Central Lancashire Online Knowledge (CLoK)

Title	New Insights into Serbian Cave Bear (Ursus spelaeus) Diet and Ecology Using Bone Collagen δ13C and δ15N Analysis in the Context of European Cave Bear Extinction
Type	Article
URL	https://clok.uclan.ac.uk/id/eprint/56023/
DOI	https://doi.org/10.1080/14614103.2025.2521944
Date	2025
Citation	Jones, Jennifer, Stevens, Rhiannon E., Mihailović, Dušan, Mihailović, Bojana and Marín-Arroyo, Ana B. (2025) New Insights into Serbian Cave Bear (Ursus spelaeus) Diet and Ecology Using Bone Collagen δ13C and δ15N Analysis in the Context of European Cave Bear Extinction. Environmental Archaeology: The Journal of Human Palaeoecology. ISSN 1461-4103
Creators	Jones, Jennifer, Stevens, Rhiannon E., Mihailović, Dušan, Mihailović, Bojana and Marín-Arroyo, Ana B.

Environmental Archaeology
The Journal of Human Palaeoecology

ISSN: 1461-4103 (Print) 1749-6314 (Online) Journal homepage: www.tandfonline.com/journals/yenv20

New Insights into Serbian Cave Bear *(Ursus spelaeus)* Diet and Ecology Using Bone Collagen δ^{13}C and δ^{15}N Analysis in the Context of European Cave Bear Extinction

Jennifer R. Jones, Rhiannon E. Stevens, Dušan Mihailović, Bojana Mihailović & Ana B. Marín-Arroyo

To cite this article: Jennifer R. Jones, Rhiannon E. Stevens, Dušan Mihailović, Bojana Mihailović & Ana B. Marín-Arroyo (09 Jul 2025): New Insights into Serbian Cave Bear *(Ursus spelaeus)* Diet and Ecology Using Bone Collagen δ^{13}C and δ^{15}N Analysis in the Context of European Cave Bear Extinction, Environmental Archaeology, DOI: 10.1080/14614103.2025.2521944

To link to this article: https://doi.org/10.1080/14614103.2025.2521944

ENVIRONMENTAL ARCHAEOLOGY
https://doi.org/10.1080/14614103.2025.2521944

New Insights into Serbian Cave Bear *(Ursus spelaeus)* Diet and Ecology Using Bone Collagen δ^{13}C and δ^{15}N Analysis in the Context of European Cave Bear Extinction

Jennifer R. Jones [a,b], Rhiannon E. Stevens [c], Dušan Mihailović [d], Bojana Mihailović[e] and Ana B. Marín-Arroyo [b]

[a]Centre for Field Archaeology and Forensic Taphonomy, University of Central Lancashire, Preston, UK; [b]Grupo de I+D+i EVOADAPTA (Evolución Humana y Adaptaciones durante la Prehistoria), Departamento de Ciencias Históricas, Universidad de Cantabria, Santander, Spain; [c]Institute of Archaeology, University College London, London, UK; [d]Department of Archaeology, University of Belgrade Faculty of Philosophy, Belgrade, Serbia; [e]Department of Archaeology, National Museum of Belgrade, Belgrade, Serbia

ABSTRACT

The extinction of the cave bears (*Ursus spelaeus*) and the factors leading to their demise have been widely discussed. Environmental change, dietary inflexibility, human predation, and resource competition all potentially contributed to their decline. Determining the ecological and dietary behaviour of cave bears is crucial in contextualising their extinction. Here, bone collagen δ^{13}C and δ^{15}N evidence from the site of Šalitrena Pećina (Serbia), from a cave bear population dating to 40.2–37.9 kyr cal. BP is used to explore their dietary behaviour. Large ranges in δ^{13}C and δ^{15}N values suggest consumption of varied plants across an isotopically diverse landscape. Pan-European comparisons of cave bear δ^{13}C and δ^{15}N values are indicative of local adaptions to the landscape with flexibility in plant types consumed across different ecological zones. A mosaic pattern of extinction, influenced by habitat and environmental pressures associated with cooling conditions likely impacted on extinction of the species. Reflecting on the ecology of cave bears, can help to support conservation efforts for species under threat today. European brown bears (*Ursus arctos*), mirror past cave bear population distributions. Supporting habitat creation and connectivity between populations may help to minimise the impact of environmental change and anthropogenic activity on European brown bears.

ARTICLE HISTORY
Received 19 March 2024
Revised 9 June 2025
Accepted 11 June 2025

KEYWORDS
Cave bear (*Ursus spelaeus*); dietary analysis; ecological niche; Balkans; stable isotopes; Late Pleistocene

Introduction

The Late Pleistocene was characterised by megafauna extinctions (Koch and Barnosky 2006; Lister and Stuart 2008). Cave bears (*Ursus spelaeus* Rosenmüller, 1794), once widespread across continental Europe, became extinct around 28–25 kyr BP, with late populations spread across the countries of Spain (Grandal-D'Anglade et al. 2006), Italy (Terlato et al. 2019), Poland (Baca et al. 2016; Nadachowski 2009), Hungary (Lengyel and Mester 2002), Germany (Bocherens et al. 2014; Münzel et al. 2011), and Slovakia (Sabol et al. 2014) indicating a simultaneous extinction across their spatial range. The latest cave bear specimens found to date are from the NE Italian sites of Paina Cave from units 5 and 6, which date to 19,686 ± 54 (ETH-79366) and Trene Cave, macro unit B, dating to 19,948 ± 55 BP (ETH-79368) (Terlato et al. 2019). The extinction of cave bears has become the subject of academic debate, with climate change (Lister and Stuart 2008; Pacher and Stuart 2009), human predation (Gretzinger 2019; Terlato et al. 2019; Wojtal et al. 2020), predation by carnivores (Bocherens 2015; Diedrich 2012; 2014b) and dietary inflexibility (Naito 2020) all being proposed as contributing to their demise. Several of the aforementioned factors threaten a host of species today, which is of great concern given the global biodiversity crisis. Research into the palaeoecology (habitats, diets, and behaviour) of past species using stable isotope and multi-proxy methods can provide insights into the factors that contributed to the extinction of past species (Jones and Britton 2019), which in turn can aid with developing conservation strategies for current day fauna that are at threat of disappearing. Today, brown bears (*Ursus arctos* Linnaeus, 1758) are threatened in Europe, with only four isolated populations remaining from a once-thriving species (Zedrosser et al. 2001). Anthropogenic factors, including hunting, deforestation, and loss of habitats through agriculture have been identified as threats to existing populations

CONTACT Jennifer R. Jones jjones30@uclan.ac.uk School of Law and Policing, Maudland Building, University of Central Lancashire, Fylde Road, Lancashire, PR2 2HE, UK

Supplemental data for this article can be accessed online at https://doi.org/10.1080/14614103.2025.2521944.

(Swenson et al. 2000), affecting their diet and hibernation patterns. Understanding the palaeoecology of extinct bear populations can help develop successful conservation strategies to protect the declining bear populations in Europe today.

Exploring Potential Drivers Behind Cave Bear (*Ursus spelaeus*) Extinction

Initial theories have suggested that humans played an important role in cave bear extinction through both competition with the species, and predation (Kurtén 1958). Archaeological evidence has shown that Neanderthals and cave bears (sensu lato) often interacted in similar niches. Cut marks and carnivore tooth puncture marks on cave bear and brown bear bones associated with Neanderthal-made Mousterian technology were found at Grotta Rio Secco and Grotta Fumane in Italy (Romandini et al. 2018), and these taphonomic alterations show that bear species were at times preyed on by humans, and that all three species competed for resources, putting pressure on habitat niches. Neanderthals also used cave bear bones as part of their toolkit as evidenced by the bone retouchers at Sclandia Cave (Belgium) (Abrams et al. 2014). Cave bears also appear to have had a symbolic role, as suggested by the Mousterian incised cave bear vertebra from Pešturina cave in Serbia (Majkić et al. 2018). With the arrival of modern humans, such interactions continued, for example at Gargas cave (France) where a cut and sawn cave bear fibula and a modified incisor showed that the species was also being used as a raw material (Vercoutere, Juan-Foucher, and Foucher 2006). Archaeologically, predation of cave bears by humans has been observed at sites such as Hohle Fels, where a Gravettian cave bear vertebra was found with a flint projectile embedded (Münzel and Conard 2004). Wider archaeological evidence indicates a complex relationship between humans and cave bears, with populations occupying the same caves, such as Chauvet, at different times (Pettitt and Bahn 2015). It is possible that increased periods of cave occupation linked to a larger human population and bigger group sizes may have contributed to the extinction of cave bear populations, as suggested from studies at Grotte XVI in the Dordogne (France) (Grayson and Delpech 2003). DNA analysis of cave bear specimens has implied that there was a drastic decline in its populations starting at about 50 kyr BP with a loss of genetic diversity (Stiller 2010), coinciding with the arrival of modern humans in Europe. More recent mtDNA evidence has further strengthened this hypothesis, showing a decreasing female cave bear population size at around 40 kyr BP, which corresponds with the onset of the Aurignacian, supporting the hypothesis that modern humans were a contributing factor to the extinction of the species (Gretzinger 2019). The arrival of modern humans appears to have accelerated the extinction process of the cave bear.

Predation by carnivores may also have had an impact on cave bear populations (Diedrich 2012; Diedrich 2014a). A decline in mammoth steppe fauna is thought to have pushed carnivores such as wolves, leopards, steppe lions and hyenas towards preying on hibernating cave bears (Diedrich 2012). The presence of hyena tooth marks and perforations on cave bear cub femora from sites in Central Europe suggests that spotted hyenas were scavenging cub remains from dens (Diedrich 2014a). However, the extent to which this occurred is not fully known. Cave bears were alternating space use with humans and carnivores, which may have resulted in resource competition, contributing to their extinction.

Undoubtedly, the highly variable climatic throughout MIS 3 and the harsh conditions of MIS 2 provided the backdrop to the extinction of various megafauna (Barnosky et al. 2004; Koch and Barnosky 2006), and this, in combination with factors such as predation may have resulted in cave bear extinction (Mondanaro 2019). Specifically, climatic cooling, affecting vegetation productivity, may have been at least partly responsible in some regions for cave bear decline (Lister and Stuart 2008; Pacher and Stuart 2009), although Western cave bear lineages have been found in cold locations as far east as the Altai Mountains (Knapp 2009), suggesting an ability to cope with more extreme conditions. Climatic change, in combination with a degree of human predation, may explain the demise of this species, showing the interrelated nature of these possible agents of extinction. Humans, cave bears and other species would all have had to adapt and cope with changing conditions, potentially causing niche overlaps and behavioural shifts. Understanding the diet and ecology of cave bears is central to the debate surrounding the extinction of the species and the extent to which environmental change and niche competition may have affected their survival.

Cave Bear Diet and Ecology

Cave bear cranial morphology alongside tooth wear patterns suggested that this species was predominantly herbivorous (Kurtén 1958; Kurtén 1976; Pacher and Stuart 2009), although geometric morphometrical studies (Figueirido, Palmqvist, and Pérez-Claros 2009), and dental microwear analysis, which reflects dietary behaviour during the last few days-weeks prior to death indicate some omnivorous behaviour, particularly during the predormancy period (Peigné et al. 2009; Ramírez-Pedraza 2019). Research into cave bear diet has applied bone collagen $\delta^{13}C$ and $\delta^{15}N$ analysis of individuals found in Late Pleistocene sites across Europe, which has supported a hypothesis of a predominantly herbivorous diet (Bocherens 2019; Nelson et al. 1998; Van Heteren and Figueirido 2018). At the Romanian site of Peştera cu Oase a negative shift in $\delta^{13}C$ values (mean value −21.5‰ from 21 specimens) is consistent with other European cave bear populations, whereas the elevated $\delta^{15}N$ values (between 5.7 and 9.8‰) observed in all but one specimen has suggested omnivorous diets for some individuals (Richards 2008; Trinkaus and Richards 2013). Counter-arguments infer that elevated $\delta^{15}N$ values may be reflecting a hibernation effect (D'Anglade and Mosquera 2008). Consumption of plants with elevated $\delta^{15}N$ values including fungi, forbs, and graminoids may also be partially responsible for some of the stable isotope values observed in European cave bears (Bocherens 2019).

In recent years compound-specific isotopic analysis of Late Pleistocene cave bears from Romania has contributed to the debate surrounding the diet of the species, as it can differentiate between trophic levels (i.e. omnivorous or carnivorous feeding patterns) and dietary sources (i.e. consumption of plants with high $\delta^{15}N$ values) (Naito 2016; Naito 2020). Results from the phenylalanine $\delta^{15}N$ values indicate that the elevated values in Romanian cave bear specimens are likely due to either a baseline shift in $\delta^{15}N$ values, or consumption of plants with high $\delta^{15}N$ values, or indeed a combination of these two, leading to the hypothesis that dietary inflexibility may have been linked to their extinction (Naito 2020). Such studies have highlighted the value of understanding the diet of local cave bear populations. Indeed, the presence of mosaic landscapes across Europe during MIS 3 and MIS 2 (Jones et al. 2020; Jones et al. 2021; Pederzani et al. 2023; Reade 2020; Wong et al. 2020) demonstrates the importance of characterising the ecology and behaviour of species on a local scale. The large variations in stable isotope results from cave bears analysed to date have indicated that local geography, climate, and environment were key factors influencing cave bear diet and ecology.

Within Europe there has been a range of cave bear isotope studies in Romania (Naito 2020; Richards 2008), Belgium (Bocherens et al. 1997), Spain (Pérez-Rama, Fernández-Mosquera, and Grandal-d'Anglade 2011b), Germany (Münzel et al. 2011; Münzel et al. 2013), France (Bocherens et al. 2006), Italy (Terlato et al. 2019), and the Ural Mountains (Gimranov et al. 2023; Kosintsev et al. 2023) amongst other places. There is a lack of information on the dietary behaviour of cave bears in Serbia (Borić 2022) despite remains of the species being identified in 36 archaeological sites and karstic features within the Balkan Peninsula (Cvetković and Dimitrijević 2014). Only in recent years have larger-scale and multidisciplinary investigations into Palaeolithic archaeology in Serbia been undertaken (Borić 2022; Mihailović 2014; Mihailović and Mihailović 2023), allowing archaeozoological and biomolecular investigations into species such as cave bears in the region. Given the heavy debate surrounding the meaning behind the elevated $\delta^{15}N$ values of bears at the Romanian sites (Bocherens 2019; D'Anglade and Mosquera 2008; Naito 2020; Richards 2008; Trinkaus and Richards 2013), it is surprising that to date little is understood about the diet of cave bears in the adjacent country of Serbia.

This paper uses newly generated bulk collagen $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis of cave bear specimens from the site of Šalitrena Pećina (Serbia) to explore their diet, hibernation behaviour and species ecology. To date, there are no bone collagen $\delta^{13}C$ and $\delta^{15}N$ values from cave bears in Serbia, meaning that the results from Šalitrena Pećina provide essential information on this species in a new region. Comparisons to existing isotopic results of cave bears analysed from other European Late Pleistocene sites will help to understand geographical variations in cave bear diet and ecologies and how the population sampled from Šalitrena Pećina relates to other contemporary Late Pleistocene cave bears.

Cave Bears at Šalitrena Pećina

Šalitrena Pećina cave is located in the Republic of Serbia, around 100 km south-west of Belgrade near Mionica (Figure 1). The site is situated in the canyon of the Ribnica River, facing west to overlook the river. Šalitrena Pećina cave is currently 20 m above the current river level, lying 277 masl (Marín-Arroyo and Mihailović 2017). Excavations at the site in 2004, and 2006–2008 revealed a series of archaeologically important deposits spanning from the Middle and Upper Palaeolithic, with rich assemblages of archaeozoological and technological material (Marín-Arroyo et al. 2023; Marín-Arroyo and Mihailović 2017). Previous publications have predominantly focussed on the anthropogenically derived deposits in the entrance to the cave and have established the chronology for the site (Marín-Arroyo et al. 2023; Marín-Arroyo and Mihailović 2017).

The cave bear remains studied here derived from Level 3 at Šalitrena Pećina located in the interior excavation area of the cave and to date have not been the subject of previous research at the site. A dating campaign to understand the chronology of the site provided a radiocarbon date of 36,150 ± 750 (OxA-27948) for Level 3, which was taken from a *Megaloceros* tooth (Marín-Arroyo and Mihailović 2017). The full faunal spectrum of archaeozoological remains recovered from Level 3 can be seen in Table 1. Cave bear remains were the most commonly identified species within the deposit (Table 1).

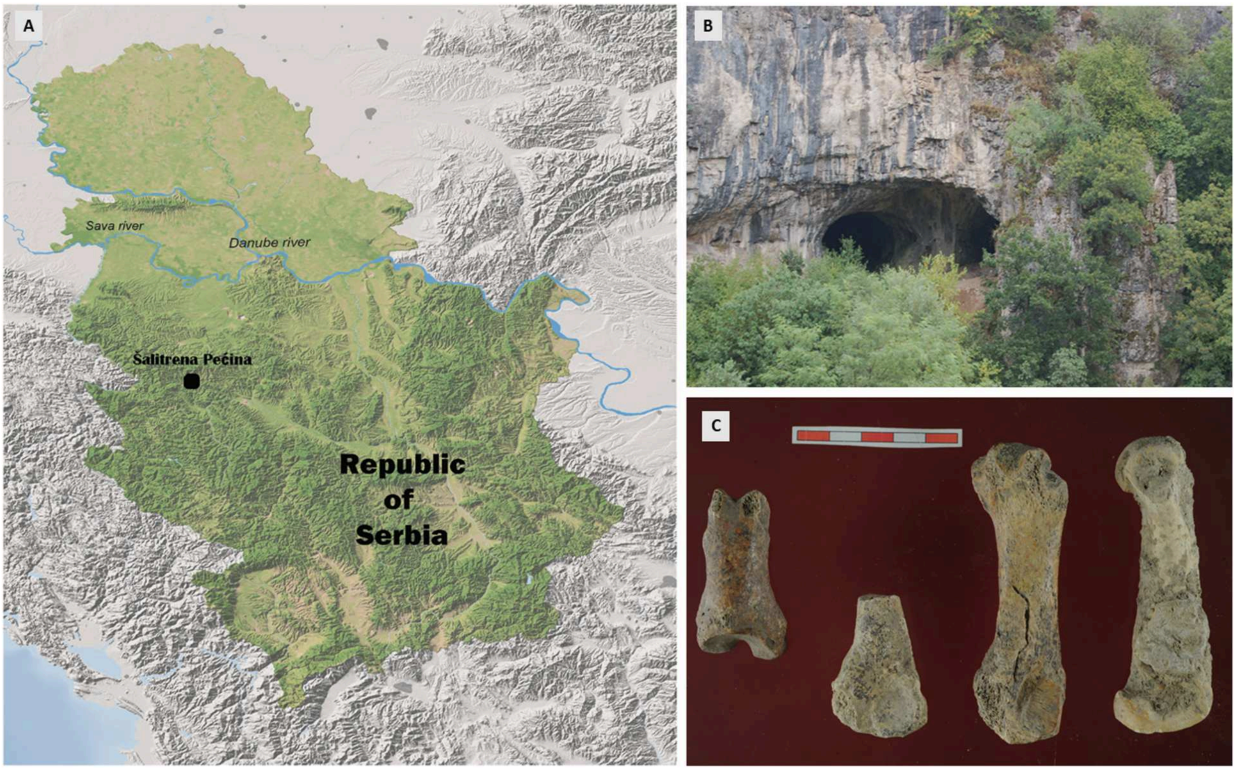

Figure 1. Location of Šalitrena Pećina cave within the Republic of Serbia (A), the exterior of the cave (B) and some of the post-cranial cave bear remains found in Level 3 from the interior of the cave (C).

Taphonomic analysis of archaeozoological remains from Level 3, noted by A.B. Marín-Arroyo during analysis, revealed extensive carnivore activity observed through gnaw marks, with occasional episodes of human activity seen through the presence of fracture patterns and cut marks. The zooarchaeological assemblage from Trench F, which forms the corridor to the interior part of the cave exhibited a high proportion of bone polishing (19% of the specimens), which is consistent with cave bear trampling (Marín-Arroyo and Mihailović 2017) (Figure 2). The cave's interior section, where the Level 3 material derives from, appears to have been a den for cave bears, as well as a place where secondary carnivore scavenging activities took place, with humans and bears alternating their occupation patterns in this space (Marín-Arroyo and Mihailović 2017).

Table 1. The full faunal spectrum recorded from Level 3, within the interior of Šalitrena Pećina cave, showing the dominance in the representation of cave bears within this level.

Species	NISP
Mammuthus primigenius	10
Equus ferus	13
Bos primigenius	1
Bos/Bison sp.	37
Capra ibex	24
Rupicapra rupicapra	6
Megaloceros sp.	3
Cervus elaphus	44
Capreolus capreolus	1
Sus scrofa	2
Ursus spelaeus	185
Crocuta spelaea	41
Canis lupus	15
Vulves vulpes	6
Panthera pardus	3
Panthera spelaea	1
Lynx lynx	1
Felis silvestris	1
Mustela sp.	1
Leporidae	5
Rodentia	1
Bird	8
Large mammal	134
Medium mammal	361
Small mammal	62
Indeterminate	2612
Total	**3578**

Materials and Methods

The Level 3 cave bear remains were identified by A.B Marín-Arroyo during archaeozoological analysis of the wider faunal assemblage from Šalitrena Pećina. Cave bear remains were identified using reference collections held at the Department of Archaeology at the University of Belgrade to determine taxa and skeletal element, in addition to consultation of fossil collections from the Natural History Museum in London. Skeletal reference guides including Pales and Lambert (1976) and Torres Pérez-Hidalgo (1984) were also used.

For the bone collagen $\delta^{13}C$ and $\delta^{15}N$ analysis 11 cave bear specimens from 10 different bones were sampled, with the material deriving from Level 3 within squares W20, W21, X22, V20, V21 and U21 (Figure 2). All bones selected for analysis were fully

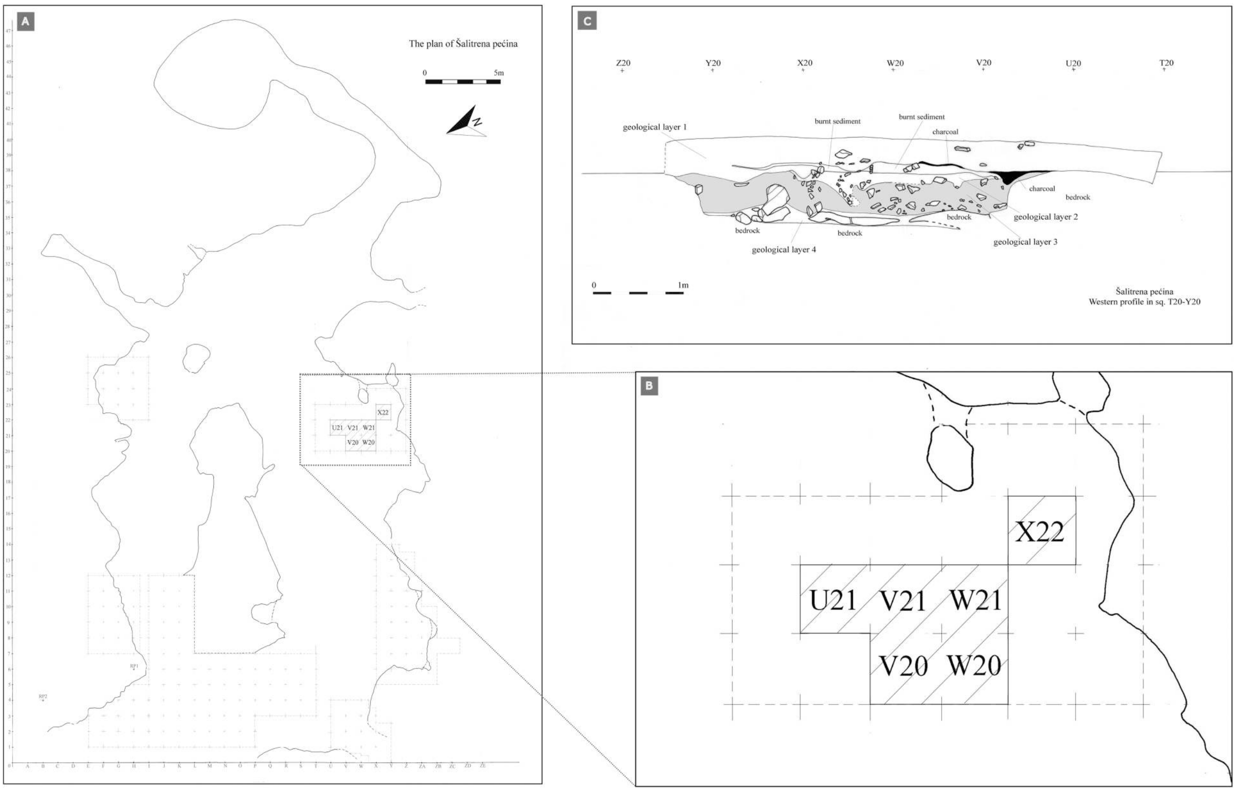

Figure 2. A site plan of the interior of Šalitrena Pećina cave (A), with a focus on the squares within the interior section of the cave where the cave bear remains were found (B), and the stratigraphic section showing geological Level 3 (shaded in grey), where the cave bear remains were derived from (C). Larger versions of panels A, B and C can be seen in Supplementary Figures 1–3.

fused and specimens are all thought to have been at least 2–3 years old (based on the earliest fusing bones represented in the assemblage) at the time of death. Age estimates follow *Ursus arctos* fusion ages, which are considered an appropriate analogy for extinct cave bears (Weinstock 2009). The exact number of individuals represented in the samples is unknown, due to the challenges of using NISP and MNI quantification when studying disarticulated bone assemblages, which can respectively over- and under-estimate the number of individuals represented (Grayson 1979; Lyman 2008). Sampling of the cave bear specimens aimed to target individuals from different squares and sub-squares within the cave to try and ensure that different individuals were represented. Two samples were taken from specimen 424 (sample numbers SAL62 and SAL63) to explore the scale of intra-individual variation. A complete list of specimens studied, locations, and results achieved is presented in Table 3.

Samples were prepared at the Dorothy Garrod laboratory at the McDonald Institute (University of Cambridge), following the methodology outlined in (Stevens et al. 2013). Collagen was extracted and then weighed prior to analysis using a Costech elemental analyser coupled to a Finnigan MAT253 mass spectrometer. The carbon and nitrogen results achieved are reported using the delta scale in units ‘per mil’ (‰) relative to internationally accepted standards VPDB and AIR, respectively (Hoefs 1997). All specimens were analysed in duplicate to ensure reproducibility, and an average of these values was used. Based on replicate analyses of international (IAEA: caffeine and glutamic acid-USGS-40) and in-house laboratory standards (nylon, alanine, and bovine liver) analytical precision of quality-control standard replicates was ≤ 0.09 for δ^{13}C and δ^{15}N (see Supplementary Table 1 for replicate results achieved). Comparative ungulate remains discussed in this paper, taken from Marín-Arroyo et al. (2023) were also prepared and analysed at the same facility using an identical methodology.

Bone collagen δ^{13}C and δ^{15}N data from Late Pleistocene European cave bear assemblages was used as a comparison for the Šalitrena Pećina cave bears, and the full comparative dataset, with bibliographic references is available in Supplementary Table 2.

Results and Discussion

The Cave Bear Remains from Level 3 at Šalitrena Pećina

Regarding the archaeozoological remains of the cave bears from Level 3 at Šalitrena Pećina, the assemblage comprised of a NISP of 185, of which 137 were dental remains (Table 2). Of the teeth studied 35 of these were deciduous teeth from cubs within their first 1–

Table 2. NISP counts of cave bear skeletal elements found within Level 3 inside of Šalitrena Pećina cave (columns 1 and 2), with further detail on the fragments of teeth that could be identified (columns 3–9).

Summary of the skeletal elements identified		Summary of the isolated teeth remains						
			Lower isolated teeth			Upper isolated teeth		
Skeletal element	NISP (total =185)	Tooth Side	R	L	unsided	R	L	unsided
Skull	9	I indet.	0	0	0	0	1	0
Mandible	3	I1/I2	1	2	0	0	0	0
Teeth	137	I1	1	1	0	1	0	1
Cervical vertebra	2	I2	4	2	1	0	1	1
Lumbar vertebra	1	I3	4	4	0	5	5	2
Ribs	5	I4	0	0	0	0	0	0
Ulna	1	C lacteal	9	8	1	5	8	2
Carpal	3	C	2	2	0	3	2	0
Tarsal	1	P4	4	3	0	0	0	0
Metapodial	3	M1	3	1	0	1	2	0
Phalanx 1	7	M2	2	1	0	2	2	0
Phalanx 2	7	M3	1	1	0	0	0	0
Phalanx 3	5	M indet.	0	0	2	0	0	0
Long bone	1	Total	31	25	4	17	21	6

2 months of life and the remaining 48 fragments of postcranial remains were from the lower limb, including 23 carpal, tarsal and phalanges, five long bones, eight axial elements (vertebrae and ribs) and 12 mandible and skull pieces (Table 2). Regarding the MNI of the population, the assemblage represents at least three senile individuals, five adults, two juveniles and nine infants based on repeated teeth of different ages, in addition to wider consideration of tooth dimensions and toothwear that enable different individuals to be distinguished (Table 2). Due to the fragmentation of the dental remains it was only possible to estimate the sex of four individuals using canine measurements, with three canines (two left and one right) being from males, and one likely being a female (See Supplementary Table 3).

Šalitrena Pećina Cave Bear Diet and Ecology inferred from $\delta^{13}C$ and $\delta^{15}N$ analysis

Collagen was successfully extracted and analysed from 10 of the 11 bone specimens, which all had a collagen yield of >3% indicative of well-preserved collagen (Ambrose 1990; Van Klinken 1999). Only one specimen (SAL67) yielded insufficient collagen for analysis (Table 2). Standard quality control criteria were used to assess the δ^{13}C, and δ^{15}N data. All analysed samples had C: N atomic ratios between 3.1 and 3.2 indicating of good bone collagen preservation (Ambrose 1990; DeNiro 1985). The %C values for the samples ranged between 21.0% to 43.0%, with %N ranging between 7.7 and 16.1%, with most specimens falling at the upper end of this range (Table 3). The δ^{13}C values ranged from −22.4‰ to −18.8‰ (mean = −21.0‰, 1σ = 0.96), with δ^{15}N values ranging from 2.5‰ to 7.8‰ (mean = 5.8‰, 1σ = 1.71) (Figure 3).

The cave bear δ^{13}C and δ^{15}N values observed from Šalitrena Pećina are mostly consistent with the bears consuming a diet based on C3 resources, as would be expected for this period in Europe. The δ^{13}C and δ^{15}N values fall mainly within the range for the hunted ungulates from the site, except for one individual that has a δ^{13}C value higher than the herbivores of −18.8‰ (Figure 3, Table 3). The range of 3.6‰ of the cave bear δ^{13}C values is larger than that of any other species analysed (Figure 3, Table 3). The cave bears show a general trend towards lower δ^{13}C values in comparison to the other herbivores, which could be due to these individuals foraging in wooded environments, a phenomenon observed in other European cave bears (Krajcarz 2016), and has been noted in bone collagen δ^{13}C values at sites including Toll cave (Moià, Catalonia, NE Iberia) (Ramírez-Pedraza 2019), and Scladina in Belgium (Bocherens et al. 1997). The lower δ^{13}C red deer value

Table 3. Cave bear bone collagen δ^{13}C and δ^{15}N results with quality indicators, taken from inside Level 3 in the inside of the cave at Šalitrena Pećina. Fusion age estimation follows Weinstock (2009).

Sample number	Square	Sub Square	Bone ID Number	Element	Min. Fusion age (years)	% collagen	δ^{13}C ‰	δ^{15}N ‰	%C	%N	C: N
SAL62	W20	C	424	Metapodial	4–6	3.9	−22.4	7.8	39.3	14.7	3.1
SAL63	W20	C	424	Metapodial	4–6	3.9	−21.4	5.2	39.6	14.8	3.1
SAL69	W20	D	735	Phalanx 1	2–3	4.1	−20.5	2.5	40.0	14.9	3.1
SAL64	W20	D	734	Carpal	n/a	3.3	−21.2	5.9	21.0	7.7	3.2
SAL66	W21	A	651	Phalanx 3	2–3	3.3	−18.8	6.7	37.9	14.3	3.1
SAL71	W21	B	693	Phalanx 2	2–3	4.5	−21.1	5.0	30.2	11.2	3.2
SAL68	X22	D	700	Radial carpal	n/a	3.8	−21.3	4.3	36.1	13.5	3.1
SAL70	V20	A	524	Ulna	5–7	3.6	−21.2	5.7	37.5	14.2	3.1
SAL61	V20	B	661	Phalanx 1	2–3	3.7	−21.3	7.8	43.0	16.1	3.1
SAL67	V21	D	599	Metapodial	4–6	0		No collagen preserved			
SAL65	U21	D	641	Ulna	5–7	5.4	−21.6	6.7	38.3	14.3	3.1

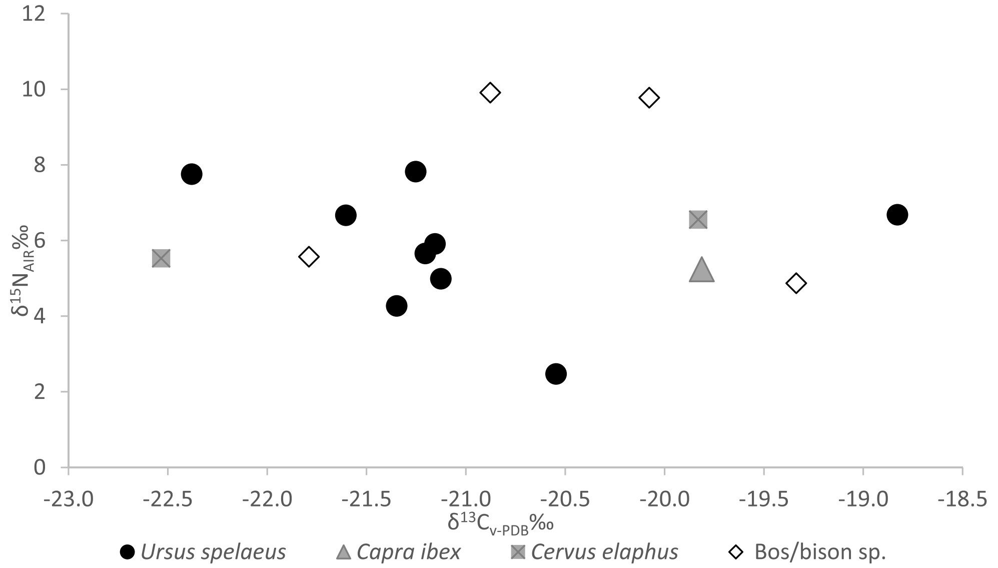

Figure 3. Cave bear $\delta^{13}C$ and $\delta^{15}N$ values from Šalitrena Pećina generated in this study plotted with the faunal baseline values from herbivores previously analysed from the site (see Marín-Arroyo et al. 2023).

from Šalitrena Pećina (Figure 3) also suggests a potential canopy effect, indicating that wooded environments were present within the locality of the site (Marín-Arroyo et al. 2023). This supports the possibility of cave bears at the site foraging in woodland locations. Whilst the cave bear and red deer $\delta^{13}C$ values are low, they are not so low as to suggest a dense forests, more an open woodland context.

Lower $\delta^{13}C$ values have also been associated with a hibernation effect, where fat stores are used as an energy source throughout the winter months, meaning that there is no excretion of urine or faeces (Nelson et al. 1975). The lack of bodily secretions during the winter months has direct implications on fractionation within bodily tissues, resulting in a depletion in ^{13}C and enrichment in ^{15}N (Bocherens et al. 1997; Fernández-Mosquera, Vila-Taboada, and Grandal-d'Anglade 2001; Hilderbrand et al. 1996), and may have contributed to the cave bear $\delta^{13}C$ and $\delta^{15}N$ values observed at Šalitrena Pećina.

One individual (SAL66) has a $\delta^{13}C$ value of −18.8‰ ($\delta^{15}N$ value of 6.7‰), which is higher than any other cave bear specimen in Europe to date (Table 3). This value is also outside the range of contemporary ungulates at the site (Figure 3). The authors considered the possibility that this specimen may have been a brown bear, especially given that the third phalanx can be challenging to differentiate morphologically (Torres Pérez-Hidalgo 1984). It is not possible to confirm the identification using ZooMS as this method cannot currently distinguish between different bear species (García-Vázquez et al. 2023). No brown bear remains have been found in the wider faunal assemblage from the site (Marín-Arroyo et al. 2023; Marín-Arroyo and Mihailović 2017), and brown bear remains are rare in cave deposits prior to the extinction of the cave bears (Münzel et al. 2011), which supports the morphological identification of this specimen as a cave bear, although DNA analysis would be needed to confirm this identification. The site is located 400 km from the sea, meaning that elevated $\delta^{13}C$ values associated with marine plant consumption (Schoeninger and DeNiro 1984) can be excluded. Freshwater aquatic plant consumption could potentially explain the elevated cave bear $\delta^{13}C$ value as aquatic plant $\delta^{13}C$ values are influenced by the isotopic composition, concentration, and source of dissolved inorganic carbon (Clementz, Holroyd, and Koch 2008). However, evidence for cave bears consuming aquatic plants has not been noted to date when reviewing published evidence (Bocherens 2019). Consuming specific terrestrial plant types which have distinct $\delta^{13}C$ values could also explain the elevated bear $\delta^{13}C$ result (Heaton 1999). The consumption of lichen is associated with elevated $\delta^{13}C$ values. This is typically seen in the archaeological bone collagen $\delta^{13}C$ and $\delta^{15}N$ values of species such as caribou and reindeer, which rely heavily on this food source (Britton 2023a; Salmi et al. 2020; Stevens et al. 2008), but has been suggested as a contributor to the diet of muskoxen on the mammoth steppe (Schwartz-Narbonne 2019), suggesting that this is not a trait unique to deer. Evidence for cave bears and lichen consumption is rare, likely occuring during times when other resources were not available, and consumption of plants such as lichens have been proposed for some cave bears in Europe (Vila Taboada, Mosquera, and Grandal d'Anglade 2001). Limited consumption of lichens, or similar species may have influenced the $\delta^{13}C$ value of the individual from Šalitrena Pećina and could indicate wide-ranging resource exploitation within the cave bears found at the site.

Similar $\delta^{13}C$ values of below −19‰ have been observed in herbivorous Late Pleistocene brown bears found at Neue Laubenstein-Bärenhöhle (−18.7‰) and Schlüssellochhöhle (−18.7‰) in Germany (Döppes et al. 2008), Sclandia (−18.6‰) and Spy (−18.4‰) in Belgium (Bocherens et al. 1999; Bocherens et al. 2013), and Goats Hole Cave in the UK (−17.3‰, −17.9% and a further two individuals with values of −18.6%) (Jacobi and Higham 2008; Richards 2000). The lower $\delta^{13}C$ value of the Šalitrena Pećina individual SAL66, which is consistent with values observed in wider European brown bear populations suggests that on occasion the niches of these two species may have overlapped, potentially during periods of habitat pressure linked to environmental change, although further research is needed to explore this hypothesis.

The $\delta^{15}N$ values of the bears from Šalitrena Pećina range from 2.5 to 7.8‰ (Table 1, Figure 2). This range is within those seen for the *Bos/Bison* sp. at the site, reflecting an isotopically variable landscape due to different environmental zones being present (Marín-Arroyo et al. 2023). The Šalitrena Pećina cave bear results typically map within the local faunal baseline from the site, indicating a predominantly plant-based diet, which is consistent with the interpretations of cave bear stable isotope results from many sites across Europe (Bocherens 2019). The relatively large range in $\delta^{15}N$ values of cave bears at Šalitrena Pećina could suggest diversity in the diet between individuals, reflecting either varying foraging zones, or preference by some individuals for nitrogen-fixing plants, such as those from the *Fabaceae* family as suggested by other authors (Vila Taboada, Mosquera, and Grandal d'Anglade 2001).

Some of the inter-individual variation in the $\delta^{15}N$ values may be due to younger sub-adult bear collagen having a long-term isotopic signature reflecting a combination of both feeding on maternal milk as well as reflecting their mother's hibernation metabolism (Bocherens et al. 2004a; Pérez-Rama, Fernández-Mosquera, and Grandal-d'Anglade 2011b). Newborn bears are expected to have $\delta^{15}N$ values two trophic levels above their mothers, estimated to be around 6‰ (Lidén and Angerbjörn 1999) due to metabolic cycling of the mother's proteinaceous tissues during the hibernation process, which drops to 1 trophic level (~3‰) as the cub ages and consumes maternal milk (Lidén and Angerbjörn 1999; Nelson et al. 1998). Bears have a particularly long lactation period (Oftedal and Gittleman 1989), with the nursing effect gradually becoming more muted as bones grow and turnover occurs (Lidén and Angerbjörn 1999). Bulk collagen values in younger individuals represent a shorter time period than in mature adults, meaning that they maintain some of the isotopic signatures from infancy. Although all sampled elements from Šalitrena Pećina were fused it is not possible to know the exact age of the individuals analysed. The earliest fusing skeletal elements within the assemblage (phalanges) are estimated to fuse between 2 and 3 years (Stiner 1998; Weinstock 2009), which could potentially still reflect a residual nursing signature if the animals died around that age. As the age at death of these individuals is not known alternative explanations must be considered.

Hibernation can cause organic tissues to be depleted in ^{13}C and enriched in ^{15}N (Bocherens et al. 1997; Fernández-Mosquera, Vila-Taboada, and Grandal-d'Anglade 2001; Hilderbrand et al. 1996). The higher variability in the $\delta^{15}N$ values of the bear bones analysed may be linked to differences in the hibernation patterns between the individuals analysed. The hibernation effect on $\delta^{15}N$ is thought to be about 1‰, based on black bears (Lohuis, Harlow, and Beck 2007), and further elevations in $\delta^{15}N$ values may reflect longer hibernation periods, resulting from prolonged winters arising from typically cooler climatic conditions (D'Anglade and Mosquera 2008; Fernández-Mosquera, Vila-Taboada, and Grandal-d'Anglade 2001). The inter-individual (and intra-individual within specimen 424) differences in $\delta^{15}N$ values observed within the Šalitrena Pećina specimens may be reflecting differences in hibernation periods between individuals sampled in this study, linked to climatic change affecting food availability. To explore this further, the analysis of $\delta^{18}O_{phos}$ of ungulate teeth from Šalitrena Pećina would help with understanding seasonal temperatures and amplitudes at the site, which have been successfully applied to MIS 3 sites such as Axlor in Spain (Pederzani et al. 2023) and Abri du Maras in France (Britton 2023b).

Bone specimen 424 (samples SAL62 and SAL63) showed intra-individual variability, with the two samples having a 2.6‰ difference in $\delta^{15}N$ values and a 1‰ difference in $\delta^{13}C$ values (Table 3). It is known that bone turnover in cortical bone can differ between the inner and outer surface, which has been observed in *Ursus arctos* femoral collagen, with the shaft of the bone representing isotopic values during adolescence when bone growth was rapid (Matsubayashi and Tayasu 2019). Specimen 424 was a fused metapodial with a minimum fusion age of between 4 and 6 years. Bone turnover has not been as clearly modelled experimentally for metapodials, but individual differences in the $\delta^{13}C$ and $\delta^{15}N$ values observed may be linked to the bone representing formation periods potentially with longer periods of hibernation being more strongly represented in one of the samples. Further studies of analogous modern-day hibernating bear species to explore changing $\delta^{13}C$ and $\delta^{15}N$ values between skeletal elements within an individual, as well

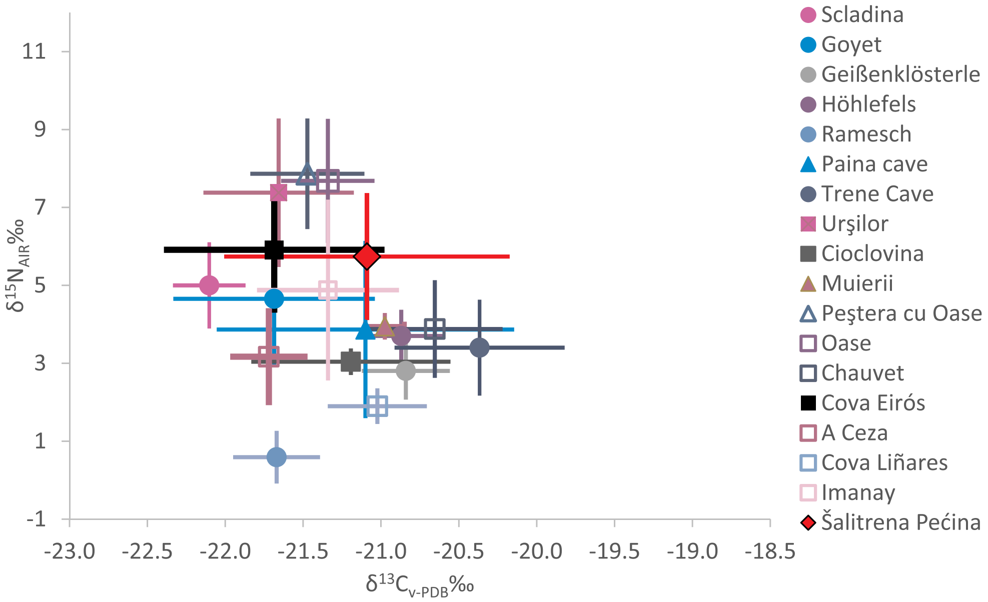

Figure 4. Cave bear δ^{13}C and δ^{15}N values from across Europe are presented as their mean value with error bars showing one standard deviation from the men. The Šalitrena Pećina data are shown as a diamond compared with other European sites shown as circles and squares.

as throughout different skeletal elements, would be valuable to examine the impact of hibernation in bone tissues of varying turnover rates.

Šalitrena Pećina Cave Bear Diet and Ecology in a European Context

To understand the Šalitrena Pećina cave bear results in context, they have been compared to findings from other European cave bear populations in Europe from the Late Pleistocene. Table 3 shows the bone collagen δ^{13}C and δ^{15}N value summary statistics for cave bears analysed across Europe, excluding sites where fewer than four individuals were present. This means that the sites of Herdengel, Hartelsgraben, Lieglloch, Drachenloch, Bärenloch, Conturines, Camiac, Tito Bustillo, Arcoia, and Pala de Rebolal were excluded from this table. Cave bears from Tayn Cave (Middle Urals) and Medvezhiya Cave (Northern Urals) (Kosintsev et al. 2023) have been studied but could not be included here as raw values and quality indicators were not available.

Figure 4 displays mean cave bear values from study sites and error bars showing 1σ from the mean, with individual δ^{13}C and δ^{15}N values shown in Figure 5 to show the spread of data across the population.

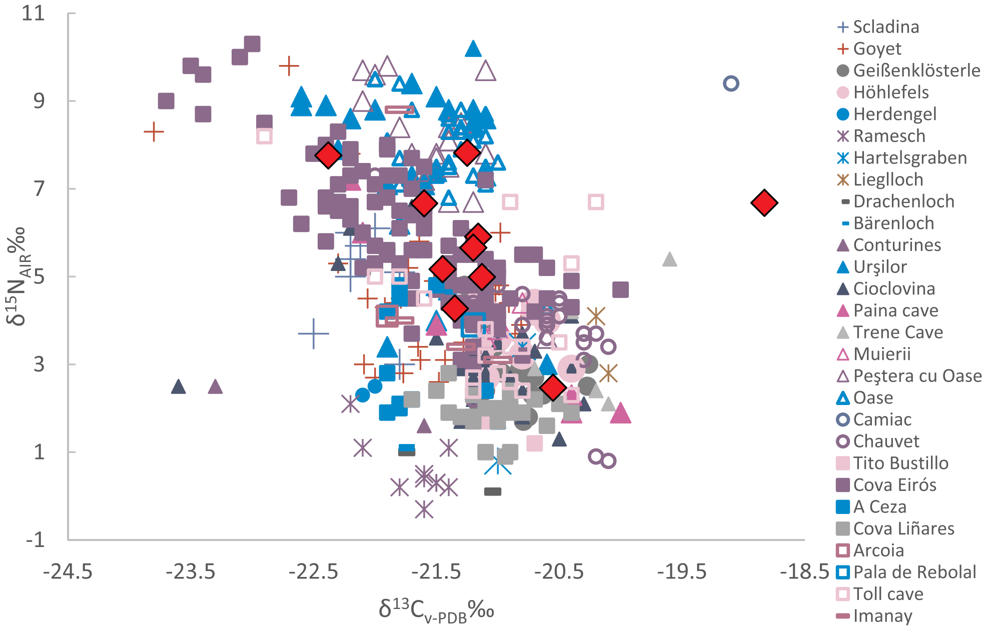

Figure 5. A bivariate plot showing cave bear δ^{13}C and δ^{15}N values across Europe. The Šalitrena Pećina specimens are displayed as large diamonds. Please see the supplementary file-Table 2 for the references for the data.

Table 4. Existing Comparative Late Pleistocene European cave bear bone collagen δ^{13}C and δ^{15}N Summary statistics.

Site and location					δ^{13}C					δ^{15}N					
Site	Location	Chronology	Altitude (m)	N	Mean	Min	Max	1σ	Range	Mean	Min	Max	1σ	Range	References
Scladina	Belgium	Early MIS 3	107	8	−22.1	−22.5	−21.8	0.2	0.7	5.0	3.0	6.1	1.1	3.1	Bocherens et al. (2011)
Goyet	Belgium	Late MIS 3	178	26	−21.7	−23.8	−20.8	0.6	3.0	4.7	2.6	9.8	1.8	7.2	Grocke et al. (2017)
Geißenklösterle	Germany	Early and Late MIS 3	577	18	−20.8	−21.3	−20.3	0.3	1.0	2.8	1.7	4.8	0.7	3.1	Münzel et al. (2011)
Höhlefels	Germany	Late MIS 3	602	10	−20.9	−21.2	−20.4	0.3	0.8	3.7	2.7	4.4	0.6	1.7	Münzel et al. (2011)
Ramesch	Austria	Early and Late MIS 3	1960	10	−21.7	−22.2	−21.4	0.3	0.8	0.6	−0.3	2.1	0.7	2.4	Bocherens et al. (2011)
Paina cave	Italy	Late MIS 3/ Early MIS 2	350	6	−21.1	−22.2	−20.0	1.0	2.2	3.9	1.9	7.2	2.3	5.3	Terlato et al. (2019)
Trene Cave	Italy	Late MIS 3/Early MIS 2	360	6	−20.4	−21.2	−19.6	0.5	1.6	3.4	2.1	5.4	1.2	3.3	Terlato et al. (2019)
Urşilor	Romania	MIS 3	491	28	−21.7	−22.6	−20.6	0.5	2.0	7.4	3.0	10.2	1.9	7.2	Robu et al. (2013)
Cioclovina	Romania	MIS 3	896	30	−21.2	−23.6	−20.3	0.6	3.3	3.0	1.3	6.6	1.2	5.3	Robu et al. (2013)
Muierii	Romania	MIS 3	779	4	−21.0	−21.1	−20.8	0.1	0.3	4.0	3.6	4.4	0.3	0.8	Robu et al. (2013)
Peştera cu Oase	Romania	Early MIS 3	655	22	−21.5	−22.1	−20.6	0.4	1.5	7.9	3.6	9.8	1.4	6.2	Richards (2008)
Oase	Romania	MIS 3	655	34	−21.3	−22.0	−20.6	0.3	1.4	7.7	1.7	9.5	1.6	7.8	Robu et al. (2013)
Chauvet	France	Early and Late MIS 3	164	26	−20.7	−22.0	−20.1	0.4	1.9	3.9	0.8	7.3	1.3	6.5	Bon et al. (2011)
Šalitrena Pećina	Serbia	Early MIS 3	277	10	−21.1	−22.4	−18.8	0.9	3.6	5.7	2.5	7.82	1.6	5.4	This study
Cova Eirós	Spain	Late MIS 3	870	97	−21.7	−23.7	−20.0	0.7	3.7	5.9	3.0	10.3	1.6	7.3	Perez-Rama et al. (2011b)
A Ceza	Spain	Early MIS 3	1202	10	−21.7	−21.9	−21.1	0.2	0.8	3.2	1.9	4.8	1.2	2.9	Krajcarz (2016)
Cova Liñares	Spain	Early MIS 3	1108	23	−21.0	−21.7	−20.4	0.3	1.3	1.9	0.9	2.8	0.5	1.9	Vila Taboda et al. (1999)
Toll Cave	Spain	Early MIS 3	862	20	−21.1	−22.9	−20.2	0.6	2.7	4.0	2.3	8.2	1.7	5.9	Ramírez-Pedraza (2019)
Imanay	Russia	Early and Late MIS 3	246	5	−21.3	−21.8	−20.8	0.5	1.0	4.9	3.1	8.8	2.3	5.7	Gimranov et al. (2023)

Notes: Data and references for cave bear data can be found in the Supplementary table 2. Only sites with >4 individuals analysed have been included within the summary statistics presented here.

Recent chrono-spatial modelling, based predominantly on herbivores has shown baseline differences in $\delta^{15}N$ values within isoscapes of Europe during MIS 3 and MIS 2, which may be partly responsible for some inter-site differences (Reade et al. 2023), and an increase in altitude has been noted to produce decreased $\delta^{15}N$ values of cave bears (Krajcarz 2016). Here, the discussion of the results focuses on comparisons of population ranges and standard deviations rather than absolute value differences between sites, which may be reflecting geographical, altitudinal and temporal variations in baseline values. This approach will allow for meaningful population level insights into the dietary behaviour of cave bears between different sites. Interpretations of the results by the original authors are also taken into account (Table 4).

The large intra-site range in $\delta^{13}C$ values at Šalitrena Pećina is mirrored in sites such as Goyet, Cioclovina, Cova Eirós all of which have a range >3‰ (Figure 5, Table 3). The largest ranges in $\delta^{15}N$ values (>7‰) are observed at Urşilor, Goyet, Cova Eirós and Oase (Table 3, Figure 5). The Šalitrena Pećina range in $\delta^{15}N$ values (5.3‰) is consistent with the ranges seen at Cioclovina, and Paina cave (Table 3, Figure 5). Some of the intra-population variation in the $\delta^{13}C$ and $\delta^{15}N$ values analysed at these sites may be due to differing ages of bears being selected for study, with some nursing signatures potentially being recognised, although the publications do not note that these individuals sampled were particularly young.

A degree of the inter-individual variation between the cave bear $\delta^{13}C$ and $\delta^{15}N$ values may be linked to differences in hibernation locations, or temporal variations reflecting the intensity of the winters experienced (D'Anglade and Mosquera 2008; Pérez-Rama, Fernández-Mosquera, and Grandal-D'anglade 2011a). Changing hibernation patterns resulting from climatic change has been cited as an important factor in cave bear extinction (Vila Taboada, Mosquera, and Grandal d'Anglade 2001), and insufficient resources in the crucial pre-dormancy period during times of longer hibernation could have dire consequences. Incremental $\delta^{13}C$ and $\delta^{18}O$ analysis, as conducted on bears at Biśnik cave (Krajcarz, Krajcarz, and Marciszak 2014), could help to explore changing seasonal conditions experienced by cave bears directly, although as a highly destructive method this has understandably not been widely applied. Overall, the intra-population variability in the $\delta^{13}C$ and $\delta^{15}N$ values observed within wider European populations suggests that even when factoring in metabolic effects relating to environmental conditions, and geographical baseline variations, cave bear diet was not homogenous, reflecting a varying landscape with different resources available, as suggested by other authors such as (Robu et al. 2013).

The European cave bear $\delta^{13}C$ and $\delta^{15}N$ values indicate a predominantly herbivorous diet, of wide-ranging plant resources based on what was locally available, with some exceptions such as the omnivorous behaviour as suggested by the $\delta^{13}C$ and $\delta^{15}N$ values of cave bears from Peştera cu Oase (Richards 2008). Dental microwear evidence has provided a more nuanced understanding of dietary behaviour. Comparisons of cave bear dental microwear patterns with modern bear species of known diets has suggested that the species was predominantly herbivorous with periods of omnivorous behaviour (Brent Jones and Desantis 2016). At Toll Cave (Moià, Catalonia, NE Iberia) specimens dating to >49 kyr BP had $\delta^{13}C$ and $\delta^{15}N$ values indicating a herbivorous diet, although dental microwear indicated omnivorous activity occurred, suggesting plasticity in cave bear diet at least in Southern latitudes (Ramírez-Pedraza 2019). Microwear evidence from 43 individuals at Goyet cave (Belgium) suggested omnivory prior to hibernation (Peigné et al. 2009), and pitting of cave bear teeth observed at Spanish sites indicates that cave bears occasionally consumed bones (Pinto-Llona 2013). In summary, current evidence indicates some flexibility in the dietary behaviour of cave bears. The long-term bone collagen record suggests a predominantly plant-based diet, whereas indicators from teeth suggest that occasional exploitation of non-plant resources occurred. Ultimately, cave bears appeared to have adapted to the localised environments where they were feeding, resulting in dietary differences between groups, as suggested at sites in the Swabian Jura (Bocherens et al. 2011b; Münzel et al. 2013). The results from Šalitrena Pećina, combined with the pan-European comparisons presented within this paper support the hypothesis that cave bears had relatively flexible herbivorous diets linked to localised food sources available.

Implications for Understanding Cave Bear Ecology and Extinction

Regarding hypotheses surrounding the extinction of cave bears, one current theory is that cave bear diet was highly specialised, with a heavy reliance on plants and little flexibility (Naito 2020), suggesting that when changes in the climate and environment happened during the Late Pleistocene, they were not able to adapt. The studies from Šalitrena Pećina indicate dietary plasticity of the cave bears studied, albeit within an herbivorous spectrum, suggesting an ability to exploit diverse environmental zones in the landscape. Studies of $\delta^{13}C$ and $\delta^{15}N$ values from cave bear populations on a pan-European scale indicate that the diet of this species was varied, even within populations, exploiting an isotopically diverse range of plant-based foods (Table 3, Figures 4 and 5). Although the diet of cave bears was predominantly herbivorous, it was not homogenous throughout time and space and shows that they had the flexibility to adapt to the localised conditions and resources that were available.

When we consider models of extinction of other species, for example, the Neanderthals, which happened in a mosaic pattern across Europe (Higham 2014; Vidal-Cordasco et al. 2023), it appears that cave bear extinction may have followed a similar mode, with cave bears adapting to changing environments through plasticity in their dietary behaviour. As the colder conditions of MIS 2 approached, the associated changing vegetation suggested by (Pacher and Stuart 2009) may have partly been responsible for cave bear extinction, limiting the carrying capacity of the land, and causing competition for already pressured resources with other agents that were also occupying these landscapes. Human predation or niche competition may have also played a role, as genetic evidence shows that cave bear populations were already in decline from 50 kyr to 40 kyr BP (Gretzinger 2019; Stiller 2010), coinciding with the arrival of modern humans. Together, current evidence suggests that a reduction in available resources combined with factors such as longer winter hibernations (D'Anglade and Mosquera 2008; Pérez-Rama, Fernández-Mosquera, and Grandal-D'anglade 2011a), and competition for resources during a climatically turbulent time may all have influenced the extinction of the species.

Reflecting on Past Extinctions to Support Threatened Species Today

The findings from this research raise important considerations for facilitating the survival of species currently under threat today. Brown bears, once common across Europe, now survive in pockets of occupation across the mountainous regions across Eurasia (Zedrosser et al. 2001), paralleling the mosaic patterns of late cave bear survival. Factors that contributed to the extinction of the cave bears including competition for resources and habitats, as well as predation by humans, are major threats to brown bears in Europe today (Lavadinović et al. 2013). A changing climate affecting vegetation diversity and availability, is impacting on brown bear distribution (Penteriani et al. 2019), as seen during the later phases of cave bear extinction. Reflecting on the scenarios that facilitated brown bear survival, when their cave bear counterparts became extinct, can be valuable in informing on current conservation efforts.

Archaeologically brown bears have shown resilience and adaptability when facing pressures. They survived when cave bears did not, and this may be partly due to them exhibiting dietary partitioning to avoid potential competition for resources with other species (Bocherens 2015; Rey-Iglesia 2019). For example, brown bears from Yukon and Alaska had lower $\delta^{13}C$ and $\delta^{15}N$ values, indicative of an herbivorous diet, when co-existing with the carnivorous giant short-faced bears. However, following the extirpation of the short-faced bear, brown bears exhibited elevated $\delta^{13}C$ and $\delta^{15}N$ values, interpreted as an increase in meat consumption (Bocherens 2015). In Europe the extinction of the cave bears likely provided space in the herbivore niche for brown bears to occupy (Ersmark 2019; Münzel et al. 2011), and their adaptability in changing conditions even if faced with competitors contributed to their survival during the late Pleistocene. The ability to adapt to competition relies on having appropriate resources available in alternative niches. Today, the loss of environments, and competition with humans through intensification of land use means that opportunities to adapt by shifting niches are limited. Modelling of current day habitat suitability for brown bears to maintain appropriate varied ecosystems is one way to help with conservation efforts (Scharf and Fernández 2018). Active creation and maintenance of habitats that offer a variety of food sources for brown bears is also a crucial conservation strategy (Cisneros-Araujo et al. 2021). Such approaches would provide bears with a greater opportunity to diversify their resource base and would ultimately facilitate their survival.

As with the cave bears, a major challenge facing brown bears today is anthropogenic activity limiting access to resources and habitats. The impact of agricultural activity on brown bears have been observed since at least the twentieth Century at Mont Ventoux (France), where Holocene specimens had lower $\delta^{15}N$ values than their omnivorous twentieth century counterparts in the region, interpreted as the ancient specimens being denied access to livestock as a protein source due to careful husbandry strategies barring access to domestic animals (Bocherens et al. 2004b). Determining the extent to which anthropogenic activity impacts on existing brown bear populations is a crucial aspect of conservation of the species. Managing human modifications to habitats to ensure that a range of food sources are available would help to buffer the impact of environmental change and human activity on bear populations. Maintaining pathways and connections between habitats (Cisneros-Araujo et al. 2021) is crucial in facilitating access to resources and reducing competition for land resulting from intense anthropogenic activity.

Human pressure on environments is happening on an unprecedented scale today. When modern humans and cave bears started occupying the same spheres the former subsequently became extinct. With careful management, we can try to prevent European brown bears from suffering the same fate. As briefly explored here, a key aspect of this is drawing links between bear ecologies in the past with present-day bear populations and learning from these lessons. Understanding the adaptive behaviours practised by fauna in the past is an important aspect of developing successful management strategies for species under threat today.

Conclusions

This paper has explored the diet of cave bears at the site of Šalitrena Pećina, dating to 36,150 ± 750 BP (OxA-27948) (Marín-Arroyo and Mihailović 2017), representing the first results from morphologically identified cave bears published from Serbia and proving a unique insight into the diet and ecology of the species. The inter-individual ranges of the $\delta^{13}C$ and $\delta^{15}N$ observed indicate that whilst being predominantly herbivorous and generally within the baseline stable isotope ranges for local herbivores at the site, their observed values reflect a variety of plant-based food sources and ecological habitats. Some of the inter-individual variability appears to be linked to dietary differences, indicating flexibility in diet likely related to wide-ranging isotopic zones in the site's locality. The high intra-individual variability within samples taken from specimen 424 suggests that further research into bear bone turnover would be beneficial in understanding the timescales represented within different skeletal elements and the factors that may influence values on an intra-element basis, such as residual nursing effects and hibernation patterns. When compared to Late Pleistocene cave bears from across Europe, the Šalitrena Pećina specimens show some of the largest ranges in $\delta^{13}C$ and $\delta^{15}N$ values, which might reflect diversity in the environments in the locality of the cave, as suggested through existing ungulate $\delta^{13}C$ and $\delta^{15}N$ evidence (Marín-Arroyo et al. 2023).

Understanding variability in cave bear behaviour is crucial in helping to reconstruct their ecology and can contribute to the debate surrounding their extinction. It seems that cave bears were relatively adaptable, demonstrating flexibility in diet within the herbivorous food spectrum. The onset of MIS 2 and the associated cooling that occurred at that time may have affected many facets of cave bear life, including hibernation duration, plant availability, and may have put pressure on ecosystems, especially when competing with humans and other species in similar ecological niches. Understanding factors that may have contributed to cave bear extinction can help contribute towards productive conservation management strategies for bear species currently under threat. By characterising past bear behaviour, we can help devise nature-based solutions that will help support the survival of other bear populations in the world today. Active habitat creation with a diverse range of resources and connecting habitat zones, as well as limiting the impact of anthropogenic activity in areas inhabited by brown bears, will all help to support the species.

Acknowledgements

Excavations at Šalitrena Pećina were organised by the National Museum of Serbia and funded by the Ministry of Culture of the Republic of Serbia. The authors are grateful for access provided to the Collection for Palaeolithic and Mesolithic in the National Museum of Serbia and facilities at the Faculty of Philosophy, University of Belgrade in order to sample these remains. We would like to thank the anonymous reviewers for their valuable comments and suggestions that have helped to further improve this manuscript.

Disclosure Statement

No potential conflict of interest was reported by the author(s).

Funding

This research has been supported by the European Commission through an ERCCoG project (SUBSILIENCE-Ref818299), the Spanish Ministry of Science, Innovation and Universities (HAR2012- 33956; HAR2017- 84997- P), and the British Academy (Postdoctoral Fellowship and Small Grants102618). JJ was supported by the Spanish Ministry of Science and Innovation (IJCI-2017-33689) when undertaking aspects of this research. The work of DM was supported by the NEEMO project of the Science Fund of the Republic of Serbia (7746827).

Notes on contributors

Dr Jennifer R. Jones is a Senior Lecturer in Archaeological Science at the University of Central Lancashire. Her research explores human-animal-environment relationships in the past. She uses stable isotope analysis alongside traditional zooarchaeological methods to reconstruct past human diet, animal management strategies and faunal palaeoecologies. She has worked on material from Middle and Upper Palaeolithic sites in Europe as well as remains from the North Atlantic Islands from Prehistory through to the Viking era.

Dr. Rhiannon E. Stevens is a Professor in Archaeological Science at University College London. She specialises in the use of stable isotopes and radiocarbon dating to explore paleoclimates, palaeoenvironments, Palaeodiets and Palaeomobility. She has worked extensively on palaeolithic sites from Eurasia to reconstruct past human responses to climatic and environmental changes.

Dušan Mihailović is a full professor at the Department of Archaeology, Faculty of Philosophy, University of Belgrade. As a director and co-director of numerous international and national projects, Mihailović was instrumental in the discovery and excavation of numerous palaeolithic sites in Servia, Montenegro, Bosnia and Herzegovina. His field of expertise covers lithic technology and wider aspects of investigation of the palaeolithic and Mesolithic in the Balkans.

Bojana Mihailović is a museum curator at the National Museum in Belgrade. Since 2004 she has been leading the archaeological excavations at Šalitrena Pećina cave. Her research focuses on lithic technology and palaeolithic and Mesolithic archaeology in South-eastern Europe, and is particularly interested in public engagement, and involving the public in the protection of cultural heritage.

Ana B. Marin-Arroyo is a Professor at the University of Cantabria (Spain) where she leads the EVOADAPTA research group. She is an archaeozoologist specialising in studying the palaeolithic in the Southern European peninsula using cutting edge interdisciplinary methods. She is particularly interested in human resilience and adaptation to changing environments, specifically adaptations in subsistence strategies.

ORCID

Jennifer R. Jones http://orcid.org/0000-0002-9247-7994
Rhiannon E. Stevens http://orcid.org/0000-0002-6140-4549
Dušan Mihailović http://orcid.org/0000-0002-8607-8196
Ana B. Marín-Arroyo http://orcid.org/0000-0003-3353-5581

References

Abrams, G., S. M. Bello, K. Di Modica, S. Pirson, and D. Bonjean. 2014. "When Neanderthals Used Cave Bear (*Ursus spelaeus*) Remains: Bone Retouchers from Unit 5 of Scladina Cave (Belgium)." *Quaternary International* 326–327:274–287. https://doi.org/10.1016/j.quaint.2013.10.022.

Ambrose, S. H. 1990. "Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis." *Journal of Archaeological Science* 17 (4): 431–451. https://doi.org/10.1016/0305-4403(90)90007-R.

Baca, M., D. Popović, K. Stefaniak, A. Marciszak, M. Urbanowski, A. Nadachowski, and P. Mackiewicz. 2016. "Retreat and Extinction of the Late Pleistocene Cave Bear (*Ursus spelaeus* sensu lato)." *The Science of Nature* 103 (11): 1–17. https://doi.org/10.1007/s00114-016-1414-8.

Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. "Assessing the Causes of Late Pleistocene Extinctions on the Continents." *Science* 306 (5693): 70–75. https://doi.org/10.1126/science.1101476.

Bocherens, H., et al. 2011. "Niche Partitioning between two Sympatric Genetically Distinct Cave Bears (*Ursus spelaeus* and *Ursus ingressus*) and Brown Bear (*Ursus arctos*) from Austria: Isotopic Evidence from Fossil Bones." *Quaternary International* 245 (2): 238–248. https://doi.org/10.1016/j.quaint.2010.12.020.

Bocherens, H. 2015. "Isotopic Tracking of Large Carnivore Palaeoecology in the Mammoth Steppe." *Quaternary Science Reviews* 117:42–71. https://doi.org/10.1016/j.quascirev.2015.03.018.

Bocherens, H. 2019. "Isotopic Insights on Cave Bear Palaeodiet." *Historical Biology* 31 (4): 410–421. https://doi.org/10.1080/08912963.2018.1465419.

Bocherens, H., A Argant, J Argant, D Billiou, E Crégut-Bonnoure, B Donat-Ayache, M Philippe, and M Thinon 2004b. "Diet Reconstruction of Ancient Brown Bears (*Ursus arctos*) from Mont Ventoux (France) Using Bone Collagen Stable Isotope Biogeochemistry (13 C, 15N)." *Canadian Journal of Zoology* 82 (4): 576–586. https://doi.org/10.1139/z04-017.

Bocherens, H., D. Billiou, A. Mariotti, M. Patou-Mathis, M. Otte, D. Bonjean, and M. Toussaint. 1999. "Palaeoenvironmental and Palaeodietary Implications of Isotopic Biogeochemistry of Last Interglacial Neanderthal and Mammal Bones in Scladina Cave (Belgium)." *Journal of Archaeological Science* 26 (6): 599–607. https://doi.org/10.1006/jasc.1998.0377.

Bocherens, H., D. Billiou, M. Patou-Mathis, D. Bonjean, M. Otte, and A. Mariotti. 1997. "Paleobiological Implications of the Isotopic Signatures (13C, 15N) of Fossil Mammal Collagen in Scladina Cave (Sclayn, Belgium)." *Quaternary Research* 48 (3): 370–380. https://doi.org/10.1006/qres.1997.1927.

Bocherens, H., A. Bridault, D. G. Drucker, M. Hofreiter, S. C. Münzel, M. Stiller, and J. van der Plicht. 2014. "The Last of Its Kind? Radiocarbon, Ancient DNA and Stable Isotope Evidence from a Late Cave Bear (*Ursus spelaeus* ROSENMÜLLER, 1794) from Rochedane (France)." *Quaternary International* 339–340:179–188. https://doi.org/10.1016/j.quaint.2013.05.021.

Bocherens, H., D. G. Drucker, D. Billiou, J. M. Geneste, and J. van der Plicht. 2006. "Bears and Humans in Chauvet Cave (Vallon-Pont-d'Arc, Ardèche, France): Insights from Stable Isotopes and Radiocarbon Dating of Bone Collagen." *Journal of Human Evolution* 50 (3): 370–376. https://doi.org/10.1016/j.jhevol.2005.12.002.

Bocherens, H., M. Germonpré, M. Toussaint, and P. Semal. 2013. "Stable Isotopes. Spy Cave." In *125 Years of Multidisciplinary Research at the Betche aux Rotches (Jemeppe-sur-Sambre, Province of Namur, Belgium). 123/2012*, edited by H. Rougier, and P. Semal, 357–370. Brussels: Royal Belgian Institute of Natural Sciences, Royal Belgian Society of Anthropology and Praehistory & NESPOS Society.

Bocherens, H., M. Philippe, A. Argant, and J. Argant. 2004a. "Cave Bear Palaeoecology and Stable Isotopes; Checking the Rules of the Game." *Cahiers Scientifiques Hors sırie* 2: 183–188.

Bon, C., V. Berthonaud, P. Fosse, B. Gély, F. Maksud, R. Vitalis, M. Philippe, J. van der Plicht, and J.-M. Elalouf. 2011. "Low Regional Diversity of Late Cave Bears Mitochondrial DNA at the Time of Chauvet Aurignacian Paintings." *Journal of Archaeological Science* 38 (8): 1886–1895. http://doi.org/10.1016/j.jas.2011.03.033.

Borić, D., et al. 2022. "Neanderthals on the Lower Danube: Middle Palaeolithic Evidence in the Danube Gorges of the Balkans." *Journal of Quaternary Science* 37 (2): 142–180. https://doi.org/10.1002/jqs.3354.

Brent Jones, D., and L. R. G. Desantis. 2016. "Dietary Ecology of the Extinct Cave Bear: Evidence of Omnivory as Inferred from Dental Microwear Textures." *Acta Palaeontologica Polonica* 61 (4): 735–741.

Britton, K., et al. 2023a. "Multi-isotope Analysis of Bone Collagen of Late Pleistocene Ungulates Reveals Niche Partitioning and Behavioural Plasticity of Reindeer during MIS 3." *Scientific Reports* 13 (1): 1–13. https://doi.org/10.1038/s41598-023-42199-7.

Britton, K., et al. 2023b. "Multi-isotope Zooarchaeological Investigations at Abri du Maras: The Paleoecological and Paleoenvironmental Context of Neanderthal Subsistence Strategies in the Rhône Valley during MIS 3." *Journal of Human Evolution* 174:103292. https://doi.org/10.1016/j.jhevol.2022.103292.

Cisneros-Araujo, P., T. Goicolea, M. C. Mateo-Sánchez, J. I. García-Viñás, M. Marchamalo, A. Mercier, and A. Gastón. 2021. "The Role of Remote Sensing Data in

Habitat Suitability and Connectivity Modeling: Insights from the Cantabrian Brown Bear." *Remote Sensing* 13 (6): 1138. https://doi.org/10.3390/rs13061138.

Clementz, M. T., P. A. Holroyd, and P. L. Koch. 2008. "Identifying Aquatic Habits of Herbivorous Mammals through Stable Isotope Analysis." *Palaios* 23 (9): 574–585. https://doi.org/10.2110/palo.2007.p07-054r.

Cvetković, N. J., and V. M. Dimitrijević. 2014. "Cave Bears (Carnivora, Ursidae) from the Middle and Late Pleistocene of Serbia: A Revision." *Quaternary International* 339–340:197–208. https://doi.org/10.1016/j.quaint.2013.10.045.

D'Anglade, A. G., D. F. Mosquera, et al. 2008. "Hibernation Can Also Cause High δ15N Values in Cave Bears: A Response to Richards et al." *Proceedings of the National Academy of Sciences of the United States of America* 105 (11): E14–E14. https://doi.org/10.1073/pnas.0800915105.

DeNiro, M. J. 1985. "Postmortem Preservation and Alteration of In Vivo Bone Collagen Isotope Ratios in Relation to Palaeodietary Reconstruction." *Nature* 317 (6040): 806–809. https://doi.org/10.1038/317806a0.

Diedrich, C. G. 2012. "Cave Bear Killers and Scavengers from the Last Ice Age of Central Europe: Feeding Specializations in Response to the Absence of Mammoth Steppe Fauna from Mountainous Regions." *Quaternary International* 255:59–78. https://doi.org/10.1016/j.quaint.2011.06.048.

Diedrich, C. G. 2014a. "Neanderthal Bone Flutes': Simply Products of Ice Age Spotted Hyena Scavenging Activities on Cave Bear Cubs in European Cave Bear Dens." *Royal Society Open Science* 2 (4): 140022. https://doi.org/10.1098/rsos.140022.

Diedrich, C. G. 2014b. "Palaeopopulations of Late Pleistocene Top Predators in Europe: Ice Age Spotted Hyenas and Steppe Lions in Battle and Competition about Prey." *Paleontology Journal* 2014 (1): 106203.

Döppes, D., W. Rosendahl, M. Pacher, W. Imhof, G. Dalmeri, and H. Bocherens. 2008. "Stabile Isotopenuntersuchungen an spätglazialen und holozänen Braunbärenfunden aus Höhlen im Alpenraum." *Stalactite* 2 (58): 64–66.

Ersmark, E., et al. 2019. "Genetic Turnovers and Northern Survival during the Last Glacial Maximum in European Brown Bears." *Ecology and Evolution* 9 (10): 5891–5905. https://doi.org/10.1002/ece3.5172.

Fernández-Mosquera, D., M. Vila-Taboada, and A. Grandal-d'Anglade. 2001. "Stable Isotopes Data (δ13C, δ15N) from the Cave Bear (*Ursus spelaeus*): A new Approach to Its Palaeoenvironment and Dormancy." *Proceedings of the Royal Society B: Biological Sciences* 268 (1472): 1159–1164. https://doi.org/10.1098/rspb.2001.1639.

Figueirido, B., P. Palmqvist, and J. A. Pérez-Claros. 2009. "Ecomorphological Correlates of Craniodental Variation in Bears and Paleobiological Implications for Extinct Taxa: An Approach Based on Geometric Morphometrics." *Journal of Zoology* 277 (1): 70–80. https://doi.org/10.1111/j.1469-7998.2008.00511.x.

García-Vázquez, A., A. C. Pinto-Llona, J. Maroto, T. Torres, and A. Grandal-D'anglade. 2023. "Characterising the Cave Bear *Ursus spelaeus* Rosenmüller by ZooMS: A Review of Peptide Mass Fingerprinting Markers." *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 114 (1-2): 83–93. https://doi.org/10.1017/S1755691023000038.

Gimranov, D., H. Bocherens, N. Kavcik-Graumann, D. Nagel, and G. Rabeder. 2023. "The Cave Bears from Imanay Cave (Southern Urals, Russia)." *Historical Biology* 35 (4): 580–588. https://doi.org/10.1080/08912963.2022.2056837.

Grandal-D'Anglade, A., J. Ramon Vidal-Romani, M. Vaqueiro-Rodríguez, and E. Mendez-Quintas. 2006. "O Rebolal: A new Cave in Galicia (NW Spain) with Recent Cave Bear Remains: Preliminary Report." *Επιστημονική Επετηρίδα του Τμήματος Γεωλογίας (ΑΠΘ)* 98:173–178.

Grayson, D. K. 1979. "On the Quantification of Vertebrate Archaeofaunasle." In *Advances in Archaeological Method and Theory*, edited by M. B. Schiffer, Vol. 2, 199–237. New York: Springer.

Grayson, D. K., and F. Delpech. 2003. "Ungulates and the Middle-to-Upper Paleolithic Transition at Grotte XVI (Dordogne, France)." *Journal of Archaeological Science* 30 (12): 1633–1648. https://doi.org/10.1016/S0305-4403(03)00064-5.

Gretzinger, J., et al. 2019. "Large-scale Mitogenomic Analysis of the Phylogeography of the Late Pleistocene Cave Bear." *Scientific Reports* 9 (1): 1–11. https://doi.org/10.1038/s41598-019-47073-z.

Gröcke, D. R., P. E. Sauer, A. Bridault, D. G. Drucker, M. Germonpré, and H. Bocherens. 2017. "Hydrogen Isotopes in Quaternary Mammal Collagen from Europe." *Journal of Archaeological Science: Reports* 11: 12–16. http://doi.org/10.1016/j.jasrep.2016.11.020.

Heaton, T.H.E. 1999. Spatial, Species, and Temporal Variations in the 13C/12C Ratios of C3 Plants: Implications for Palaeodiet Studies. *Journal of Archaeological Science 26*(6), pp. 637–649. https://doi.org/10.1006/jasc.1998.0381

Higham, T., et al. 2014. "The Timing and Spatiotemporal Patterning of Neanderthal Disappearance." *Nature* 512 (7514): 306–309. https://doi.org/10.1038/nature13621.

Hilderbrand, G. V., S. D. Farley, C. T. Robbins, T. A. Hanley, K. Titus, and C. Servheen. 1996. "Use of Stable Isotopes to Determine Diets of Living and Extinct Bears." *Canadian Journal of Zoology* 74 (11): 2080–2088. https://doi.org/10.1139/z96-236.

Hoefs, J. 1997. *Stable Isotope Geochemistry*. Berlin: Springer.

Jacobi, R. M., and T. F. G. Higham. 2008. "The "Red Lady" Ages Gracefully: New Ultrafiltration AMS Determinations from Paviland." *Journal of Human Evolution* 55 (5): 898–907. https://doi.org/10.1016/j.jhevol.2008.08.007.

Jones, J., and K. Britton. 2019. "Multi-scale, Integrated Approaches to Understanding the Nature and Impact of Past Environmental and Climatic Change in the Archaeological Record, and the Role of Isotope Zooarchaeology." *Journal of Archaeological Science: Reports* 23:968–972. https://doi.org/10.1016/j.jasrep.2019.02.001.

Jones, J. R., A. B. Marín-Arroyo, M. S. Corchón Rodríguez, and M. P. Richards. 2021. "After the Last Glacial Maximum in the Refugium of Northern Iberia: Environmental Shifts, Demographic Pressure and Changing Economic Strategies at Las Caldas Cave (Asturias, Spain)." *Quaternary Science Reviews* 262:106931. https://doi.org/10.1016/j.quascirev.2021.106931.

Jones, J. R., A. B. Marín-Arroyo, L. G. Straus, and M. P. Richards. 2020. "Adaptability, Resilience and Environmental Buffering in European Refugia during the Late Pleistocene: Insights from La Riera Cave (Asturias, Cantabria, Spain)." *Scientific Reports* 10 (1): 1217.

Knapp, M., et al. 2009. “First DNA Sequences from Asian Cave Bear Fossils Reveal Deep Divergences and Complex Phylogeographic Patterns.” *Molecular Ecology* 18 (6): 1225–1238. https://doi.org/10.1111/j.1365-294X.2009.04088.x.

Koch, P. L., and A. D. Barnosky. 2006. “Late Quaternary Extinctions: State of the Debate.” *Annual Review of Ecology, Evolution, and Systematics* 37 (1): 215–250. https://doi.org/10.1146/annurev.ecolsys.34.011802.132415.

Kosintsev, P. A., K. Y. Konovalova, G. V. Simonova B Presented, and A. V. N. Bolshakov. 2023. “Content of 13C and 15N Isotopes in Bone Collagen of Geographical, Age, and Sex Groups of the Ural Cave Bear (Mammalia, Carnivora, Ursidae, Ursus (Spelaearctos) kanivetz Verestchagin, 1973).” *Doklady Biological Sciences* 513:539–543. https://doi.org/10.1134/S0012496623700076.

Krajcarz, M., et al. 2016. “Isotopic Variability of Cave Bears (δ15N, δ13C) across Europe during MIS 3.” *Quaternary Science Reviews* 131:51–72. https://doi.org/10.1016/j.quascirev.2015.10.028.

Krajcarz, M. T., M. Krajcarz, and A. Marciszak. 2014. “Paleoecology of Bears from MIS 8–MIS 3 Deposits of Biśnik Cave Based on Stable Isotopes (δ13C, δ18O) and Dental Cementum Analyses.” *Quaternary International* 326–327:114–124. https://doi.org/10.1016/j.quaint.2013.10.067 Accession: 080799107.

Kurtén, B. 1958. “Life and Death of the Pleistocene Cave Bear: A Study in Paleontology.” *Acta Zoologica Fennica* 95:4–59.

Kurtén, B. 1976. *The Cave Bear Story. Life and Death of a Vanished Animal*. New York: Columbia University Press.

Lavadinović, V., Z. Popović, Z. Ristić, and D. Beuković. 2013. “Threats and International Tools for Sustainable Brown Bear (*Ursus arctos* L.) Management.” *Ekologia Bratislava* 32 (4): 345–351.

Lengyel, G., and Z. Mester. 2002. “A New Look at the Radiocarbon Chronology of the Szeletian in Hungary.” *Eurasian Prehistory* 5 (2): 73–83.

Lidén, K., and A. Angerbjörn. 1999. “Dietary Change and Stable Isotopes: A Model of Growth and Dormancy in Cave Bears.” *Proceedings of the Royal Society B: Biological Sciences* 266 (1430): 1779–1783. https://doi.org/10.1098/rspb.1999.0846.

Lister, A. M., and A. J. Stuart. 2008. “The Impact of Climate Change on Large Mammal Distribution and Extinction: Evidence from the Last Glacial/Interglacial Transition.” *Comptes Rendus Geoscience* 340 (9–10): 615–620. https://doi.org/10.1016/j.crte.2008.04.001.

Lohuis, T. D., H. J. Harlow, and T. D. I. Beck. 2007. “Hibernating Black Bears (*Ursus americanus*) Experience Skeletal Muscle Protein Balance during Winter Anorexia.” *Comparative Biochemistry and Physiology-B Biochemistry and Molecular Biology* 147 (1): 20–28. https://doi.org/10.1016/j.cbpb.2006.12.020.

Lyman, R. L. 2008. *Quantitative Paleozoology*. Cambridge: Cambridge University Press.

Majkić, A., F. D’Errico, S. Milošević, D. Mihailović, and V. Dimitrijević. 2018. “Sequential Incisions on a Cave Bear Bone from the Middle Paleolithic of Pešturina Cave, Serbia.” *Journal of Archaeological Method and Theory* 25 (1): 69–116. https://doi.org/10.1007/s10816-017-9331-5.

Marín-Arroyo, A. B., J. R. Jones, E. Cristiani, R. E. Stevens, D. Mihailović, and B. Mihailović. 2023. “Late Pleistocene Hominin Settlement Patterns in the Central Balkans: Šalitrena Pećina, Serbia.” In *Late Pleistocene Hominin Settlement Patterns in the Central Balkans: Šalitrena Pećina, Serbia. Proceedings of the British Academy*, edited by A. Ruiz-Redondo, and W. Davies, 107–155. Oxford: Oxford University Press (OUP).

Marín-Arroyo, A. B., and B. Mihailović. 2017. “The Chronometric Dating and Subsistence of Late Neanderthals and Early Anatomically Modern Humans in the Central Balkans Insights from Šalitrena Pećina (Mionica, Serbia).” *Journal of Anthropological Research* 73 (3): 413–447. https://doi.org/10.1086/693054.

Matsubayashi, J., and I. Tayasu. 2019. “Collagen Turnover and Isotopic Records in Cortical Bone.” *Journal of Archaeological Science* 106:37–44. https://doi.org/10.1016/j.jas.2019.03.010.

Mihailović, D. 2014. *Paleolit na centralnom Balkanu. arheološko društvo*. Beograd: Srpsko.

Mihailović, D. D., and B. R. Mihailović. 2023. “Chronology and Succession of Palaeolithic Technocomplexes in Serbia. Зборник Народног музеја Србије. Археологија = Recueil du Musée national de Serbie.” *Archéologie* 26 (1): 11–37.

Mondanaro, A., et al. 2019. “Additive Effects of Climate Change and Human Hunting Explain Population Decline and Extinction in Cave Bears.” *Boreas* 48 (3): 605–615. https://doi.org/10.1111/bor.12380.

Münzel, S., and N. J. Conard. 2004. “Cave Bear Hunting in Hohle Fels Cave in the Ach Valley of the Swabian Jura.” *Revue de Paleobiologie* 23 (2): 877–885. https://doi.org/10.13140/RG.2.1.2271.0249.

Münzel, S. C., F. Rivals, M. Pacher, D. Döppes, G. Rabeder, N. J. Conard, and H. Bocherens. 2013. “Behavioural Ecology of Late Pleistocene Bears (*Ursus spelaeus*, *Ursus ingressus*): Insight from Stable Isotopes (C, N, O) and Tooth Microwear.” *Quaternary International* 339:148–163. https://doi.org/10.1016/j.quaint.2013.10.020.

Münzel, S. C., M. Stiller, M. Hofreiter, A. Mittnik, N. J. Conard, and H. Bocherens. 2011. “Pleistocene Bears in the Swabian Jura (Germany): Genetic Replacement, Ecological Displacement, Extinctions and Survival.” *Quaternary International* 245 (2): 225–237. https://doi.org/10.1016/j.quaint.2011.03.060.

Nadachowski, A. et al. 2009. *Late Pleistocene Environment of the Częstochowa Upland (Poland) Reconstructed on the Basis of Faunistic Evidence from Archaeological Cave Sites*. Krakow: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.

Naito, Y. I., et al. 2016. “Evidence for Herbivorous Cave Bears (*Ursus spelaeus*) in Goyet Cave, Belgium: Implications for Palaeodietary Reconstruction of Fossil Bears Using Amino Acid δ15N Approaches.” *Journal of Quaternary Science* 31 (6): 598–606. https://doi.org/10.1002/jqs.2883.

Naito, Y. I., et al. 2020. “Heavy Reliance on Plants for Romanian Cave Bears Evidenced by Amino Acid Nitrogen Isotope Analysis.” *Scientific Reports* 10 (1): 6612. https://doi.org/10.1038/s41598-020-62990-0.

Nelson, D. E., A. Angerbjörn, K. Lidén, I. Turk, A. Angerbjoè Rn, K. Lideâ, and I. Turk. 1998. “Stable Isotopes and the Metabolism of the European Cave Bear.” *Oecologia* 116 (1-2): 177–181. https://doi.org/10.1007/s004420050577.

Nelson, R. A., J. D. Jones, H. W. Wahner, D. B. McGill, and C. F. Code. 1975. “Nitrogen Metabolism in Bears: Urea Metabolism in Summer Starvation and in Winter Sleep and Role of Urinary Bladder in Water and Nitrogen Conservation.” *Mayo Clinic Proceedings* 50 (3): 141–146.

Oftedal, O. T., and J. L. Gittleman. 1989. "Patterns of Energy Output during Reproduction in Carnivores." In *In Carnivore Behavior, Ecology, and Evolution*, edited by John L. Gittleman, 355–378. Boston, MA: Springer US.

Pacher, M., and A. J. Stuart. 2009. "Extinction Chronology and Palaeobiology of the Cave Bear (*Ursus spelaeus*)." *Boreas* 38 (2): 189–206. https://doi.org/10.1111/j.1502-3885.2008.00071.x.

Pales, L., and C. H. Lambert. 1976. Atlas Ostéologique pour Mammifères I. Editions du Centre National de la Recherche Scientifique.

Pederzani, S., K. Britton, J. R. Jones, L. A. Pérez, J. M. Geiling, and A. B. Marín-Arroyo. 2023. "Late Pleistocene Neanderthal Exploitation of Stable and Mosaic Ecosystems in Northern Iberia Shown by Multi-isotope Evidence." *Quaternary Research 116* : 108–132. https://doi.org/10.1017/qua.2023.32.

Peigné, S., C. Goillot, M. Germonpré, C. Blondel, O. Bignon, and G. Merceron. 2009. "Predormancy Omnivory in European Cave Bears Evidenced by a Dental Microwear Analysis of *Ursus spelaeus* from Goyet, Belgium." *Proceedings of the National Academy of Sciences of the United States of America* 106 (36): 15390–15393. https://doi.org/10.1073/pnas.0907373106.

Penteriani, V., A. Zarzo-Arias, A. Novo-Fernández, G. Bombieri, and C. A. López-Sánchez. 2019. "Responses of an Endangered Brown Bear Population to Climate Change Based on Predictable Food Resource and Shelter Alterations." *Global Change Biology* 25 (3): 1133–1151. https://doi.org/10.1111/gcb.14564.

Pérez-Rama, M., D. Fernández-Mosquera, and A. Grandal-D'anglade. 2011a. "Effects of Hibernation on the Stable Isotope Signatures of Adult and Neonate Cave Bears." *Hors-série* 4:79–88.

Pérez-Rama, M., D. Fernández-Mosquera, and A. Grandal-d'Anglade. 2011b. "Recognizing Growth Patterns and Maternal Strategies in Extinct Species Using Stable Isotopes: The Case of the Cave Bear *Ursus spelaeus* ROSENMÜLLER." *Quaternary International* 245 (2): 302–306. https://doi.org/10.1016/j.quaint.2010.09.009.

Pettitt, P., and P. Bahn. 2015. "An Alternative Chronology for the art of Chauvet Cave." *Antiquity* 89 (345): 542–553. https://doi.org/10.15184/aqy.2015.21.

Pinto-Llona, A. C. 2013. "Macrowear and Occlusal Microwear on Teeth of Cave Bears *Ursus spelaeus* and Brown Bears *Ursus arctos:* Inferences concerning Diet." *Palaeogeography, Palaeoclimatology, Palaeoecology* 370:41–50. https://doi.org/10.1016/j.palaeo.2012.11.017.

Ramírez-Pedraza, I., et al. 2019. "Microwear and Isotopic Analyses on Cave Bear Remains from Toll Cave Reveal Both Short-Term and Long-Term Dietary Habits." *Scientific Reports* 9 (1): 1–12. https://doi.org/10.1038/s41598-019-42152-7.

Reade, H., et al. 2020. "Deglacial Landscapes and the Late Upper Palaeolithic of Switzerland." *Quaternary Science Reviews* 239:106372. https://doi.org/10.1016/j.quascirev.2020.106372.

Reade, H., J. A. Tripp, D. Fré Mondeau, K. L. Sayle Id, T. F. G. Higham, M. Street, and R. E. Stevens. 2023. "Nitrogen Palaeo-Isoscapes: Changing Spatial Gradients of Faunal δ15N in Late Pleistocene and Early Holocene Europe." *PloSOne* 18 (2): e0268607. https://doi.org/10.1371/journal.pone.0268607.

Rey-Iglesia, A., et al. 2019. "Evolutionary History and Palaeoecology of Brown Bear in North-East Siberia re-examined Using Ancient DNA and Stable Isotopes from Skeletal Remains." *Scientific Reports* 9 (1): 1–12. https://doi.org/10.1038/s41598-019-40168-7.

Richards, M. P. 2000. "Human and Faunal Stable Isotope Analysis from Goat's Hole and Foxhole Caves, Gower." In *Paviland Cave and the 'Red Lady': A Definitive Report*, edited by S. Aldhouse-Green, 71–75. Bristol: Western Academic and Specialist Press.

Richards, M. P., et al. 2008. "Isotopic Evidence for Omnivory among European Cave Bears: Late Pleistocene *Ursus spelaeus* from the Peştera cu Oase, Romania." *Proceedings of the National Academy of Sciences of the United States of America* 105 (2): 600–604. https://doi.org/10.1073/pnas.0711063105.

Robu, M., J. K. Fortin, M. P. Richards, C. C. Schwartz, J. G. Wynn, C. T. Robbins, and E. Trinkaus. 2013. "Isotopic Evidence for Dietary Flexibility among European Late Pleistocene Cave Bears (*Ursus spelaeus*)." *Canadian Journal of Zoology* 91 (4): 227–234. https://doi.org/10.1139/cjz-2012-0222.

Romandini, M., G. Terlato, N. Nannini, A. Tagliacozzo, S. Benazzi, and M. Peresani. 2018. "Bears and Humans, a Neanderthal Tale. Reconstructing Uncommon Behaviors from Zooarchaeological Evidence in Southern Europe." *Journal of Archaeological Science* 90:71–91. https://doi.org/10.1016/j.jas.2017.12.004.

Sabol, M., A. Bendík, M. Grivalský, M. Grivalský, J. Lizák, and I. Michlík. 2014. "Latest and Highest Fossil Record of Cave Bears (Ursus ex gr. spelaeus) in Slovakian Western Carpathians." *Quaternary International* 339:189–196.

Salmi, A. K., M. Fjellström, T. Äikäs, M. Spangen, M. Núñez, and K. Lidén. 2020. "Zooarchaeological and Stable Isotope Evidence of Sámi Reindeer Offerings." *Journal of Archaeological Science: Reports* 29:102129. https://doi.org/10.1016/j.jasrep.2019.102129.

Scharf, A. K., and N. Fernández. 2018. "Up-scaling Local-Habitat Models for Large-Scale Conservation: Assessing Suitable Areas for the Brown Bear Comeback in Europe." *Diversity and Distributions* 24 (11): 1573–1582. https://doi.org/10.1111/ddi.12796.

Schoeninger, M. J., and M. J. DeNiro. 1984. "Nitrogen and Carbon Isotopic Composition of Bone Collagen from Marine and Terrestrial Animals." *Geochimica et Cosmochimica Acta* 48 (4): 625–639. https://doi.org/10.1016/0016-7037(84)90091-7.

Schwartz-Narbonne, R., et al. 2019. "Reframing the Mammoth Steppe: Insights from Analysis of Isotopic Niches." *Quaternary Science Reviews* 215:1–21. https://doi.org/10.1016/j.quascirev.2019.04.025.

Stevens, R. E., R. Jacobi, M. Street, M. Germonpré, N. J. Conard, S. C. Münzel, and R. E. M. Hedges. 2008. "Nitrogen Isotope Analyses of Reindeer (Rangifer tarandus), 45,000 BP to 9,000 BP:Palaeoenvironmental Reconstructions." *Palaeogeography, Palaeoclimatology, Palaeoecology* 262 (1-2): 32–45. https://doi.org/10.1016/j.palaeo.2008.01.019.

Stevens, R. E., E. Lightfoot, J. Hamilton, B. W. Cunliffe, and R. E. M. Hedges. 2013. "One for the Master and One for the Dame: Stable Isotope Investigations of Iron Age Animal Husbandry in the Danebury Environs." *Archaeological and Anthropological Sciences* 5 (2): 95–109. https://doi.org/10.1007/s12520-012-0114-3.

Stiller, M., et al. 2010. "Withering Away-25,000 Years of Genetic Decline Preceded Cave Bear Extinction." *Molecular Biology and Evolution* 27 (5): 975–978. https://doi.org/10.1093/molbev/msq083.

Stiner, M. C. 1998. "Mortality Analysis of Pleistocene Bears and Its Paleoanthropological Relevance." *Journal of*

Human Evolution 34 (3): 303–326. https://doi.org/10.1006/jhev.1997.0198.

Swenson, J. E., N. Gerstl, B. Dahle, and A. Zedrosser. 2000. “Action Plan for the Conservation of the Brown Bear (*Ursus arctos*) in Europe.” *Nature and environment* 114 (114): 1–72.

Terlato, G., H. Bocherens, M. Romandini, N. Nannini, K. A. Hobson, and M. Peresani. 2019. “Chronological and Isotopic Data Support a Revision for the Timing of Cave Bear Extinction in Mediterranean Europe.” *Historical Biology* 31 (4): 474–484. https://doi.org/10.1080/08912963.2018.1448395.

Torres Pérez-Hidalgo, T. J. 1984. *Ursidos del pleistoceno-holoceno de la Península Ibérica*. Madrid: Universidad Politécnica de Madrid.

Trinkaus, E., and M. P. Richards. 2013. “Stable Isotopes and Dietary Patterns of the Faunal Species from the Peştera cu Oase.” In *In Life and Death at the Peştera cu Oase: A Setting for Modern Human Emergence in Europe*, edited by E. Trinkaus, S. Constantin, and J. Zilhão, 211–226. Oxford: Oxford University Press (OUP).

Van Heteren, A. H., and B. Figueirido. 2018. “Diet Reconstruction in Cave Bears from Craniodental Morphology: Past Evidences, new Results and Future Directions.” *Historical Biology* 31 (4): 500–509. https://doi.org/10.1080/08912963.2018.1547901.

Van Klinken, G. J. 1999. “Bone Collagen Quality Indicators for Palaeodietary and Radiocarbon Measurements.” *Journal of Archaeological Science* 26 (6): 687–695. https://doi.org/10.1006/jasc.1998.0385.

Vercoutere, C., C. S. Juan-Foucher, and Pascal Foucher. 2006. “Human Modifications on Cave Bear Bones from the Gargas Cave (Hautes-Pyrénées, France).” *Επιστημονική Επετηρίδα του Τμήματος Γεωλογίας (ΑΠΘ)* 98:257–262.

Vidal-Cordasco, M., G. Terlato, D. Ocio, and A. B. Marín-Arroyo. 2023. “Neanderthal Coexistence with Homo Sapiens in Europe Was Affected by Herbivore Carrying Capacity.” *Science Advances* 9 (38): p.eadi4099. https://doi.org/10.1126/sciadv.adi4099.

Vila Taboada, M., D. Fernández Mosquera, F. López González, and J. R. Vidal Romaní. 1999. *Paleoecological implications inferred from stable isotopic signatures (δ13C,δ15N) in bone collagen of Ursus spelaeus ROS*. Vol. 24, 73–87.

Vila Taboada, M., F. Mosquera, and A. Grandal d’Anglade. 2001. “Cave Bear’s Diet: A new Hypothesis Based on Stable Isotopes.” *Cadernos Lab. Xeolóxico de Laxe Coruña* 26: 431–439.

Weinstock, J. 2009. “Epiphyseal Fusion in Brown Bears: A Population Study of Grizzlies (*Ursus arctos* horribilis) from Montana and Wyoming.” *International Journal of Osteoarchaeology* 19 (3): 416–423. https://doi.org/10.1002/oa.980.

Wojtal, P., J. Svoboda, M. Roblíčková, and J. Wilczyński. 2020. “Carnivores in the Everyday Life of Gravettian Hunters-Gatherers in Central Europe.” *Journal of Anthropological Archaeology* 59:101171. https://doi.org/10.1016/j.jaa.2020.101171.

Wong, G. L., B. M. Starkovich, D. G. Drucker, and N. J. Conard. 2020. “New Perspectives on Human Subsistence during the Magdalenian in the Swabian Jura, Germany.” *Archaeological and Anthropological Sciences* 12 (9): 1–31. https://doi.org/10.1007/s12520-020-01119-w.

Zedrosser, A., B. Dahle, J. E. Swenson, and N. Gerstl. 2001. “Status and Management of the Brown Bear in Europe.” *Ursus (International Association for Bear Research and Management)* 12:9–20.