Stable isotopes data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) from the cave bear (*Ursus spelaeus*): a new approach to its palaeoenvironment and dormancy

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Palaeoclimatic data that can be extracted from the isotopic signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which are found in fossil bone collagen, should be analysed according to the specific metabolism of each species. Although *Ursus spelaeus* is an extinct species, its metabolism is assimilated to current, closely related species of bear. In this study, bone collagen isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of cave bears from Late Pleistocene Alpine sites were compared to those that have already been documented. The $\delta^{13}\text{C}$ signature did not seem to follow a systematic trend according to climatic conditions, probably as a consequence of the high variability present in the values of C3 plants, which were the basis of feeding. On the contrary, the $\delta^{15}\text{N}$ signature displayed higher values in sites corresponding to colder periods in which the $\delta^{15}\text{N}$ signature appeared to be dominated by the physiology of dormancy. Then, due to the reuse of urea in synthesizing amino acids, the $\delta^{15}\text{N}$ signature systematically increased along with dormancy duration. This was related to the length of winter and, in turn, depended on climate.

Keywords: *Ursus spelaeus*; $\delta^{13}\text{C}$; $\delta^{15}\text{N}$; bone collagen; palaeoenvironment; dormancy

1. INTRODUCTION

Carbon and nitrogen isotopic signatures, which are found in fossil tissues (bone and dentine), have often been used for reconstructing the features of palaeoclimate (Ambrose & De Niro 1989; Bocherens *et al.* 1994, 1996; Cormie & Schwarcz 1994). The usual strategy followed in extracting palaeoclimatic data from the isotopic signatures of ^{13}C and ^{15}N in fossil tissues is based on two different approaches: (i) comparison between these signatures and those which are currently found in the same or other related species under well-known climatic conditions, and (ii) comparison between different fossil species from the same site, assuming they are contemporary.

Both approaches have clear problems when applied to extinct species. In the first case, extinct animals are compared to current ones following purely phylogenetic criteria and, even if it is presumed that their metabolisms were similar, the main isotopic signature conditioning, i.e. climate, is ignored. In the second case, it is presumed that the climate where the life of the different species took place is the same, but comparison forces us to reject physiological conditioning.

In order to be able to obtain results that allow for the creation of palaeoclimatic reconstruction, it is necessary, in our opinion, to compare the isotopic signatures of individuals of the same species and age range from well-known geographical areas and, most importantly, use an accurate chronological framework. This is particularly important in the case of extinct species, in which the impossibility of having precise current referents forces us to assume more hypotheses than for extant species.

One of these species is the cave bear (*Ursus deningeri-spelaeus*), which is considered as having been endemic in Europe (Kurtén 1976). The environment and metabolism of this

species are usually considered similar to those of the American black bear (*Ursus americanus*) or the brown bear (*Ursus arctos*). As with these bears, the cave bear would retire to a refuge (usually a cave) when food was scarce, regardless of the amount of reserves accumulated as fat and become dormant (Nelson *et al.* 1998; Lidén & Angerbjörn, 1999).

Dormancy in bears is not real hibernation, although during this stage they do develop a particular metabolism whereby they do not feed, drink, defecate or urinate. Metabolic waste, such as urea, the storage of which can be lethal, is almost entirely recycled, as will be explained later. After dormancy, a bear will only have lost between 15 and 25% of its body weight at the expense of a decrease in fat but not in protein or bone (Anderson 1992). Dormancy duration is variable. Periods of five to seven months in cold regions (Rogers 1987) to cases where there was no dormancy at all (Hellgren & Vaughan 1987) have been documented in American black bears. In brown bears, variability is lower (Naves & Palomero 1993). Clearly, permanence in bear dens is longer in those regions with longer winters (Johnson & Pelton 1980). The causes of cave bear death inside caves were recently analysed by Stiner (1998) and were found to have been disease, accident and starvation.

The cave bear has a specific tooth, skull and jaw morphology, which is the principal reason why it is thought to have followed a basically herbivorous regime (Kurtén 1976). In recent years, different approaches have been adopted in reconstructing this species' diet through analysis of stable isotopes, usually ^{13}C and ^{15}N , preferably in bone and dentine collagen and hydroxyapatite (Bocherens *et al.* 1994, 1997; Fernández-Mosquera 1998; Nelson *et al.* 1998; Lidén & Angerbjörn 1999; Vila-Taboada *et al.* 1999). The results derived from these studies may be summed up in the following points.

- (i) A preferably herbivorous diet based on C3 plants.

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Table 1. Isotopic data published so far of cave bear bone collagen from European sites

(The following references were used: Fernández-Mosquera (1998) for Eirós, Vila-Taboada *et al.* (1999) for Liñares, Bocherens *et al.* (1994) for Aldène, Mialet and Olaskoa, Bocherens *et al.* (1997) for Scladina-1, Bocherens *et al.* (1999) for Scladina-4 and Nelson *et al.* (1998) for Divje Babe.)

site	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>n</i>	age (years BP)
Eirós	-21.1 ± 0.6	5.0 ± 0.5	8	$24\,090 \pm 440$
Liñares	-21.0 ± 0.3	3.0 ± 0.4	20	$35\,220\text{--}1440$
Aldène	-20.8 ± 0.4	3.1 ± 1.5	3	$<250\,000$
Mialet	-20.2 ± 0.4	2.8 ± 1.6	5	no data
Olaskoa	-20.5	2.7	1	<i>ca.</i> 10 000
Scladina-1	-22.1 ± 0.2	4.9 ± 1.2	7	<i>ca.</i> 40 000
Scladina-4	-23.2 ± 0.3	3.6 ± 0.6	4	$120\,000\text{--}130\,000$
Divje Babe	-20.5 ± 0.4	1.9 ± 0.7	11	48 000

- (ii) A marked lactation effect that caused an increase in $\delta^{15}\text{N}$ values in the bone collagen of young individuals and in the dentine values of young and adult individuals, the latter of which maintained the lactation signature due to non-renewal of dentine collagen after weaning.
- (iii) In some cases, there is a hint of a possible influence of winter dormancy on their isotopic signatures (Bocherens *et al.* 1997; Nelson *et al.* 1998; Lidén & Angerbjörn 1999).

This study was aimed at obtaining palaeoclimatic data from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures found in the bone collagen of *Ursus spelaeus* from different Alpine sites and proposing a comparison with data from other isotopically well-described and well-documented sites. Using a comparison of data from adult individuals of the same species, we were able to evaluate how different climates (geographical or chronological) influenced the same metabolism and, thus, delimit the responses of isotopic signatures to climatic conditions. The data from these sites, i.e. absolute age (if known), the average values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and sample sizes, are shown in table 1. Only data from adult individuals were included. The geographical locations of these sites are shown in figure 1.

2. MATERIAL AND METHODS

Palaeoclimatic data extraction from fossil collagen stable isotopes should be interpreted according to the location and conditions of each site. Even though all sites are in the Eastern Alps, a decision was taken to select samples that covered a wide range of altitudes (from 878 up to 2800 m above sea level (a.s.l.)) and ages (from 121 to 28 kiloyears before present (kyr BP)) in order to observe how climatic conditions had an influence on isotopic signatures. Twenty-seven adult cave bear ribs from eight different Alpine sites were assembled (figure 1).

Samples were cleaned by sandblasting and then alternative acetone/distilled water sonicated, sawn, crushed and finely ground. Collagen extraction was performed according to Bocherens *et al.* (1997) based on alternative reactions and filtrations with HCl and NaOH. The extracted collagen was weighed

Figure 1. Geographical location of the cave bear sites studied in this work. Sites with data published in this paper are represented by solid symbols and the initial numbers of samples analysed appear in parentheses: Co, Conturines (three); Li, Lieglloch (three); RK, Ramesch Knochenhöhle (three); Gs, Gamssulzenhöhle (three); Hd, Herdengelhöhle (six); Hg, Hartelsgraben (three); PZ, Potocka Zijalka (three); Sw, Schwabenreithöhle (three). Sites from the literature are represented by hollow circles: L, Liñares (Vila-Taboada *et al.* 1999); E, Eirós (Fernández-Mosquera 1998); Sc, Scladina (Bocherens *et al.* 1997, 1999); Olaskoa–Pyrenees—exact location unknown (Bocherens *et al.* 1994); Al, Aldène (Bocherens *et al.* 1991, 1994); Mi, Mialet (Bocherens *et al.* 1994); DB, Divje Babe (Nelson *et al.* 1998).

in order to calculate the percentage of collagen in the bone. The carbon and nitrogen isotope compositions, percentage of carbon and nitrogen in collagen and the C:N atomic ratio were measured using an Elemental Analyser Carlo-Erba 1108 connected to a Finnigan Mat Delta Plus mass spectrometer, with analytic reproducibility better than 0.1‰ for carbon and 0.2‰ for nitrogen. The results were referred to international standards, i.e. PDB (Pee Dee Bee limestone) and atmospheric N_2 , respectively. Isotopic ratios are presented using δ notation, where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{15}\text{N}/{}^{14}\text{N}$ and ${}^{13}\text{C}/{}^{12}\text{C}$.

3. RESULTS AND DISCUSSION

Only 12 (none of them from Gamssulzenhöhle) out of the 27 initial samples yielded an atomic C:N ratio of collagen within the range 2.9–3.6, which is usually considered as a criterion for proper preservation of the original isotopic composition (De Niro 1985). The results obtained (table 2) were absolutely comparable to those that have been documented (figure 2). Therefore, the palaeoclimatic information that could be extracted from these data did not differ from that which has been generally accepted so far, that is to say a preferentially herbivorous diet based on C_3 plants typical of mild and wet climates.

The variability in the values obtained should be considered in the light of the data presented in table 1,

Table 2. Isotopic signatures of the analysed samples

(Chronology and altitude as well as a description of the Alpine sites are given in the following references: Rabeder (1992) for Conturines, Rabeder (1997a,b) for Lieglloch, Rabeder (1997a) and Frank & Rabeder (1997b) for Ramesch, Rabeder (1997a) and Frank & Rabeder (1997a) for Herdengel, Rabeder (1997a,c) for Hartelsgraben, Frank & Rabeder (1997c) for Schwabenreith and G. Rabeder (personal communication) for Potocka Zijalka (30 980 $\pm$ 330/–310 years BP). Absolute age for Llus-2 at Lieglloch ^{14}C AMS (Ua-15978) 28 130 $\pm$ 600 years BP (this paper) and for Llus-3 at Lieglloch dated as 25–35kyr BP by P4 index.)

site	bone number	absolute age (kyr)	altitude (m a.s.l.)	bone % N	% collagen	% C	% N	atomic C:N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Ramesch	Rus-3	42–44.5	1960	3.2	13.2	21.7	8.1	3.1	–22.5	2.4
Herdengel	Hdus-2	36.2–40	878	2.2	9.2	12.7	5.0	2.9	–22.1	2.3
Herdengel	Hdus-3	36.2–40	878	3.2	10.2	13.1	4.8	3.1	–22.0	2.5
Schwabenreith	Sus-3	55–121	959	2.7	27.9	33.3	13.1	3.0	–22.9	2.5
Lieglloch	Llus-2	28.1	1290	2.5	6.8	25.5	9.8	3.0	–20.2	4.1
Lieglloch	Llus-3	25–35	1290	2.0	1.8	27.2	10.8	2.9	–20.1	2.8
Hartelsgraben	Hgus-1	27.3–43.4	1230	1.2	4.4	21.3	8.5	2.9	–21.0	0.8
Hartelsgraben	Hgus-7	27.3–43.4	1230	1.5	4.0	26.0	9.6	3.1	–20.8	3.4
Conturines	Cous-1	41.9–47.5	2800	3.3	8.6	25.7	9.4	3.2	–23.3	2.5
Conturines	Cous-2	41.9–47.5	2800	3.6	8.6	27.4	10.7	3.0	–21.9	1.9
Conturines	Cous-3	41.9–47.5	2800	3.5	7.0	19.5	7.5	3.0	–21.6	1.6
Potocka Zijalka	Pzus-2	30.9	1700	3.4	10.5	30.9	11.9	3.0	–20.4	4.2

Figure 2. Isotopic signatures for the Alpine sites (solid symbols) and the average values of those used for comparison (hollow symbols). Error bars represent standard deviations.

where the studied sites with the highest numbers of samples and accurate dating (Liñares, Eirós and Divje Babe) showed deviations of ± 0.3 – 0.6 for the $\delta^{13}\text{C}$ signature and ± 0.4 – 0.7 for the $\delta^{15}\text{N}$ signature. These values are very similar to those proposed by Cormie &

Schwarcz (1994) for contemporary individuals from the same geographical area (± 0.5 for the $\delta^{13}\text{C}$ signature and ± 0.6 for the $\delta^{15}\text{N}$ signature). Our results displayed a higher variability (except in the case of Herdengel) in both signatures. This may of course have been due to the small number of samples analysed for each site and, above all, to the wide time-span that has been assigned to these sites.

Similarly, if all the existing data so far are taken into account (figure 2), with their respective time assignments, we observe that the signature of $\delta^{13}\text{C}$ varies from -23.5 up to -19.8 and the signature of $\delta^{15}\text{N}$ from 0.8 ‰ up to 6.1 ‰. This variability should be considered as a response to environmental conditions, since all the data compared belonged to adult individuals of the same species. It has been implicitly assumed that the response to climatic changes must be the same, regardless of the site.

The isotopic signature of ^{13}C was more negative in the case of the Alpine bears than in the rest of the bear populations to which they were compared, except for that of Scladina-4. Using comparison with other herbivorous examples, Bocherens *et al.* (1994) suggested that the lower content of ^{13}C in *U. spelaeus* could be due to their preference for closed habitats. This cannot be the reason in the case of the Conturines sites (2800 m a.s.l.) or Ramesch (1960 m a.s.l.) due to the step orography of the surrounding area, which makes development of dense forests impossible.

Bocherens *et al.* (1997) also proposed that the storage of lipids (low in ^{13}C) and their later use as a source of carbon for synthesizing amino acids during dormancy justified the lower value of the $\delta^{13}\text{C}$ signature in *U. spelaeus* as compared to the rest of the herbivores. It is difficult to determine the influence of this mechanism on the isotopic signature of bone collagen when only data from *U. spelaeus* are compared. First, we could expect a difference in the signature of $\delta^{13}\text{C}$ for sites that were associated with either cold or mild periods, i.e. longer or shorter dormancy periods. However, comparison between the $\delta^{13}\text{C}$ signature

Figure 3. $\delta^{15}\text{N}$ average value from the sites considered, climatic proxy $\delta^{18}\text{O}_{\text{atm}}$ as recorded at the Vostok ice core and the insolation curve for 65°N (adapted from Petit *et al.* 1999). Data from Aldène, Mialet and Schwabenreith were not considered as their chronology was not accurate enough. Data from Sciadina-4 (average $\delta^{15}\text{N} = 3.6 \pm 0.6$, ca. 120 kyr BP) are not represented due to its large age difference. Bar lengths correspond to time-spans. The dots show accurate radiocarbon datings.

of Eirós and Liñares (table 1), two sites which are very close geographically even though one was associated with a significantly colder period (Eirós, 24 kyr BP) than the other (Liñares, 35 kyr BP), showed that the values of the $\delta^{13}\text{C}$ signature were the same for both sites (Vila-Taboada *et al.* 1999) and equivalent to those of Aldène and Mialet, these last two lacking a precise chronology. Similarly, some of the Alpine site samples that, according to their chronology, were associated with warmer periods than those of Eirós or Liñares (figure 3) showed a more negative $\delta^{13}\text{C}$ signature.

It is possible that the high rate of bone renewal during dormancy (Anderson 1992) led to a significant incorporation of collagen considerably depleted in ^{13}C over a relatively short period of time. The signal found would not change once the maximum collagen renewal value had been reached as the ^{13}C pool of the lipid storage was the same during dormancy. However, the difficulty in determining the starting value accurately (that of the diet) due to the high variation in the $\delta^{13}\text{C}$ signature of C3 plants (Cerling & Harris 1999) did not allow for determination of the final contribution of

dormancy to the signature found. In any case, similarity between the rest of the values that, in turn, came from very different periods of time led us to conclude that the $\delta^{13}\text{C}$ signature does not reflect changes in climatic conditions precisely enough.

The $\delta^{15}\text{N}$ signature in collagen is determined by diet and metabolism. Changes in the original signature are to be expected if we take into account the range of values presented by soils, even in restricted geographical areas and the plant signature will also be varied due to its capacity to fix N_2 (Högberg *et al.* 1996; Michelsen *et al.* 1996). However, in those cases where we were able to determine the influence of climate on diet and metabolism quantitatively, the variability shown by the $\delta^{15}\text{N}$ signature in the collagen could not be explained purely via the original signature of the diet, given that it is also possible to identify climatic and physiological changes (Cormie & Schwarcz 1994, 1996). It has been shown that, in certain herbivores, periods of drought induce hydric stress, the result of which is an increase in the $\delta^{15}\text{N}$ signature due to internal recycling of nitrogen (Sealey *et al.* 1987; Cormie & Schwarcz 1994, 1996; Iacumin *et al.* 1997).

With regard to the values of the $\delta^{15}\text{N}$ signatures obtained, the value of 0.81 from Hartelsgraben stood out as the lowest, whilst the highest value (4.17) belonged to a sample from Potocka Zizalka, which is within the range of values mentioned in the literature (figure 2). When all the available data were compared, the coincidence of values obtained in contemporary sites from different geographical zones contrasted with the discrepancy between values from sites which were close to each other, but with different chronologies and even between different levels within the same site. Attributing the $\delta^{15}\text{N}$ signature variations in spatially and temporally contiguous coincidences to the original signature of the diet would be too simple and, in any case, difficult to justify, given the total lack of $\delta^{15}\text{N}$ data in the soils and plants throughout the extensive geographical and temporal spectrum of our data set. Consequently, the only possibility of obtaining palaeo-environmental information from the sites studied was through their chronology. As mentioned above, several of the sites studied were associated with periods that were colder than others, which directly affected the metabolism of the nitrogen in bears due to dormancy (Nelson *et al.* 1975; Nelson 1989).

During dormancy, protein synthesis increases and amino-acid catabolism decreases, but is not eliminated (Nelson 1989). Nitrogenated waste is transformed into urea in the liver, which, during dormancy, is hydrolysed and reabsorbed in the urinary bladder (Nelson *et al.* 1975). When urea breaks down, its amino groups are reused for the synthesis of amino acids, thereby beginning the cycle all over again. In this process, the higher affinity for joining the urea of the light isotope ^{14}N causes an enrichment in ^{15}N in amino acids, which form in this way (Peterson & Fry 1987). This reuse of urea components for the synthesis of amino acids will increase their trophic level, leading to an increase in the $\delta^{15}\text{N}$ signature in each cycle. In addition, tropocollagen is almost entirely formed by glycine and proline/hydroxyproline, non-essential amino acids, the enrichment of ^{15}N in which is higher than that in essential ones (Gaebler *et al.* 1966).

Given the chronologies of the sites studied, it was observed that those which displayed higher $\delta^{15}\text{N}$ values corresponded to globally colder periods (figure 3), which led to longer dormancy periods. The signals found at Eirós, Potocka Zijalka and LLus-2 reflected a strong influence of dormancy on their $\delta^{15}\text{N}$ values, whereas those sites assigned to warmer stages did not show such a contribution of dormancy to diet value, except in the case of Scladina-1. According to our hypothesis, the environmental conditions at Scladina-1 up to 40 kyr BP would have been colder than in the other sites situated further to the south. Palaeoenvironmental reconstruction of Scladina-1 indicated an open steppe environment, in contrast to the wooded environment obtained for Scladina-4 (Cordy & Bastin 1992) in a hotter interstadial and with lower $\delta^{15}\text{N}$ values. The comparison of $\delta^{15}\text{N}$ values from different levels of this site corroborated the tendency observed in the other sites towards an increase in the $\delta^{15}\text{N}$ signature during colder periods. The high variability of the $\delta^{15}\text{N}$ signature from Aldène and Mialet will be a consequence of the different climatic conditions during the wide time-span that these sites represent, although accurate datings from them are needed in order to confirm this interpretation.

4. CONCLUSIONS

In accordance with the data presented, we believe that dormancy duration must be taken into account when interpreting $\delta^{15}\text{N}$ results, both in *U. spelaeus* and in modern bears. Our hypothesis is based on the physiology of dormancy, which indicated a progressive and systematic increase in the $\delta^{15}\text{N}$ signature. However, the $\delta^{13}\text{C}$ signature did not seem to follow a systematic trend according to climatic conditions, at least as recorded in *U. spelaeus* bone collagen. However, ignorance of the rate of replacement of the collagen and, above all, the original values of the diet of each individual, which, in turn, may have depended on climatic variations, prevented us from quantifying the magnitude of this effect. According to our hypothesis, the original value of the diet would have been added to the effect produced by the recycling of urea during dormancy, which would only be detectable in cases of longer dormancy.

Finally, this work has shown that, because of the general climatic instability experienced during the Upper Pleistocene until the Holocene (Daansgard *et al.* 1993), having accurate datings is particularly important when making inferences about palaeoclimatic data from stable isotopes found in fossil remains. Further measurements with an increased sample size and accurate datings will be necessary in order to test our hypothesis about the use of $\delta^{15}\text{N}$ signatures in cave bear bone collagen as a tool for environmental reconstruction.

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