*	Bocherens et al. 2011	3.4	-20.1	7.1
KSL-16	Kesslerloch	*Gulo gulo*	Bocherens et al. 2011	3.4	-20.2	5.2
KSL-18	Kesslerloch	*Lynx lynx*	Bocherens et al. 2011	3.4	-19.4	4.2
KSL-8	Kesslerloch	*Panthera leo* sp.	Bocherens et al. 2011	3.3	-18.8	5.4
KSL-9	Kesslerloch	*Panthera leo* sp.	Bocherens et al. 2011	3.2	-18.5	5.8
RAN-32lion	Ranchot	*Panthera leo* sp.	Bocherens et al. 2011	3.2	-18.4	7.0
SCH-8	Schussenquelle	*Ursus arctos*	Bocherens et al. 2011	4.9	-20.6	3.3
SCH-9	Schussenquelle	*Ursus arctos*	Bocherens et al. 2011	6.0	-20.3	2.8
TUB-82	Hohle Fels	*Ursus arctos*	Bocherens et al. 2011	3.2	-19.3	4.0
TUB-56	Buttentalhöhle	*Ursus arctos*	Bocherens et al. 2011	3.3	-18.7	4.7

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