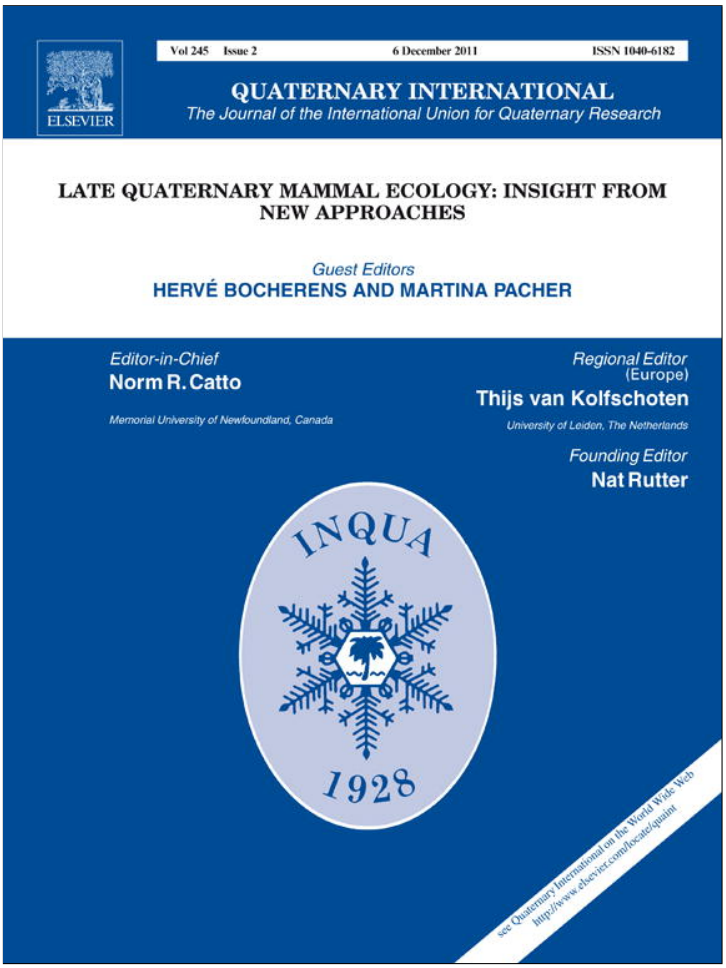

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Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus)* and brown bear (*Ursus arctos*) from Austria: Isotopic evidence from fossil bones

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ABSTRACT

In the Austrian caves of Gamssulzen and Ramesch, two genetically distinct cave bears, *Ursus ingressus* and *Ursus spelaeus eremus,* apparently lived side by side for 15,000 years, together with brown bears *Ursus arctos*. The possible ecological partitioning of these three types of bears was investigated using multi-isotopic tracking of organic ($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$) and inorganic ($\delta^{13}C_{carb}$, $\delta^{18}O_{carb}$, $\delta^{18}O_{PO4}$) fractions of bone. The cave bears from Ramesch, *Ursus spelaeus eremus*, were ecologically distinct from the cave bears from Gamssulzen, *Ursus ingressus*, both being ecologically distinct from brown bears from Ramesch, *Ursus arctos*. Both cave bear types were purely herbivorous but likely consumed different plant types and/or plants from different habitats, while brown bears included some animal proteins in their diet. Bone apatite $\delta^{18}O$ values strongly suggest that both types of cave bears used isotopically distinct water sources, indicating that they may not have occupied the same landscape, either separated in space or in time due to climatic shifts. Therefore, the influence of environmental conditions strongly constrained the genetic structure of these bears.

1. Introduction

The cave bear (*Ursus spelaeus* Rosenmüller 1794) is probably the Upper Pleistocene species that has yielded the highest number of fossil remains in Europe. Since its recognition by the scientific community as an extinct species, this taxon has been extensively studied, especially its palaeoecology. Based on functional anatomy, Kurtén (1958) suggested that this extinct group of bears had a herbivorous diet, a hypothesis that was recently confirmed by taphonomical and stable isotopic investigations (e.g., Bocherens et al., 1994, 1997, 2001, 2006; Fernandez-Mosquera, 1998; Stiner, 1999; Bocherens, 2008). Indeed, the high proportion of males in hibernating populations of cave bears point to a depletion of dietary resources available to this species during winter. This is not the case for male carnivorous bears which do not need to hibernate, as opposed to females who give birth during hibernation (Stiner, 1999). The stable nitrogen isotopic ($\delta^{15}N$) results on cave bear bones from Europe are mostly as low as or even lower than those of herbivorous species, pointing to the near-absence of animal protein in their diet. Isolated reports indicate higher $\delta^{15}N$ values as indicators of omnivory or carnivory (Hilderbrand et al., 1996; Richards et al., 2008). However, cave bears with high $\delta^{15}N$ values have unusually low stable carbon isotopic ($\delta^{13}C$) values that are not

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found in coeval predators, such as wolves, lions or hyaenas, but rather mimic those observed in some late Pleistocene herbivores such as woolly mammoth, and those observed for herbivores living in dense forest habitats (Bocherens, 2008). Also, large isotopic variations in bear tissues during hibernation could lead to a similar range of variation in some mineralised tissues of cave bears (e.g., Bocherens, 2004; Grandal d'Anglade and Fernández Mosquera, 2008; Pérez-Rama et al., 2011). Therefore, material to be analysed isotopically has to be selected carefully to avoid possible interference between dietary and physiological patterns in fossil bears. For these reasons, claims of animal protein consumption by cave bears based on isotopic measurements are still premature and better understandings of isotopic variations in plants of the Late Pleistocene and of the impact of physiological factors are required to distinguish between the effects of environmental changes and dietary shifts.

Recent studies involving morphometry, radiochronology, and palaeogenetic investigations of Upper Pleistocene cave bears have demonstrated the occurrence of at least two different genetic types of cave bears in Europe, sometimes considered different species (e.g., Hofreiter et al., 2004; Rabeder and Hofreiter, 2004; Stiller et al., 2009). The study of ancient mitochondrial DNA led to the definition of at least four different haplogroups among cave bears (Hofreiter et al., 2002; Orlando et al., 2002). One of these haplogroups is sufficiently distinct from the others to deserve a new species name, *Ursus ingressus*, and three different subspecies are defined among *Ursus spelaeus*, for example, *Ursus spelaeus spelaeus*, *Ursus spelaeus eremus* and *Ursus spelaeus ladinicus* (Rabeder and Hofreiter, 2004; Rabeder et al., 2004). This taxonomic diversity raises the question of possible ecological differences among what was previously classed as "cave bears". In some cases, the two cave bear species exhibit a chronological difference, with very little overlap, as in southwestern Germany between 37,000 and 26,000 ^{14}C BP (Hofreiter, 2002; Hofreiter et al., 2007), while in Austria *Ursus ingressus* and *Ursus spelaeus eremus* apparently lived sympatrically for 15,000 years (Hofreiter et al., 2004). In addition, specimens of brown bears, *Ursus arctos,* have been found in one of the Austrian caves together with those cave bears, with direct radiocarbon dating of some material showing a late Pleistocene age, contemporaneous with the cave bears, rather than all brown bears being Holocene as previously suggested.

Co-existence of two sympatric species of bears is also known today. For instance, grizzly bear *Ursus arctos horribilis* and American black bear *Ursus americanus* coexist in north-western North America (e.g., Herrero, 1972; Aune, 1994; MacHutchon et al., 1998), as do Asiatic black bears and brown bears in India (Sathyakumar, 2001). In such cases, there is potential dietary competition both among species and among sexes within species, and each species/sex tends to specialise with regard to habitat and diet resources (e.g., Apps et al., 2006; Belant et al., 2006; Garneau et al., 2008). However, both modern brown and black bears are omnivorous and can shift their dietary preferences quite easily (e.g., Beckmann and Berger, 2003). In the Late Pleistocene, when omnivorous brown bears coexisted with more specialised bear species such as the carnivorous giant short-faced bear *Arctodus simus* in north-western North America and with the herbivorous cave bear *Ursus spelaeus* in Europe, isotopic evidence demonstrated that ancient brown bears occupied the opposite end of the dietary spectrum. In these situations, brown bears were herbivorous in North America as long as short-faced bears were around (Barnes et al., 2002) and were mainly carnivores in Europe when they shared the landscape with cave bears (Bocherens and Drucker, 2006; Münzel et al., 2008; Bocherens et al., 2011). The case of two co-existing bears with predominantly herbivorous dietary habits is without modern analogue and raises many ecological questions. Were all cave bears herbivorous when they co-occurred? When they lived together for significant periods, did they partition their ecological niches? How flexible were the dietary habits of cave bears in relation to individual choices and phylogenetic affiliation? Is there a link between the occurrence of different cave bear types and climatic fluctuations?

The present study investigates these aspects using different "cave bear" populations, characterised by ancient DNA sequencing, and using mainly the stable isotope approach of environmental and dietary reconstruction. Organic and mineral fractions in bone record the isotopic parameters of consumed food and water during their formation (e.g., Bocherens and Drucker, 2007; Koch, 2007). In particular, δ^{13}C and δ^{15}N values in bone collagen as well as δ^{13}C values in the carbonate fraction of bone reflect those of the consumed food, and differences are clearly visible between plants, animal proteins, and freshwater resources (e.g, Richards et al., 2001; Drucker and Bocherens, 2004). Also, differences in δ^{13}C and δ^{15}N values can be observed between different types of plants of similar photosynthetic pathway, as between plants growing under closed-canopy forest and those from more open environments, as well as between plants growing at different altitudes (review in Heaton, 1999; Drucker et al., 2008). Typically, plants exhibit lower δ^{15}N values and higher δ^{13}C values with increasing altitude (Mariotti et al., 1980; Körner et al., 1991; Zhu et al., 2010) and these isotopic variations are recorded in animals consuming these plants (Männel et al., 2007). In addition, oxygen isotopic (δ^{18}O) values in the carbonate and phosphate of the mineral fraction of bone relate to those of drinking water, which relate to elevation and climate, with δ^{18}O values decreasing with lower temperatures and higher altitudes (e.g., Longinelli, 1984; D'Angela and Longinelli, 1990; Iacumin et al., 1996; Kohn et al., 1996; Drucker et al., 2009). Bears spend about half of their life in hibernation, a period during which their metabolism is highly modified (Hellgren, 1995). It was therefore necessary to test the assumption that oxygen isotopic composition (δ^{18}O) of bears covaried with those of environmental water and that the fact that hibernating bears do not drink or urinate does not significantly affect the δ^{18}O values recorded in the skeletal apatite of these animals. A previous study addressed this point using bears from zoological gardens with poor control of their history, thus being inconclusive (Reinhard et al., 1996). In this study, the correlation between ambient $\delta^{18}O_{H2O}$ and bone apatite δ^{18}O values was tested using recent wild grizzly bears (*Ursus arctos horribilis*) from Alberta, Canada, obtained from the mammalogy section of the Alberta Provincial Museum in Edmonton (Canada), with detailed record of their origin.

2. Material and methods

2.1. Fossil material

The analysed fossil bear material came from two caves in Austria, Ramesch and Gamssulzen. Both caves are located 10 km apart, Ramesch at an altitude of 1960 m above sea level (asl) and Gamssulzen at an altitude of 1300 m asl (Fig. 1). Both caves are located on the same massif named "Warscheneck" at the eastern slope of the "Totes Gebirge" in the Northern calcareous Alps. Today the karst landscape between the caves is characterised by forests, meadows and rocks. Due to the absence of natural obstacles between the two caves, it is very likely that the browsing areas of both cave bear species overlapped (Hille and Rabeder, 1986; Rabeder, 1995). Both caves contain remains of males and females, but the sex-index (quantity of females as percentage of all bears) of cave bears is lower in the Ramesch cave (about 50%) than in the Gamssulzen cave (about 75%: Rabeder et al., 2008).

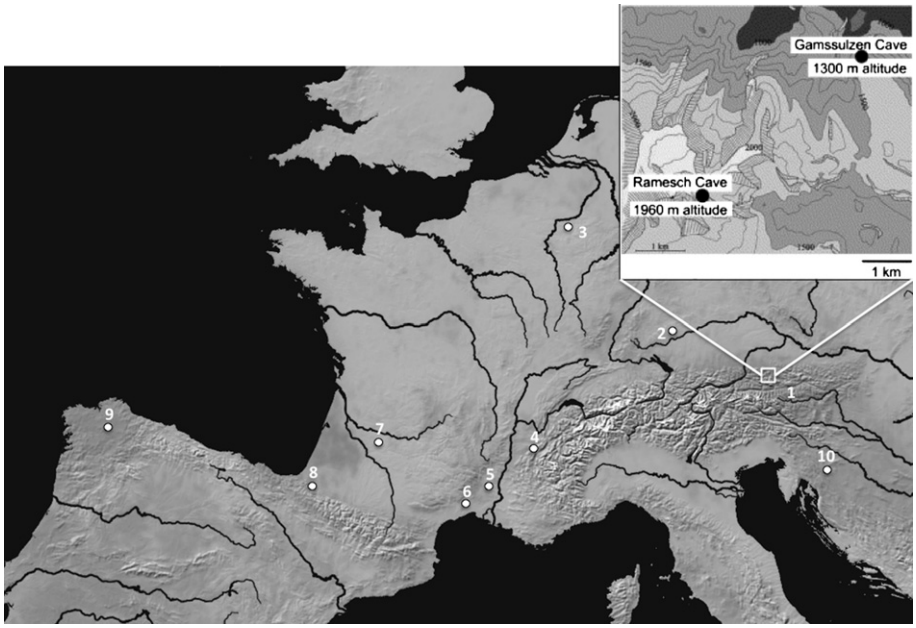

Fig. 1. Location of the Ramesch and Gamssulzen caves as well as those of the sites from which cave bear bones were analysed and that are discussed in the text (1: Ramesch and Gamssulzen, 2: Swabian Jura (Geißenklösterle and Hohle Fels), 3: Ardennes (Goyet and Scladina), 4: Balme-à-Collomb, 5: Chauvet, 6: Aldène and Mialet, 7: Font-de-Gaume, 8: Olaskoa, 9: Linares and Cova Eiros, 10: Didje Babe).

Small pieces were cut from long bones, metapodial bones, skulls or ribs of the three bear species occurring in these sites (i.e. ten cave bear *Ursus spelaeus eremus* and six brown bear *Ursus arctos* in Ramesch, and nine cave bear *Ursus ingressus* in Gamssulzen). The directly ^{14}C-dated specimens exhibit ages ranging from around 30,000 ^{14}C BP to more than 50,000 ^{14}C BP (Table 1). This was also the case for one of the brown bears from Ramesch, demonstrating contemporaneity of brown bear with cave bears during the Late Pleistocene in this region, contrary to previous age estimations (Rabeder et al., 2000, p.30).

2.2. Modern material

Nine modern grizzly bear ribs or femurs were selected from the mammalogy section of the Provincial Museum of Alberta, Edmonton, Canada. Only adult or subadult individuals were selected as young individuals may have δ^{18}O values influenced by suckling, as it has been shown that mother's milk consumption has an impact on δ^{18}O values of human infants (Wright and Schwarcz, 1998). The place of death of these grizzly bear individuals was recorded and, assuming that these bears lived close to the area where they died, it is possible to calculate the expected weighted mean annual isotopic values of local rainfall, using the OIPC (Online Isotopes in Precipitation Calculator: Bowen and Revenaugh, 2003; Bowen, 2010) and taking a range of altitudes corresponding to about a 20-km circle around the bear death location. This allowed the calculation of average δ^{18}O values of the precipitation water in the area where the bears lived to compare it with the δ^{18}O values measured for the bear bones.

2.3. Palaeogenetics

All bones were investigated using techniques to measure ancient DNA (aDNA). Although some (LPZ-1 to 12 and LPZ-29 to 35) have been previously published in Hofreiter et al. (2004), others (LPZ-13 to 16, LPZ-36 and LPZ-37, see Table 1) were processed as part of this study for the first time. For the latter ones, aDNA was extracted from 170 to 350 mg of powdered bone using a silica-based aDNA extraction protocol (Rohland and Hofreiter, 2007). DNA extractions as well as amplification reactions were conducted in a laboratory, physically separated from all post-PCR experiments, and only dedicated to ancient DNA work. Amplifications were performed using the primers CBL164 (3F) 5′-GCATATAAGCATGTACATATTATGC-3′ and CBH221 (3R) 5′-CGGACTAAGTGAAATACAT GCT-3′ using the amplification conditions described in Hofreiter et al., (2004) to amplify a 103 base pairs (bp) fragment (56 bp excluding primers) of the mitochondrial control region. The amplified region contains diagnostic nucleotide positions that can be used to distinguish between brown bears and cave bears as well as among cave bears. All amplifications were replicated to assure sequence accuracy and to prevent erroneous determination of nucleotide positions due to miscoding lesions in aDNA. Mock controls were taken at all steps to monitor possible contamination. Subsequently, all PCR products were individually barcoded, pooled in equimolar ratios and then sequenced on the 454 FLX platform using the DMPS protocol (Stiller et al., 2009). Sequences were sorted by barcode using the "untag"-tool (http://bioinf.eva.mpg.de/pts/), aligned and a consensus sequence for each individual was called in BioEdit (Hall, 1999). Based on their mitochondrial control region sequences, all individuals were eventually identified to species level.

2.4. Bone preparation and isotopic measurements

Collagen extraction followed the protocol presented in Bocherens et al. (1997). This preparation was performed in the Institut des Sciences de l'Evolution (Montpellier, France), as well as N elemental analysis of whole bone powders prior to collagen extraction, performed on a Eurovector CHN elemental analyser (Bocherens et al., 2005). Carbon and N elemental and stable isotope measurements were performed at the Department of Soil Science, University of Saskatchewan, Canada, using a Europa (Crewe, England) continuous flow isotope ratio mass spectrometer (CFIRMS) interfaced with a Robo-Prep elemental analyser.

Table 1
List of fossil samples and of palaeogenetic and isotopic results. In the column genetic results, the numbers in italics starting with "FR" correspond to the accession numbers of the new DNA sequences deposited in GenBank. Climatic contexts are estimated using the $\delta^{18}O$ values of the carbonate fraction: samples with $\delta^{18}O_{carb}$ values lower than the average value minus one half of the standard-deviation are considered "cold", while those with $\delta^{18}O$carb values higher than the average value plus one half of the standard-deviation are considered "warm". $\Delta^{13}C$ stands for the difference between $\delta^{13}C_{carb}$ and $\delta^{13}C_{coll}$. $\Delta^{18}O$ stands for the difference between $\delta^{18}O_{carb}$ and $\delta^{18}O_{PO4}$. The radiocarbon dates are from Hofreiter et al. (2004). The collagen isotopic values and radiocarbon date for the cave lion from Gamssulzen are from Barnett et al. (2009).

Analysis No.	Site	Piece	DNA analysis #	Species	%N bone	collagen yield (mg g^{-1})	%C	%N	C/N	δ^{13}Ccoll	δ^{15}Ncoll
LPZ-1	Ramesch	long bone	SP-346	*U. spelaeus eremus*	3.0	97.1	34.9	12.3	3.3	−22.1	1.1
LPZ-2	Ramesch	long bone	SP-347	*U. spelaeus eremus*	2.5	38.5	24.4	8.6	3.3	−21.4	1.1
LPZ-3	Ramesch	long bone	SP-348	*U. spelaeus eremus*	3.0	47.2	32.4	11.5	3.3	−21.6	0.4
LPZ-4	Ramesch	long bone	SP-349	*U. spelaeus eremus*	3.0	55.6	31.3	11.1	3.3	−21.4	0.2
LPZ-5	Ramesch	long bone	SP-350	*U. spelaeus eremus*	3.2	119.1	39.8	14.2	3.3	−21.8	0.2
LPZ-6	Ramesch	long bone	SP-351	*U. spelaeus eremus*	3.1	73.5	36.7	12.9	3.3	−22.2	2.1
LPZ-7	Ramesch	long bone	SP-352	*U. spelaeus eremus*	2.5	42.3	30.3	10.7	3.3	−21.5	0.3
LPZ-29	Ramesch	metapodial	SP-323 (69)	*U. spelaeus eremus*	2.8	122.2	39.4	13.9	3.3	−21.6	−0.3
LPZ-30	Ramesch	metapodial	SP-323 (160)	*U. spelaeus eremus*	3.5	130.8	39.3	13.8	3.3	−21.5	0.3
LPZ-36	Ramesch	metapodial	SP-323 (68) *FR733659*	*U. spelaeus eremus*	3.5	136.4	37.2	13.1	3.3	−21.6	0.5
LPZ-31	Ramesch	metapodial	SP-323 (163)	*U. arctos*	4.1	146.3	38.4	13.5	3.3	−20.4	3.5
LPZ-32	Ramesch	metapodial	SP-323 (221)	*U. arctos*	3.3	127.6	35.6	12.5	3.3	−21.1	2.5
LPZ-33	Ramesch	metapodial	SP-323 (477)	*U. arctos*	3.7	166.1	39.5	13.9	3.3	−20.7	3.4
LPZ-34	Ramesch	metapodial	SP-323 (531)	*U. arctos*	3.4	136.4	37.5	13.1	3.3	−18.4	2.9
LPZ-35	Ramesch	metapodial	SP-323 (603)	*U. arctos*	4.1	204.1	39.9	14.0	3.3	−20.5	3.6
LPZ-37	Ramesch	metapodial	SP-323 (456) *FR733658*	*U. arctos*	3.0	95.1	35.3	12.7	3.2	−18.5	2.5
LPZ-8	Gamssulzen	long bone	SP-337	*U. ingressus*	2.1	31.2	29.5	10.4	3.3	−21.0	1.7
LPZ-9	Gamssulzen	skull?	SP-338	*U. ingressus*	3.3	97.3	38.2	13.6	3.3	−20.4	0.7
LPZ-10	Gamssulzen	long bone	SP-339	*U. ingressus*	3.0	99.6	34.9	12.4	3.3	−20.7	1.5
LPZ-11	Gamssulzen	rib	SP-340	*U. ingressus*	3.7	131.6	38.7	13.8	3.3	−20.8	0.8
LPZ-12	Gamssulzen	long bone	SP-341	*U. ingressus*	3.3	122.3	37.7	13.4	3.3	−20.9	0.7
LPZ-13	Gamssulzen	long bone	SP-342 *FR733660*	*U. ingressus*	2.9	57.5	36.7	13.1	3.3	−21.0	1.6
LPZ-14	Gamssulzen	rib	SP-343 *FR733660*	*U. ingressus*	3.5	147.5	37.9	13.5	3.3	−21.0	0.9
LPZ-15	Gamssulzen	long bone	SP-344 *FR733660*	*U. ingressus*	3.0	116.8	37.0	13.1	3.3	−21.0	1.0
LPZ-16	Gamssulzen	long bone	SP-345 *FR733660*	*U. ingressus*	2.5	67.0	33.7	12.0	3.3	−20.8	1.4
RB60	Gamssulzen	tibia		*Panthera leo spelaea*						−17.9	5.6

The $\delta^{13}C$ and $\delta^{18}O$ measurements of the carbonate fraction and $\delta^{18}O$ analysis of phosphate were performed at the Department of Geosciences (University Tübingen, Germany). Prior to these analyses of the bone mineral fraction, bone powders were chemically pre-treated with 2% NaOCl solution, followed by a 1 M Ca-acetate acetic acid buffer solution (Bocherens et al., 1996). Samples were analysed at 70 °C using a ThermoFinnigan Gasbench II on a Finnigan Delta Plus XL CFIRMS at the University of Tübingen for $\delta^{13}C$ and $\delta^{18}O$ values of the carbonate fraction of bioapatite. Oxygen isotope composition of phosphate ($\delta^{18}O_{PO4}$) was measured on silver phosphate (Ag_3PO_4). About 4 mg of pre-treated powder were dissolved in 2 M HF, neutralised with NH_4OH and the PO_4 in solution was rapidly precipitated as Ag_3PO_4 by adding 2 M $AgNO_3$ according to the method described in Tütken et al. (2006). Ag_3PO_4 of each sample and standard was analysed in triplicate (~500 μg for a single measurement) for $\delta^{18}O_{PO4}$. The $\delta^{18}O_{PO4}$ measurements were performed using a Finnigan TC-EA at 1450 °C linked via a Finnigan Conflow III to a ThermoFinnigan Delta Plus XL CFIRMS at the University of Tübingen.

Isotopic abundances are expressed as δ (delta) values in parts per mil (‰), as follows: $\delta^{E}X = (R_{sample}/R_{standard} - 1) \times 1000$, where X is C, N or O, E is the atomic number 13, 15 or 18, and R is the isotopic ratios $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{18}O/^{16}O$, respectively. Delta values are reported relative to international reference standards: a Vienna Pee Dee Belemnite (V-PDB) for carbon, atmospheric nitrogen (AIR) for nitrogen and Vienna Standard Mean Ocean Water (V-SMOW) for O. Analytical error was estimated to be 0.1‰ for $\delta^{13}C$ values, 0.2‰ for $\delta^{15}N$ values, and 0.15‰ for $\delta^{18}O_{CO3}$ values and 0.3‰ for $\delta^{18}O_{PO4}$ values based on replicate within-run analyses of lab standards.

Isotopic results for each bear species were compared statistically using a non-parametric Mann–Whitney *U*-test (Statview). Differences with p values lower than 0.05 were considered statistically significant.

3. Results

3.1. Species identification using ancient DNA

All fossil specimens not previously analysed in Hofreiter et al. (2004) yielded sufficiently well-preserved DNA to amplify and determine the desired fragment of their mtDNA control region. Although spanning only 56 bp in between the priming sites, the mtDNA sequences harboured enough information to allow for unambiguous species identification. Thus, all specimens could be identified as being *U. ingressus*, *U. spelaeus eremus* or *U. arctos*, respectively (Table 1).

3.2. Oxygen isotopic values of modern grizzly bears

The $\delta^{18}O$ values of the carbonate fraction of modern grizzly bear bones from different habitats in Alberta ranged from 13.6 to 16.8‰ (Table 2). This range was slightly larger than that of the average $\delta^{18}O_{H2O}$ values (−18.2 to −16.0‰) estimated for the weighted mean annual precipitation in the area where the individuals had been collected. Bear bone $\delta^{18}O_{CO3}$ values exhibited a covariation with the presumed environmental water $\delta^{18}O_{H2O}$ values yielding a positive regression with a slope near unity (Fig. 2). Although the R^2 of 0.398 is lower than those usually measured for other modern species, which are typically higher than 0.80 (e.g. Iacumin et al., 1996; Hoppe, 2006), the level of significance of the R correlation coefficient ($r = 0.6308$) is close to the $p = 0.05$ level of significance for the same degree of freedom (0.666). Moreover, this equation was similar to those published for different extant large herbivorous mammals such as red deer (Iacumin et al., 1996), and the difference between the $\delta^{18}O_{carb}$ in the same range of $\delta^{18}O_{water}$ values was less than 1‰. Thus, the use of isotopically different water resources was reflected in the skeletal apatite $\delta^{18}O$ values of bears. This

d-
e-

%carb	δ^{13}Ccarb	δ^{18}Ocarb PDB	δ^{18}Ocarb SMOW	$\delta^{18}O_{PO4}$	Climatic context	Δ13C	Δ18O	Date No	Beta No	Age BP	sd
6.9	−15.7	−9.1	21.5		"average"	6.4		R3451	Beta-157666	>49860	
8.0	−14.3	−9.0	21.6	14.1	"average"	7.1	7.5	R3452	Beta-157667	43700	1270
7.3	−14.6	−8.4	22.2		"warm"	7.1		R3453	Beta-157668	>48800	
8.6	−13.5	−8.1	22.5	14.7	"warm"	7.9	7.8	R3454	Beta-157669	47600	2060
7.7	−15.1	−9.1	21.5		"average"	6.7		R3455	Beta-157670	31140	310
7.8	−15.8	−9.2	21.3	13.7	"cold"	6.4	7.6	R3456	Beta-157671	>49990	
8.6	−15.2	−8.5	22.1	15.3	"warm"	6.3	6.8	R3491	Beta-157672	>49650	
7.2	−14.5	−8.3	22.3		"warm"	5.9			Beta-171310	47420	
7.8	−14.2	−8.3	22.3	14.3	"warm"	6.9	8.0				
7.3	−14.6	−8.1	22.6	14.2	"warm"	6.1	8.4				
7.6	−13.5	−9.5	21.0		"cold"	4.9					
6.9	−14.4	−8.5	22.1		"warm"	6.1					
6.1	−14.2	−9.4	21.2		"cold"	6.9		GS33	Beta-157661	37310	580
7.1	−13.5	−9.8	20.8		"cold"	6.8		GS34	Beta-157662	44400	1380
8.3	−14.1	−9.5	21.1	13.9	"cold"	6.6	7.2	GS35	Beta-157663	45410	1560
7.3	−14.5	−8.8	21.8	13.9	"average"	6.3	7.9	GS36	Beta-157664	41060	920
5.6	−14.5	−9.5	21.1	13.3	"cold"	6.4	7.9	GS37	Beta-157665	47300	1970
									OxA-13110	49900	1500

monstrates that hibernation did not lead to complete loss of the environmental signal and that it remains possible to use $\delta^{18}O$ values of bear bones as climatic indicators.

3.3. Carbon and nitrogen isotope composition of bone collagen from ancient bears

The N content of the bear samples ranged from 2.1 to 4.1% (Table 1). This means that at least half of the collagen was still preserved in the bones from both caves, and the extraction yields confirmed this excellent quantitative preservation, which was likely linked to the low temperatures in the caves. The qualitative preservation of collagen could be evaluated using the C/N ratio and the proportions of C and N (%C, %N). All the extracted collagen exhibited atomic C/N ratios equal to 3.3, which is the nominal value for collagen. The %C ranged from 24.4 to 39.9% and the %N ranged from 8.6 to 14.2% (Table 1). These values are within the expected range for well-preserved collagen (DeNiro, 1985; Ambrose, 1990), and demonstrate that the measured isotopic values on collagen should not deviate significantly from the values recorded by the living animals.

The $\delta^{13}C_{coll}$ values ranged from −22.2 to −21.4‰, from −21.1 to −18.4‰ and from −21.0 to −20.4‰ for *Ursus spelaeus eremus*, *Ursus arctos* and *Ursus ingressus*, respectively (Table 1). The $\delta^{13}C_{coll}$ values were more negative for *Ursus spelaeus eremus* than for *Ursus ingressus* and *Ursus arctos* with no overlap, and a Mann–Whitney statistical *U*-test yielded a *p*-value of 0.0027 (Table 4). With an average $\delta^{13}C_{coll}$ value of −21.7 ± 0.3‰, *Ursus spelaeus eremus* was clearly lower than *Ursus ingressus* and *Ursus arctos*, with average $\delta^{13}C_{coll}$ values of −20.8 ± 0.2‰ and −20.2 ± 0.9‰, respectively (Table 3). When compared with a Mann–Whitney non-parametric statistical test, the $\delta^{13}C_{coll}$ values of *Ursus spelaeus eremus* were significantly different from those of *Ursus ingressus* and *Ursus arctos* ($p = 0.0027$), while those of *Ursus ingressus* and *Ursus arctos* were not significantly different ($p = 0.3472$; Table 4).

The $\delta^{15}N$ values ranged from −0.3 to 2.1‰, from 2.5 to 3.6‰ and from 0.7 to 1.6‰ for *Ursus spelaeus eremus*, *Ursus arctos* and *Ursus ingressus*, respectively (Table 1). The $\delta^{15}N$ values were higher for *Ursus arctos* than for *Ursus spelaeus eremus* and *Ursus ingressus* with no overlap. The average $\delta^{15}N$ value for *Ursus arctos* was clearly higher than for both cave bears, with average values of 3.2 ± 0.4‰, 0.6 ± 0.7‰ and 1.1 ± 0.5‰ for *Ursus arctos*, *Ursus spelaeus eremus* and *Ursus ingressus*, respectively (Table 2). The $\delta^{15}N$ values of *Ursus arctos* collagen were significantly different from those of both cave bears as indicated by Mann–Whitney *U*-test ($p = 0.0027$ for *U. spelaeus eremus* and $p = 0.0090$ for *U. ingressus*) (Table 4). In summary, the $\delta^{13}C$ and $\delta^{15}N$ values of the three bear species were clearly distinct and cluster differently on a bivariate graph (Fig. 3).

3.4. Oxygen and carbon isotope composition of bone mineral fraction from ancient bears

The $\delta^{13}C_{CO3}$ values ranged from −15.8 to −13.5‰, from −14.6 to −13.5‰ and from −14.5 to −13.5‰ for *Ursus spelaeus eremus*, *Ursus arctos* and *Ursus ingressus*, respectively (Table 1). The average $\delta^{13}C_{CO3}$ values were relatively close for the three kinds of bear and did not exhibit any statistically significant difference (Table 4). The $\delta^{18}O_{CO3(vsmow)}$ values ranged from 21.3 to 22.5‰, from 21.0 to 22.6‰ and from 20.8 to 21.8‰ for *Ursus spelaeus eremus*, *Ursus arctos* and *Ursus ingressus*, respectively (Table 1, Fig. 4). A significant difference was found between the $\delta^{18}O_{CO3(vsmow)}$ values of *Ursus spelaeus eremus* and those of *Ursus ingressus* ($p = 0.0284$) (Table 4).

The $\delta^{18}O_{PO4}$ ranged from 13.7 to 15.3‰, from 14.2 to 14.3‰ and from 13.3 to 13.9‰ for *Ursus spelaeus eremus*, *Ursus arctos* and *Ursus ingressus*, respectively (Table 1). There were not enough measurements to test statistical differences among the three bear groups,

Table 2
List of carbon and oxygen isotopic values of the carbonate fraction of bone apatite from modern grizzly bears from Alberta with the estimated $\delta^{18}O$ values of local precipitation.

Analysis number	Accession number	Piece	Date collected	Sex	Age	Latitude N	Longitude W	Altitude range	Expected high	$\delta^{18}O$ low	$\delta^{18}O_W$	sd	$\%CaCO_3$	$\delta^{13}C_{carb}$	$\delta^{18}O_{PDB}$	$\delta^{18}O_{SMOW}$
30333	Z76.107.1	rib	09.09.76	M	adult	51.33	−115.58	1500–3000	−16.6	−19.5	−18.05	1.45	6.5	−17.1	−15.4	15.0
30335	Z76.115.1	femur	24.09.76	M	adult	56.45	−118.85	700–1000	−17.2	−18.2	−17.7	0.5	7.8	−17.3	−14.5	15.9
30346	Z81.94.1	rib	22.07.81	F	adult	51.42	−116.23	1500–3000	−16.5	−19.4	−17.95	1.45	3.4	−17.1	−16.8	13.6
30348	84.21.1	rib	11.06.84	F	adult	53.47	−113.08	500–1000	−16.0	−16.9	−16.45	0.45	4.9	−16.0	−13.6	16.8
30350	87.3.4	rib	18.09.86	M	subadult	52.62	−114.65	700–1000	−15.7	−16.3	−16.0	0.3	4.2	−18.0	−14.4	16.0
30356	87.39.1	rib	09.09.87	M	adult	50.38	−114.68	1500–3000	−16.2	−19.1	−17.65	1.45	5.9	−17.5	−15.1	15.3
30358	87.43.1	femur	27.09.85	M	subadult	49.15	−113.42	1000–3000	−14.9	−18.8	−16.85	1.95	5.8	−17.3	−13.2	17.2
30364	91.24.1	femur	13.09.90	F	adult	57.35	−117.53	300–1000	−17.5	−18.8	−18.15	0.65	5.3	−18.1	−15.6	14.7
30368	91.37.1	femur	05.10.90	F	adult	54.93	−116.07	500–1300	−16.3	−17.8	−17.05	0.75	6.9	−18.8	−15.8	14.5

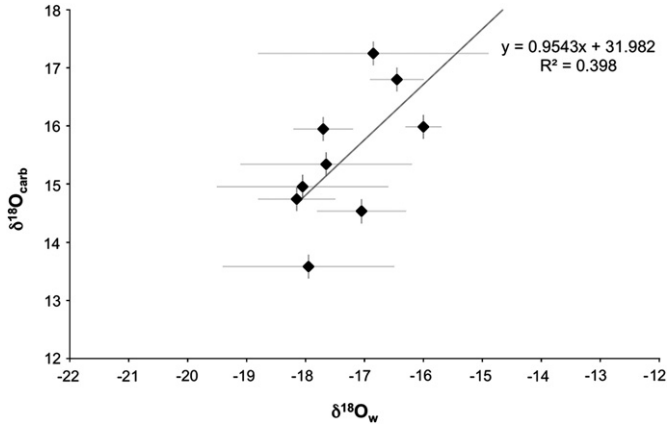

Fig. 2. Relationship between $\delta^{18}O_{H2O}$ and $\delta^{18}O_{CO3}$ in bones of modern grizzly bears from Alberta, Canada.

but the trends observed for $\delta^{18}O_{carb}$ values were also seen with the $\delta^{18}O_{PO4}$ values. For instance, the average $\delta^{18}O_{PO4}$ were higher for *Ursus spelaeus eremus* than for *Ursus ingressus*, with values of $14.5 \pm 0.6‰$ and $13.7 \pm 0.3‰$, respectively (Table 2).

The assessment of reliability for carbonate isotopic results is less straightforward than for collagen. Enamel is usually preferred to bone for Pleistocene and older samples as the latter tissue exhibit a lower crystallinity, and is therefore more prone to diagenetic alteration (e.g., Lee-Thorp and van der Merwe, 1991; Koch et al., 1997). Here, the preference wasto investigate bone despite this drawback, to ensure analysis of the same specimen for collagen and carbonate. Even when tooth and bone are sampled on one specimen, the growth and turnover timing are different in both tissues, possibly leading to discrepancies. Moreover, these bones were the same ones used for palaeogenetic studies, so the taxonomic determination was extremely robust. Investigation of the possibility of diagenetic alteration involved testing different correlations between diagenetic markers, such as N content of whole bone that reflects the intensity of collagen loss or the percent carbonate in the bone, and the investigated isotopic signatures. Percent of carbonate in bone ranges from 5.6 to 8.3%, while it can reach values of 7.8% in modern bear bone using the same preparation method (Table 3). As an additional test for possible diagenetic alteration, the difference between $\delta^{18}O_{CO3}$ and $\delta^{18}O_{po4}$ values of fossil bear bones were compared to those of modern mammal bones as suggested by Iacumin et al. (1996). The difference ($7.7 \pm 0.5‰$, $n = 9$) was close to that of modern mammal bones. Furthermore, no significant correlation existed between changes in the difference in $\delta^{18}O_{CO3}$ and $\delta^{18}O_{po4}$ and the $\delta^{18}O$ values. As no significant correlation was found between the isotopic values and any diagenetic indicator, the measured $\delta^{13}C_{CO3}$ and $\delta^{18}O_{CO3}$ values likely had not changed significantly, although minor changes cannot be completely ruled out. The following discussion on the palaeobiology of the fossil bears uses the $\delta^{18}O$ values measured on the carbonate fraction, as they are more numerous and therefore allow more robust comparisons between the different groups.

4. Discussion

4.1. Niche partitioning in Austrian fossil bears

Both cave bear types were herbivorous compared with brown bears, and also by comparison with a cave lion (*Panthera spelaea*) from Gamssulzen published by Barnett et al. (2009) (Fig. 3). Indeed, $\delta^{15}N$ values of cave bears did not exceed 2‰, while the cave lion

Table 3
Summary of isotopic data of Austrian bears. Asterisks show samples with palaeogenetic data published here for the first time.

Species (site)		$\delta^{13}C_{coll}$	$\delta^{15}N_{coll}$	$\delta^{13}C_{carb}$	$\delta^{18}O_{carb\ (PDB)}$	$\delta^{18}O_{carb\ (SMOW)}$	$\delta^{18}O_{PO4}$	$\Delta^{13}C$	$\Delta^{18}O$
U. spelaeus eremus (Ramesch)	average	−21.69	0.60	−14.89	−8.78	21.81	14.46	6.84	7.42
	sd	0.24	0.63	0.74	0.40	0.41	0.60	0.53	0.40
	n	10	10	7	7	7	4	7	4
U. arctos (Ramesch)	average	−19.93	3.07	−14.24	−8.54	22.05	14.24	5.98	8.19
	sd	1.07	0.46	0.40	0.52	0.54	0.08	0.63	0.21
	n	6	6	5	5	5	2	5	2
U. ingressus (Gamssulzen)	average	−20.85	1.15	−14.16	−9.38	21.19	13.68	6.61	7.65
	sd	0.20	0.39	0.36	0.31	0.32	0.30	0.21	0.32
	n	9	9	5	5	5	3	5	3

from Gamssulzen exhibited a $\delta^{15}N$ value close to 6‰. Such a difference of more than 4‰ between a predator, the cave lion, and both cave bears, is similar to the isotopic difference observed between herbivorous and carnivorous mammals in modern and other late Pleistocene ecosystems (e.g., Bocherens et al., 1997; Bocherens, 2000; Bocherens and Drucker, 2003; Fox-Dobbs et al., 2007). It is therefore clear that neither cave bear included any significant amount of animal protein in their dietary intake. In contrast, the brown bears from Ramesch exhibited $\delta^{15}N$ values significantly higher than those of coeval cave bears, but lower than those of the cave lion from Gamssulzen (Fig. 3). Therefore, an omnivorous diet including some animal proteins can be inferred for these brown bears, which confirms that the dietary flexibility of this species was already developed in the Late Pleistocene (Bocherens et al., 1997; Bocherens and Drucker, 2006; Döppes et al., 2008; Münzel et al., 2008). This dietary difference between brown bears and cave bears shows that ecological competition was probably limited between both types of ursids. However, the case of the two herbivorous cave bears should be investigated in more detail to try to understand how two closely related species could live side by side with similar dietary preferences.

Although both cave bears were herbivorous, differences in $\delta^{13}C$ values of their collagen points to ecological differences, linked to different dietary and/or habitat preferences. In connection with differences in $\delta^{18}O$ values, it is possible to infer differences in habitat and possibly in climatic context during the lifetime of the cave bears (Fig. 4). Isotopic differences can be used to track the environmental factors responsible for the observed pattern. Two main factors have to be considered: (1) differences in altitudes of the feeding areas, and (2) climate changes that occurred during MIS 3 (e.g., Shackleton and Hall, 2001; Genty et al., 2003; Van Meerbeeck et al., 2009). Isotopic investigations in modern mountainous contexts yielded numerous $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ data that allow some predictions about the effects of altitude expected on herbivorous mammals living across an altitudinal gradient. Plant $\delta^{13}C$ values increase with increasing altitude of about 1.4‰ per km (e.g., Körner et al., 1991; Zhu et al., 2010) while their $\delta^{15}N$ values decrease with increasing altitude (e.g., Mariotti et al., 1980; Sah and Brumme, 2003). In parallel, $\delta^{18}O$ values of precipitation decrease with altitude (Longinelli, 1984; Kohn et al., 1996). This pattern of isotopic variations holds at a given time as long as climatic conditions remain more or less the same. However, it must be kept in mind that the period between 30,000 and 50,000 years ago was subject to short-term climatic changes (e.g., Shackleton and Hall, 2001; Van Meerbeeck et al., 2009). These changes led to variations in $\delta^{18}O$ values of local precipitation, as documented in various continental deposits, such as speleothems (Genty et al., 2003; Spötl et al., 2006). Several interstadial periods lasting a few hundred years occurred during this time interval, with colder stadial intervals in between. Warmer time periods will lead to more positive $\delta^{18}O$ values at a given altitude due to increasing temperatures, as well as to more negative $\delta^{13}C$ values if the vegetation becomes denser, and higher $\delta^{15}N$ values (Drucker et al., 2009). In order to sort out effects of altitude for a given climatic context and of climatic shifts through time on isotopic values of cave bears, a closer look at the isotopic variations is needed, in terms of chronology and between the two cave bear populations.

At first glance, AMS radiocarbon dates measured on some specimens do not seem very helpful, as many results are only minimal dates, and even the finite dates cannot be used to tentatively correlate them with a climatic episode, as their standard-deviations are so large in the time range of 30,000 to 50,000 years that the calibrated dates overlap several cold and warm climatic episodes. However, having different bears in a given site with similar isotopic signatures but clearly different ages demonstrates that the ecology of these bears was similar for many millennia and there was no obvious shift of environmental conditions during the period considered here. This result does not preclude shorter deviations from this pattern. It merely shows that the bears that hibernated in a given cave between around 30 and at least 50 thousand years ago experienced relatively similar ecological conditions, and that these conditions were different for the bears hibernating in two different caves. The main question is whether this ecological difference is linked to niche partitioning of populations living in sympatry in the same region or if the two cave bear populations that lived in the same general area did so under different climatic conditions that occurred at different periods, and therefore were not in direct contact.

In the first hypothesis, the isotopic differences between the cave bears from Gamssulzen and Ramesch need to be explained for a scenario where the bears coexisted in the region. The difference in $\delta^{13}C$ values of collagen and of carbonate may reflect that plants from a landscape with denser vegetation cover were consumed by *Ursus spelaeus eremus* than by *Ursus ingressus*, or by the consumption of different plant parts by both bears. Cave bears with the lowest $\delta^{13}C$ values exhibited the highest $\delta^{18}O_{carb}$ values, a situation contrary to

Table 4
Statistical comparisons of the stable isotopic data of the Austrian bears.

Species (site)	*U. ingressus* (Gamssulzen)	*U. arctos* (Ramesch)
	($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$, $\delta^{13}C_{carb}$, $\delta^{18}O_{carb}$, $\Delta^{13}C$)	($\delta^{13}C_{coll}$, $\delta^{15}N_{coll}$, $\delta^{13}C_{carb}$, $\delta^{18}O_{carb}$, $\Delta^{13}C$)
U. spelaeus eremus (Ramesch)	($p = 0.0027$; $p = 0.1252$; $p = 0.074$; $p = 0.0284$; $p = 0.4795$)	($p = 0.0027$; $p = 0.0027$; $p = 0.1229$; $p = 0.3718$; $p = 0.1573$)
U. ingressus (Gamssulzen)	X	($p = 0.3472$; $p = 0.0090$; $p = 0.6015$; $p = 0.0472$; $p = 0.2888$)

expectation that less evaporation, and therefore lower $\delta^{18}O$ values, would occur in denser vegetation with lower $\delta^{13}C$ values. It seems therefore that difference in $\delta^{18}O$ values rather suggests that water originating from different altitudes was the cause of these differences. In the case of sympatric and contemporary bears, it would have to be assumed that individuals dwelt in different areas with different drinking waters, at least for part of their active time. There are several examples of non-interbreeding populations of the same species of large mammals in modern herbivores, such as plain and wood bison (*Bison bison bison* and *Bison bison athabascae*) and barren-ground and woodland caribou (*Rangifer tarandus groenlandicus* and *Rangifer tarandus caribou*), which coexist in the same area part of the year (e.g., Van Zyll de Jong et al., 1995; Thomas and Gray, 2002; Nagy et al., 2003). In such cases, the genetic separation is a consequence of different, non-overlapping, breeding areas, preventing males and females of both populations from meeting each other during the mating period. This could have happened with the two types of cave bears in the Totes Gebirge: if they indeed had the possibility to meet each other, they probably did so outside their breeding season.

What could be the ecological difference between both cave bear populations? The different $\delta^{13}C$ values of collagen, with no overlap between cave bears from Ramesch and Gamssulzen, were striking. The $\delta^{13}C$ values of the bone carbonate fraction were also more negative in Ramesch than in Gamssulzen, but not significantly so. Except for one cave bear from Ramesch with a $\delta^{15}N$ value in the range of the cave bears from Gamssulzen (LPZ-6), average $\delta^{13}C$ and $\delta^{15}N$ values of cave bears from Ramesch were lower than those of cave bears from Gamssulzen. This trend is opposite to the expected variation if the higher altitude of Ramesch was responsible for the difference: indeed, $\delta^{15}N$ values follow the expected altitudinal trend, but $\delta^{13}C$ values of plants and of the animals eating them tend to increase with altitude, a trend that is opposite to the one observed here (Männel et al., 2007). Interestingly, the outlying bear from Ramesch also exhibited low $\delta^{18}O$ values, pointing to an animal dwelling under cold conditions. In this case, a home range at lower altitude could have been responsible for this relatively high $\delta^{15}N$ value.

The difference in $\delta^{18}O_{carb}$ values between bears from both caves raises questions about its possible cause. Bear bones from the

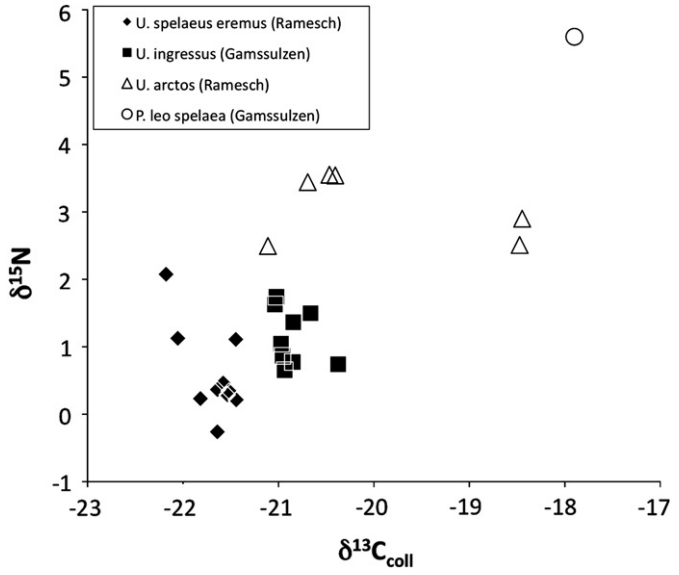

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values in bone collagen from cave bears in Ramesch and Gamssulzen cave, brown bears in Ramesch cave, and cave lion in Gamssulzen cave (data from Barnett et al., 2009).

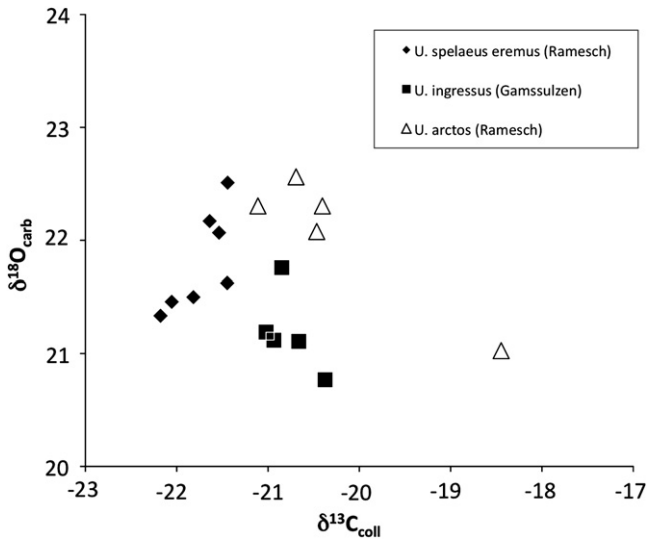

Fig. 4. $\delta^{13}C_{coll}$ and $\delta^{18}O_{CO3}$ of cave bears and brown bears from the Austrian caves.

higher altitude cave (Ramesch) exhibit higher $\delta^{18}O$ values than those in the lower altitude cave (Gamssulzen). This contrasts with the decrease of $\delta^{18}O$ values in precipitations expected with increasing altitude, but bears record their $\delta^{18}O$ values during the season when they are active, and this happens outside the caves where their remnants have been found. It is theoretically possible that the bears from the higher altitude cave spent their active life at lower altitudes than the bears that hibernated in the lower altitude cave, or at least that the drinking water available to them originated from different altitudes and therefore presented different $\delta^{18}O$ values. This would mean that both bear types spent their active times in areas with different drainage basins, both being herbivorous but avoiding direct competition by splitting their territories. In such a scenario, brown bears from Ramesch were also dwelling in the same area as cave bears hibernating in the same cave, based on their $\delta^{18}O$ values. This suggests that the different collagen isotopic values between cave bears and brown bears in Ramesch do not reflect a difference in feeding areas, but rather a real difference in dietary preferences, with brown bears including some meat in their diet compared to cave bears. Only one brown bear specimen presents overlapping $\delta^{18}O$ values with the cave bears from Gamssulzen, but the dating of this brown bear is not secure.

Another possibility to explain the different $\delta^{18}O$ values between the cave bear bones from both caves could be linked to climate changes. The period between 30,000 and 50,000 years ago was subject to short-term climatic changes (Shackleton and Hall, 2001) with changes in $\delta^{18}O$ values of local precipitation, as documented in various continental deposits, such as speleothems (Genty et al., 2003; Spötl et al., 2006). In such a context, higher $\delta^{18}O$ values of bears found in the higher cave (Ramesch) could reflect the fact that these bears used this cave as a winter den only during the warmer phases, while bears found in the lower altitude cave (Gamssulzen) hibernated there during colder phases, and therefore had lower $\delta^{18}O$ values. It is unfortunately impossible to correlate $\delta^{18}O$ values of the directly dated bear bones with the palaeoclimatic record, as the chronological resolution of the radiocarbon dates is not good enough and many dates are only minimal ages (Table 1). Interestingly, cave bears from the higher cave had, together with higher $\delta^{18}O$ values, low $\delta^{15}N$ values (Fig. 5). These low $\delta^{15}N$ values could reflect higher altitude feeding grounds, as the $\delta^{15}N$ values of plants decrease with increasing altitude (e.g., Männel et al., 2007). If this scenario is correct, genetic difference between cave bears from both caves would reflect populations that actually did not live in the area

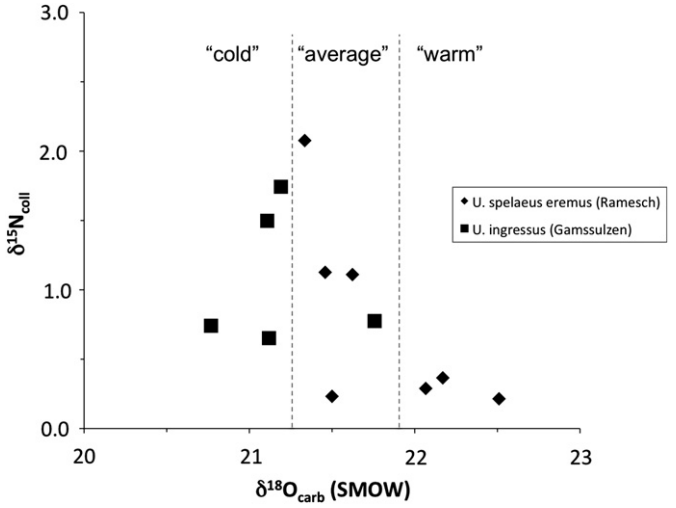

Fig. 5. $\delta^{15}N$ and $\delta^{18}O_{CO3}$ of cave bears from Ramesch and Gamssulzen.

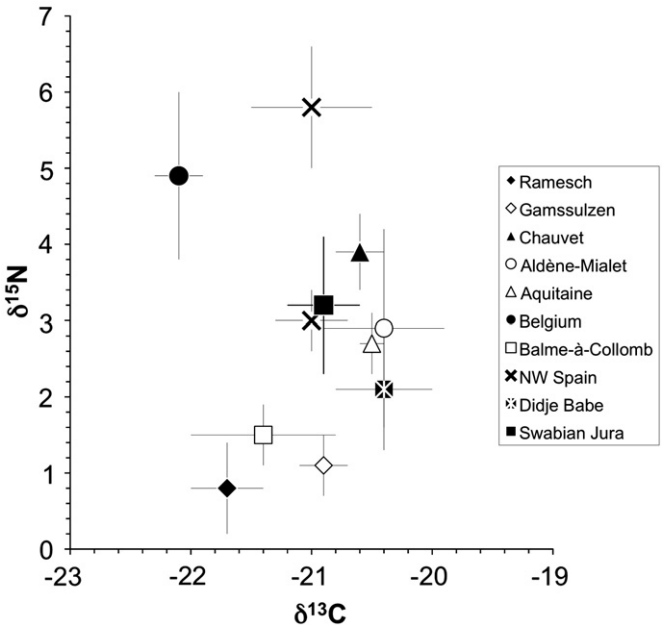

Fig. 6. Comparison of the $\delta^{13}C$ and $\delta^{15}N$ values of cave bears from different sites in Western and Central Europe (complete table as supplementary data Table S1).

at exactly the same time, but moved back and forth according to climatic fluctuations: the large *Ursus ingressus* from Gamssulzen used this moderate altitude cave as a winter den during the cooler climate phases while the smaller *Ursus spelaeus eremus* from Ramesch hibernated in this high altitude cave during the milder phases. Interestingly, this scenario based on climatic fluctuations fits the expectation that body size of bears would be smaller during warmer episodes than during colder ones, as predicted by the so-called "Bergmann's rule" (Bergmann, 1847; Meiri and Dayan, 2003), although this trend is sometimes not so clear for modern omnivorous brown bears (Kojola and Laitala, 2001). However, such a scenario does not explain what happened to the respective bears during the climate phases during which they were absent from the area, and it does not explain why Gamssulzen cave was not used as a hibernation den during the warmer phases. Perhaps the cave was not hospitable to hibernating bears because of excessive humidity or warmth, or the area may have been too dangerous for hibernating cave bears due to more numerous predators at this altitude during the warmer periods. Nevertheless, it opens the possibility that cave bear populations were highly mobile and reactive to short-term climatic changes. It would be interesting to test the possible climatic difference between *Ursus spelaeus* and *Ursus ingressus* in other areas where they co-occur, for instance in the Swabian Jura in southwestern Germany (Hofreiter et al., 2007).

4.2. Comparison with other cave bear populations

Collagen $\delta^{13}C$ and $\delta^{15}N$ have been measured over the last 20 years on several cave bear populations in Europe, mainly from sites located at relatively low altitudes. When compared to other cave bear sites from western and central Europe, the specimens from Ramesch and Gamssulzen are remarkable for their low $\delta^{15}N$ values (Fig. 6). Average $\delta^{15}N$ values of other cave bear populations in western and central Europe range from 2 to 6‰. Only cave bears from the French Alps site of Balme-à-Collomb come close to the low $\delta^{15}N$ values of the Austrian cave bears (Fig. 6). Nevertheless, cave bears from Balme-à-Collomb *Ursus spelaeus spelaeus* (France), found in a cave at 1700 m asl, a similar altitude to Ramesch (Philippe and Deverchère, 1995), exhibited a broad range of $\delta^{13}C$ values, from −22.2 to −20.3‰ (Bocherens, submitted, Fig. 6), similar to the total range observed for both cave bear types from the Austrian caves combined. The $\delta^{15}N$ values were slightly higher than for the Austrian cave bears, with an average of 1.7 ± 0.5‰, but clearly lower than for other cave bear populations from lower altitude where most of the $\delta^{15}N$ values ranged from 3 to 4.5‰ (Bocherens et al., 2006), or sites in southern France, Belgium, southwestern Germany and north-western Spain (Fig. 6). This difference supports the hypothesis that cave bears from Ramesch and Gamssulzen not only hibernated in high altitude caves, but also spent their active time foraging at higher altitude than cave bears hibernating in caves located at lower altitudes. This implies that the many cave bear populations that lived in Europe during the Late Pleistocene occupied a mosaic of different habitats, and this mosaic was highly dynamic due to the heterogeneous landscape and to short-term climatic shifts. In such a context, the population dynamics of cave bears must have been quite complex and isotopic tracking provides a way to evaluate the ecological side of this complexity.

5. Conclusion

The question of ecological separation between two genetically distinct cave bear types from Ramesch and Gamssulzen was addressed successfully by using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ measurements of fossil bear bones. The first firm conclusion is that the cave bears from Ramesch, *Ursus spelaeus eremus*, were ecologically distinct from the cave bears from Gamssulzen, *Ursus ingressus*, both being ecologically distinct from the brown bears from Ramesch, *Ursus arctos*. Both cave bear types appeared to have been purely herbivorous but likely consumed different plant types and/or plants from different habitats, while brown bears included some animal proteins in their diet. More difficult to answer is the question of whether the separation between both cave bear types was only spatial, meaning that the individual bears roamed the area at the same time, but remained physically separated in different areas, or whether both types of cave bears occupied the regions during times of different climate. The direct ^{14}C dates were not precise enough to sort out these two hypotheses, but the bone apatite $\delta^{18}O$ values strongly suggest that both types of cave bears used isotopically distinct water sources indicating that they may not have occupied the same landscape, either separated in space or in time due to climatic shifts.

If the separation between the two cave bear types was only spatial, this would require a strong territoriality for these bears, at least during the breeding period to prevent significant gene flow, since ancient DNA investigations provided evidence for genetic separation between both cave bear types (Hofreiter et al., 2004).

An alternative scenario is the possibility that both cave bears moved back and forth in the area, the *ingressus* type being present during relatively colder periods and hibernating in the lower altitude cave, and presenting a larger body mass consistent with Bergmann's rule, while the smaller *eremus* type being present during relatively warmer periods and using the higher altitude cave as a winter den. In either case, it seems that the influence of environmental conditions strongly constrained the genetic structure of these bears and further research combining multi-isotopic approaches and palaeogenetic investigations, together with a robust chronology of the skeletal remains, should allow a better understanding of population dynamics during the unstable climatic context of the Late Pleistocene, with possible implications for the conservation of modern large mammals in a global warming context.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quaint.2010.12.020.

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