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Diverse bone calcium isotope compositions in Neanderthals suggest different dietary strategies

Pierre-Jean Dodat^{a,b,*}, Emmanuelle Albalat^a, Vincent Balter^a, Christine Couture-Veschambre^b, Maurice Hardy^c, Juliette Henrion^b, Trenton Holliday^{d,e}, Bruno Maureille,^b

a : Laboratoire de Géologie de Lyon : Terre, Planètes, Environnements. UMR 5276, CNRS, Ecole Normale supérieure de Lyon. 46 Allée d'Italie, 69342 Lyon Cedex 07, France

b : Univ. Bordeaux, CNRS, Ministry of Culture, PACEA UMR 5199, F-33600 Pessac France

c : CNRS, UMR 7041, Univ. Nanterre, Ministère de la Culture, ArScAn, 92000 Nanterre, France

d : Tulane University; Department of Anthropology, 101 Dinwiddie Hall, New Orleans, Louisiana 70118, USA

e : University of the Witwatersrand; Centre for the Exploration of the Deep Human Journey, Private Bag 3, Wits 2050, Republic of South Africa

* Corresponding author.

E-mail address: pjdodat@naturalsciences.be (P.-J. Dodat).

Abstract

Zooarcheological and geochemical evidence suggests Neanderthals were top predators, but their adherence to a strictly carnivorous diet has been questioned. Recent studies have demonstrated the potential of calcium stable isotopes to evaluate trophic and ecological relationships. Here, we measure the $\delta^{44/42}\text{Ca}$ values in bone samples from Mousterian contexts at Grotte du Bison (Marine Isotope Stage 3, Yonne, France) and Regourdou (Marine Isotope

Stage 5, Dordogne, France) in two new Neanderthal individuals, associated fauna, and living local plants. We use a Bayesian mixing model to estimate the dietary composition of these Neanderthal individuals, plus a third one already analyzed. The results reveal three distinct diets: a diet including accidental or voluntary consumption of bone-based food, an intermediate diet, and a diet without consumption of bone-based food. This finding is the first demonstration of diverse subsistence strategies among Neanderthals and as such, reconciles archaeological and geochemical dietary evidence.

Keywords: Paleodiet; Late Pleistocene; Calcium isotopes, Marrow consumption, Trophic relationships.

1. Introduction

The recent first analysis of calcium stable isotope composition ($\delta^{44/42}\text{Ca}$) of Neanderthal remains (Dodat et al., 2021) illustrated how Ca stable isotopes can be used to reconstruct dietary habits of Neanderthals. The results of this study agreed with traditional isotopic data (primarily nitrogen) previously obtained on Neanderthal remains (Balter and Simon, 2006; Naito et al., 2016; Wißing et al., 2016): specifically, Regourdou 1 individual has a carnivorous diet which must have included a significant proportion of bone or bone marrow (Dodat et al., 2021). Data showing that Neanderthals were highly competent hunter-gatherers, a primarily meat-based diet raises the conundrum of a diet potentially lacking essential nutrients. In nutritional terms, the consumption of a protein-based diet is an effective way to provide energy to the body but is also a diet that lacks many essential nutrients, vitamins, or carbohydrates (Hardy, 2010), creating potential deficiencies that could impact fertility, fetal mortality or exposure to kidney failure (Fiorenza et al., 2015). In fact, humans cannot tolerate a diet composed of more than 35–40% protein no matter its origin (animal or

vegetal; Cordain et al., 2000; Hardy, 2010; Fiorenza et al., 2015). Ethnographic studies have shown that if hunter-gatherers obtain more than 50% of their energy from animal sources (Cordain et al., 2000), the consumption of animal fat containing little, or no protein limits the toxicity of such a diet. Under these conditions, the remaining energy is provided by vegetal sources (Cordain et al., 2000; Fiorenza et al., 2015). Taking these metabolic arguments into account, it is unlikely Neanderthals had a diet of ca. 100% (primarily ungulate) meat. Rather, a proportion on the order of 60–70% of the energy coming from animal sources (meat and fat) would better fit metabolic and ethnographic data (Cordain et al., 2000).

With over 40 analyzed Neanderthal remains, results of nitrogen isotopes research still makes confident assertions about homogeneity in the Neanderthal diet, displaying a preference for consuming large herbivores such as horse, reindeer, red deer, bovids, rhinoceroses, and mammoth (e.g. Balter and Simon, 2006; Bocherens, 2013; Naito et al., 2016; Wibing et al., 2016). This dietary preference aligns with evidence from zooarchaeology, bone accumulation, and anthropic marks on faunal remains (e.g. Patou-Mathis, 2000; Costamagno et al., 2006; Hublin and Richards, 2009; Marín et al., 2017). Nonetheless, recent methodological developments such as dental calculus studies now allow us direct analysis of diet and reveal the consumption of a large panel of plants by Neanderthal (Henry et al. 2011; Weyrich et al. 2017; Hardy et al. 2022). Additionally, recent discoveries at the Figueira Brava site on Portugal's Atlantic coast have even painted a picture of a very broad food spectrum for Neanderthals, including terrestrial (animal and vegetable) and marine resources (Zilhão et al., 2020).

The $\delta^{44/42}\text{Ca}$ value is one proxy for studying Neanderthal diet (Tacail et al., 2020; Dodat et al., 2021) mainly for enriched Ca source such as bone or milk. Unfortunately, it cannot evaluate the proportion of consumed animal soft tissues versus plant material because the $\delta^{44/42}\text{Ca}$ value of these two components is similar (Tacail et al., 2019). The Ca isotope

composition is however an efficient dietary proxy when applied to predators consuming whole prey, because bone, with its extremely negative $\delta^{44/42}\text{Ca}$ value, is eaten along with the soft edible parts (Martin et al., 2015; Hassler et al., 2018) resulting in a more negative $\delta^{44/42}\text{Ca}$ value of the consumer relative to the prey. The situation becomes more complicated in mammals because medium- to large-sized predators do not ingest bone deliberately, except for hyenas and to a lesser degree canids (Skulan and DePaolo, 1999; Reynard et al., 2010; Heuser et al., 2011; Clementz, 2012; Martin et al., 2017, 2018). Bone and bone marrow have similar $\delta^{44/42}\text{Ca}$ values but because of the distinct Ca concentrations of bone marrow, meat, and fresh bone (0.01%, 0.6% and 20%, respectively), a diet with a negative $\delta^{44/42}\text{Ca}$ value is indicative of accidental or voluntary bone consumption (Reynard et al., 2010; Heuser et al., 2011; Martin et al., 2017, 2018; Dodat et al., 2021). The archaeological evidence suggests that the ingestion of some trabecular bone during yellow marrow consumption, or via culinary practice is the most likely hypothesis to explain bone consumption among human populations (Fiorenza et al., 2015; Morin, 2020a).

Calcium is the main cationic constituent of hydroxylapatite (~40% weight), the primary mineral component of bone and dental tissues. Diagenesis has been recognized for decades to be pervasive for trace elements in fossil hydroxylapatite (e.g., Trueman and Tuross, 2002; Kohn and Moses, 2013). Trace elements generally accumulate in secondary minerals (usually calcite) or ultimately, during hydroxylapatite recrystallization subsequent to a Ca substitution process. However, the diagenesis of Ca should not be as pervasive as it is for trace elements for two main reasons. First, mass balance calculations between a fossil bone or tooth and the diagenetic soil water predict only limited diagenesis because the Ca concentration in ground water is negligible relative to that in hydroxylapatite, or marked diagenesis would require unrealistic groundwater $\delta^{44/42}\text{Ca}$ values (Martin et al., 2017). Second, the diagenetic Ca in fossil bone and dental tissues can be removed via leaching protocols based on the higher

solubility of calcite relative to hydroxylapatite (Sillen and LeGeros, 1991; Lee-Thorp and van der Merwe, 1991; Balter et al., 2002). Therefore, the existence of remaining secondary Ca after a leaching protocol is unlikely, unless diagenetic Ca had been incorporated into the hydroxylapatite during recrystallization (Dodat et al., 2023). Beyond the potentially strong resistance to diagenesis of bone Ca isotopes, the fact that Ca is the main cationic constituent of hydroxylapatite offers a second advantage—a very small sample requirement. Calcium isotope compositions are routinely measured at 1.5 $\mu\text{g/mL}$ on multi-collection inductively coupled plasma mass spectrometer (MC-ICP-MS). Three runs are generally performed and leaching usually induces an initial sample mass loss of 30–50%, so theoretically ca. 20 μg of bone sample is sufficient for processing. However, in practice, such a tiny amount of material cannot be handled during sample preparation. About 200 μg of material, which can be obtained using micro-sampling techniques (Tacail et al., 2019), is the amount barely visible to the naked eye, and is therefore easy to handle. This comes, however, with a potential flaw, which is the possible significant variability of the Ca isotope composition within mineralized tissues. It is likely to take advantage of this variability when using tooth enamel because the position of the micro-sampling can be controlled and reported as a function of dental age and because enamel does not remodel. Tacail et al. (2019) for instance use such dental age reconstructions to study the age at weaning of South African hominins. When using bone, it is not possible to infer the age at which bone formed and eventually remodeled, and a tiny sample amount of about 1 mg (which is the typical size used in the present study) might record unusual period of life information. Thus, we are faced with the persistent issue that, in order to get a certain degree of reproducibility for an averaged value, a larger sample size is required the more heterogeneous a material is. A substantial scattering of the Ca isotope compositions is therefore expected, which will depend on lactation, gestation, dietary shift, species-specific

metabolic trait, or a combination thereof (Tacail et al., 2020). Nevertheless, during this study a bear bone was collected from two areas of the same bone, these are samples R35 and R33.

This study presents Ca isotope compositions measured on a Neanderthal individual and eleven different faunal taxa from Grotte du Bison archaeological site in Bourgogne (Yonne, France), and on a second Neanderthal individual, two newly analyzed faunal taxa and faunal taxa from the Regourdou site in Black Périgord (France; Dodat et al., 2021). We also consider another Neanderthal individual and faunal remains from the Regourdou site already analyzed in 2021 (Dodat et al., 2021) and then characterize the diet of these three Neanderthals using Bayesian mixing models for stable isotope analyses in R (MixSIAR) based on the measured $\delta^{44/42}\text{Ca}$ values.

2. Materials and methods

2.1. Grotte du Bison fossil material

The Grotte du Bison belongs to a larger group of prehistoric caves at Arcy-sur-Cure which forms a network of nearly 4 km with a surface area of about 60 ha (Fig. 1A; Baffier and Girard, 1997). The site of Grotte du Bison is one of the most recent discovery in the history of the excavated sites caves of Arcy-sur-Cure. It was identified in 1958 by P. Poulain and was excavated for the first time in 1959 by members of A. Leroi-Gourhan's scientific team until 1963 (Leroi-Gourhan, 1961). It was later excavated by F. David (1995 to 2008) and finally by one of us (M.H.) from 2011 to 2019. The excavation campaigns resulted in discovery of at least 50 Neanderthal remains (40 isolated teeth, two maxillary fragments, six skull fragments and two postcranial pieces belonging to two different individuals), plus four partially digested teeth (potentially humans; Maureille et al., 2017) in two (I and J) of the lower sedimentological layers, attributed to a late Mousterian period. Following Tillier et al. (2013), two accelerator mass spectrometry radiocarbon dates place the layer I between 51 519–44 120 and 47 951–42

658 BC. Other chronological correlations of the Grotte du Bison layers are available in Roblin-Jouve et al. (2018). In 2019, an incomplete right fibula diaphysis attributed to a mature Neanderthal individual was recovered in layer J, which is related to the beginning of Marine Isotope Stage (MIS) 3. This is the specimen we sampled. The presence in layers I and J of *Crocota crocuta* and an unusually low carnivore-to-ungulate ratio together suggest that the faunal assemblage in these layers is not the result of accumulation by hyena alone but also by Neanderthal (Pothier Bouchard, 2016). Among the three most represented herbivore taxa, at least two (*Rangifer tarandus* and *Equus caballus*) show anthropic (e.g. cut mark, fresh bone breaks) traces suggesting consumption by Neanderthals. The accumulation of bovine bone is thought to be due to *Crocota crocuta* (Pothier Bouchard, 2016).

2.2. The Regourdou fossil material

The Regourdou cave is located at the top of Lascaux hill (Fig. 1A; Montignac-Lascaux, Dordogne, France). 'Excavations' at Regourdou began in 1954 at the landowner's (R. Constant) initiative. During the night of the 22nd to the 23rd of September 1957, part of a Neanderthal skeleton (Regourdou 1) was discovered under unprofessional circumstances (Maureille et al., 2013; Pelletier et al., 2017). A salvage excavation led to the discovery of some faunal and lithic remains, and a set of bone fragments or complete ones belonging to one Neanderthal specimen, Regourdou 1 (Bonifay, 1965; Madelaine et al., 2008). Regourdou 1 partial skeleton was recovered from Bonifay's stratigraphic layer 4 (Bonifay, 1965), which contained Discoid Mousterian lithics with the production of pseudo-Levallois points and a temperate fauna dominated by brown bears (*Ursus arctos*). Based on lithic and faunal remains layer 4 was attributed to the first part of MIS 5 (Bonifay, 1965; Pelletier et al., 2017). Regourdou 1 skeletal conservation and preservation were interpreted as a Neanderthal burial since its discovery (Piveteau, 1959; Maureille et al., 2016; Pelletier et al., 2017). The calcaneus belonging to

Regourdou 2 was found near the wall opposite to Regourdou 1 burial and it is presumed that Regourdou 2, like Regourdou 1, came from layer 4 (Madelaine et al., 2008). Regourdou 2 lacks any archaeological context, and despite its discovery as early as 1963, it was not studied until recently (Coutinho Nogueira et al., 2017), while it was suspected the existence of two adult Neanderthal individuals since many years on the basis of foot bones (e.g. Vandermeersch and Trinkaus, 1995).

The Ca isotope composition was measured for fifteen samples obtained from two new mammal species (*Capreolus capreolus*, *Bos/Bison*), and seven previously analyzed species including Regourdou 2 (Supplementary Online Material [SOM] Table S1). A study already has investigated and reconstructed the ecology and diet of Regourdou 1 Neanderthal, which was a mix of food resources, including meat and plant materials (Fiorenza et al. 2019).

2.3. *Calcium extraction and analysis*

Because cortical bone is denser and cleaner than trabecular bone, all samples were collected from cortical bone except for three trabecular bone samples (Regourdou 1 and 2, and one from a brown bear). Each trabecular bone sample is paired with a cortical bone sample collected nearby on the same piece. The samples were collected either with a scalpel in the form of a chip of about 5 mm long and 1 mm wide, or with a micro-mill generating a pit less than 1 mm in diameter and 1 mm deep (sample weight <200 µg). Samples were preferentially taken in damaged areas to preserve as much as possible the morphological and structural integrity of the fossil remains. A potential drawback of using bone instead of enamel is that a false diagnosis can be made especially when a fossil piece lacks diagnostic characters, and thus we took special care to sample only well-diagnosed material.

The analyses were carried out at the Laboratoire de Géologie de Lyon. The samples (68 new plus 30 from Dodat et al. 2021, SOM Table S1) were first grounded using an agate mortar

and pestle before being leached with diluted ultrapure acetic acid (0.1 M) for 30 min at room temperature in an ultrasonic bath to eliminate Ca-bearing secondary carbonates, particularly present as calcite (Lee-Thorp and van der Merwe, 1991; Sillen and LeGeros, 1991; Balter et al., 2002; Dodat et al., 2023). The residue was then digested in distilled HNO₃ (4.5 M) and about 10% of the solution saved for concentration measurements following Balter et Lécuyer (Balter and Lécuyer, 2004). Most of the samples were not weighed to avoid sample loss that would have been critical for such small samples. The concentration of major and trace elements was measured on leached bone samples, using ICP-MS (iCap-Q, Thermo Scientific, Bremen) and a inductively coupled plasma optical emission spectrometer (ICP-OES; iCap pro, Thermo Scientific, Bremen) for trace elements (Mn, Fe, U and rare earth elements [REE]) and major elements (Ca, P, Mg), respectively.

All samples were successfully processed to extract and purify Ca from bone matrix according to the protocol set up by Tacail et al. (2014). Briefly, the remaining 90% of the digestion solution was taken up in distilled and titrated HCl (1.0 M), followed by three chromatography steps: the first allows the recovery of Ca, Fe and Sr, the second isolates Sr, and the third separates Ca from Fe. The Ca isotope compositions were measured using a Neptune Plus MC-ICP-MS (Thermo Scientific, Bremen) using the standard-sample-standard bracketing method. All Ca isotope compositions are expressed using the delta notation, calculated as following:

$$\delta^{44/42}\text{Ca} = \left(\frac{(^{44}\text{Ca}/^{42}\text{Ca})_{\text{Sample}}}{0.5 \times (^{44}\text{Ca}/^{42}\text{Ca})_{\text{ICP-Ca-Lyon}}^{n-1} + 0.5 \times (^{44}\text{Ca}/^{42}\text{Ca})_{\text{ICP-Ca-Lyon}}^{n+1}} - 1 \right) \times 1000$$

The ICP Ca Lyon standard, used routinely in Lyon, was used as bracketing and reference material, but the results are also expressed relative to the SRM915a certified reference material. The certified reference material NIST SRM1400 (bone ash) was repeatedly purified and

measured as a sample to control the accuracy of the $\delta^{44/42}\text{Ca}$ values. During the study, six different aliquots ($n^* = 6$) of the SRM1400 certified reference material were measured which yield a value of $-1.05 \pm 0.07\text{‰}$, (2 SD, $n^* = 6$, $n = 35$), indistinguishable from all SRM1400 measurements reported in other studies ($-1.07 \pm 0.09\text{‰}$, 2 SD, $n^* = 1$, $n = 10$: Koutamanis et al., 2021; $-1.06 \pm 0.04\text{‰}$, 2 SD, $n^* = 1$, $n = 4$: Romaniello et al., 2015; $-1.02 \pm 0.07\text{‰}$, 2 SD, $n^* = 1$, $n = 4$: Lanping et al., 2018).

2.4. *MixSIAR modeling*

Calcium stable isotope compositions of Neanderthal individuals and potential food sources were analyzed with the Bayesian mixing model MixSIAR (Stock and Semmens, 2016; Stock et al., 2018), which estimates the relative contribution of food sources in the composition of diet, taking into account measurement uncertainty and variability. All statistical analyses were conducted with ‘MixSIAR’ v 3.1.12 (Stock and Semmens, 2016; Stock et al., 2018) in R v 4.0.5 (R Core Team, 2023). The SIAR Markov chain Monte Carlo algorithm was run with the predefined parameter 'extreme'. Three types of data are necessary to estimate the contribution of a potential source in the diet using a Bayesian mixing model: (1) the values and associated uncertainties of the consumers of interest (Neanderthal individuals); (2) the values and associated uncertainties of potential sources (summarized in Table 1) and, (3) the values and associated uncertainties of the trophic discrimination. Regarding potential animal dietary sources, we focused on the $\delta^{44/42}\text{Ca}$ values of the taxa present in the archaeological sites, which were aggregated into three distinct groups (SOM Table S1; Table 1), i.e., monogastric herbivores, including woolly rhinoceros, boar, horse, and mammoth, and two distinct ruminant herbivores groups according to the family taxonomic rank, cervid and bovid (summarized in Table 1). Regarding potential vegetal dietary sources, we have used current data obtained on European plants, in particular on the herb/grass types, or above ground biomass (AGB), and

plant leaf or stem samples collected at the vicinity of both archaeological sites. All the $\delta^{44/42}\text{Ca}$ values used to calculate the AGB average and standard deviation are given in SOM Table S2. We used a trophic discrimination value of $0.27 \pm 0.1\%$ for the Ca isotopic offset between bones of herbivores and carnivores (Martin et al., 2018) and a trophic discrimination value of $0.57 \pm 0.1\%$ for the Ca isotopic offset between plants and bones (Tacail et al., 2020).

3. Results

All results are given in SOM Table S1 and are reported in the text with two standard deviations (± 2 SD) unless otherwise specified. As mentioned above, the measurement of Ca isotope compositions in bone necessitates only the smallest of samples. After leaching, the remaining bone residue was often so small that it was impossible to weigh it (cf. Section 2). The concentrations of major and trace elements are thus Ca-normalized.

3.1. Calcium diagenesis

The diagenesis of Ca was evaluated by testing for a correlation between the Ca/P (which could track potential excess Ca) and the $\delta^{44/42}\text{Ca}$ values on the one hand, and diagenetic proxies (Fe/Ca, Mg/Ca, Mn/Ca, U/Ca and $\sum\text{REE}/\text{Ca}$) on the other. At Grotte du Bison, the $\delta^{44/42}\text{Ca}$ values are negatively correlated with the $\sum\text{REE}/\text{Ca}$ ratio, albeit not significantly after a Benjamini-Hochberg (BH) correction for multiple comparisons (Pearson BH-adjusted p -value = 0.087; SOM Fig. S1). At Regourdou, the Ca/P values are significantly correlated (Pearson BH-adjusted p -value = 0.017), with the $\sum\text{REE}/\text{Ca}$ ratio (SOM Fig. S1). Examination of the individual relationships reveals that these correlations are induced by single values: a wolf specimen (B42; SOM Table S1; SOM Fig. S2) at Grotte du Bison, and a lion specimen (R43; SOM Table S1; SOM Fig. S3) at Regourdou. The negative association between the $\delta^{44/42}\text{Ca}$ value and the $\sum\text{REE}/\text{Ca}$ ratio of the B42 specimen does not suggest diagenetic overprint

because altered bone $\delta^{44/42}\text{Ca}$ values tend to be more positive, not negative (Martin et al., 2017; Dodat et al., 2023). The Ca/P ratio of the R43 specimen (2.72; SOM Table S1) is at the upper limit of the 1.9 to 2.7 range, indicative of the stoichiometry of hydroxylapatite (Tzaphlidou and Zaichick, 2003, 2004). The $\delta^{44/42}\text{Ca}$ value of the R43 specimen is also negative (-1.13‰; SOM Table S1). Taken together, these results suggest that bone Ca/P and $\delta^{44/42}\text{Ca}$ values are not affected by significant diagenesis at either Grotte du Bison or Regourdou.

It is important to note that the Arcy 2015 BIS J T14 12 *Canis lupus* sample has an unexpectedly high $\delta^{44/42}\text{Ca}$ value ($-0.50 \pm 0.10\text{‰}$) and shows clear signs of partial digestion (SOM Fig. S4; SOM S1). This can be explained by the partial digestion of the bone which would have preferentially removed light Ca isotopes by kinetic fractionation. This sample will therefore not be further considered.

3.2. Calcium isotope compositions

The observed linear correlation between the $\delta^{44/42}\text{Ca}$ and $\delta^{43/42}\text{Ca}$ values (SOM Fig. S5) agrees with the expected mass-dependent fractionation slope of ~ 0.5 (Tacail et al., 2014). Measurements that deviate from this line would indicate unresolved interference in the isotope ratio measurements, which is not the case here. All $\delta^{44/42}\text{Ca}$ values are given in SOM Table S1 and shown in Figure 2.

A first observation is that there is intra-specific $\delta^{44/42}\text{Ca}$ variability that can be significant for some ruminant taxa, notably cervids. A second observation is that cervids have generally low $\delta^{44/42}\text{Ca}$ values, comparable to carnivores. We note that there is a species-specific distribution of the Ca isotope value at both sites, with monogastric herbivores having the highest $\delta^{44/42}\text{Ca}$ values, ruminant herbivores and omnivores showing intermediate $\delta^{44/42}\text{Ca}$ values and, carnivores having the lowest $\delta^{44/42}\text{Ca}$ values (Fig. 2). The statistical results of pairwise comparisons, which support these observations, are given in Figure 2. The observed Ca isotope

systematic variability in the faunal assemblage is similar to that reported at Sclayn (Belgium) and Jaurens (France) and in South China (Martin et al., 2017; Hu et al., 2022). The absence of differences between herbivores and carnivores at Regourdou is due to the very low $\delta^{44/42}\text{Ca}$ values of red deer ($-1.34 \pm 0.18\text{‰}$, $n = 6$). A final observation is that the average $\delta^{44/42}\text{Ca}$ values at Grotte du Bison ($-0.72 \pm 0.37\text{‰}$, $n = 46$) are significantly higher (Wilcoxon p -value = 10^{-10}) than at Regourdou ($-1.09 \pm 0.52\text{‰}$, $n = 48$). The $\delta^{44/42}\text{Ca}$ offset between the two sites is close to 0.4‰ and affects all taxa present at both sites (0.64‰ for red deer, 0.37‰ for reindeer, 0.34‰ for horse, 0.25‰ for wolf and 0.12‰ for bovid; SOM Table S1).

Cortical and trabecular bone samples were collected on Regourdou 1 and Regourdou 2 Neanderthals (SOM Table S1). For both individuals, trabecular bone samples have a $\delta^{44/42}\text{Ca}$ value (Regourdou 1: $-1.56 \pm 0.02\text{‰}$; Regourdou 2: $-0.78 \pm 0.07\text{‰}$) that is undistinguishable from that of cortical bone (Regourdou 1: $-1.51 \pm 0.10\text{‰}$; Regourdou 2: $-0.80 \pm 0.07\text{‰}$). For this study a brown bear bone was collected from two areas of the same cortical bone, these are samples R35 and R33) these samples show no significant difference in their isotopic composition.

4. Discussion

4.1. General comments

The $\delta^{44/42}\text{Ca}$ offset observed between the two sites could be due to Ca isotope variability at the bottom of the food web (water and/or soil). A range of 0.74‰ is measured in a global compilation of 52 water samples around the world (Tipper et al., 2010), which is compatible with the $\delta^{44/42}\text{Ca}$ offset observed between Grotte du Bison and Regourdou. Several studies (e.g., Page et al., 2008; Cenko-Tok et al., 2009; Tipper et al., 2010) suggest that the Ca isotope fractionation between plant organs is similar whatever the species. However, these studies also suggest that the Ca isotope fractionation between soil and plant organs is more specific and

likely linked to the type of plant or the local soil environment (Hindshaw et al., 2013). This suggests that the local geology and vegetation types may have an impact on the initial Ca isotope composition of a trophic chain. To unravel the respective influence of local geology and vegetation types, we analyzed vegetal (grasses, garlic mustard, common nettle and dandelion, cleavers, hazel, and oak; SOM Table S1) collected in the vicinity of the Grotte du Bison and Regourdou archaeological sites. The results reveal similar $\delta^{44/42}\text{Ca}$ values at both sites, i.e., $-0.67 \pm 0.21\text{‰}$ ($n = 10$) and $-0.60 \pm 0.19\text{‰}$ ($n = 7$) at Grotte du Bison and Regourdou, respectively (Fig. 2; SOM Table S1), and therefore do not explain the observed bone $\delta^{44/42}\text{Ca}$ offset between the two sites. A potential explanation is that these living plants are likely not representative of those that grew locally, or were consumed, tens of thousands of years ago (Fig. 1). The plant communities must have been different because Grotte du Bison is dated to the MIS 3 glacial environment while Regourdou is dated to the MIS 5 interglacial environment (Fig. 1). Temperature and aridity have been known to influence Ca isotope cycling at the water-rock-vegetation interface (Page et al., 2008; Cenki-Tok et al., 2009; Holmden and Bélanger, 2010; Hindshaw et al., 2013). Furthermore, it is well established that environmental changes and food supplies vary between two climatic periods e.g. MIS 3 and MIS 5 in our study (Fig. 1). Micro- and macro-wear analysis for taxa, such as cervids and large bovids demonstrates the variability of dietary traits of herbivores that could be conditioned by the environment and food resources (Amano et al., 2016), this variability could have repercussions on calcium isotope composition.

4.2. *Species-specific comments*

The low $\delta^{44/42}\text{Ca}$ values and associated important variability of cervids have also been observed by other authors in enamel (Martin et al., 2017; Hu et al., 2022). It is tempting to explain the cervid low $\delta^{44/42}\text{Ca}$ values by the formation of ^{44}Ca -enriched antlers (Hassler et al.,

2021). A pilot investigation (Hassler et al., 2021) highlighted that one antler of a modern red deer displays $\delta^{44/42}\text{Ca}$ values higher than the rest of the skeleton (c.a. $\leq 0.2\text{‰}$), but this represents a too small fractionation to account for the very low $\delta^{44/42}\text{Ca}$ values of cervids relative to other mammals. Further studies are necessary to clarify the influence of antlerogenesis on cervid bone and enamel low $\delta^{44/42}\text{Ca}$ values. An obvious source of Ca isotope variability for herbivores is that of the local vegetal sources. Here, we show that plant stems have lower $\delta^{44/42}\text{Ca}$ values than leaves (Fig. 2), a pattern previously observed by multiple authors and compiled by Tacail et al., 2020. Because stems and roots have similar $\delta^{44/42}\text{Ca}$ values (Tacail et al., 2019, 2020), the intra-organ Ca isotope difference between leaves and roots, the edible parts of a plant, is an additional source of Ca isotope variability among herbivores. As, the accepted mechanism to explain the decrease of the $\delta^{44/42}\text{Ca}$ values up trophic chain is bone consumption (Skulan and DePaolo, 1999; Reynard et al., 2010; Heuser et al., 2011; Clementz, 2012; Martin et al., 2015, 2017, 2018; Hassler et al., 2018), the assimilation of Ca through a non-nutritive source, such as bone or antler chewing, is likely to mimic bone consumption even for cervid species (Kierdorf, 1994; Caceres et al., 2011). The use of the MixSIAR model on red deer allow us to support the hypothesis of osteophagia to explain the low values of red deer at Regourdou (SOM Fig. S6).

Hyenas, and to a lesser degree canid, are recognized to be regular bone crushers and are known to usually exhibit extremely negative $\delta^{44/42}\text{Ca}$ values (Heuser et al., 2011; Martin et al., 2018; Hassler et al., 2021) this is the case for the hyenas at Grotte du Bison. The absence of hyenas at Regourdou unfortunately prevents us from assessing where the bone crusher carnivore stands on the isotopic scale. The range of variation of $\delta^{44/42}\text{Ca}$ values is important for carnivores, e.g., c.a. 0.7‰ for wolf at Regourdou or c.a. 0.8‰ for lion at Grotte du Bison (Fig. 2). This observation has also been made in other studies on enamel (Martin et al., 2015; Hu et al., 2022) thus, the variability seen here should be attributed to the increased probability

of integrating an unusual Ca isotope signal due to the variability of possible preys and the proportion of ingested bone.

The difference between cave bear from Grotte du Bison and brown bear from Regourdou is 0.42‰. This difference is compatible with the general offset between the two sites and is not indicative of different dietary patterns, as suggested by nitrogen isotopes (Tacail et al., 2017).

4.3. *Estimation of diet composition for the Grotte du Bison Neanderthal*

The Grotte du Bison Neanderthal displays a $\delta^{44/42}\text{Ca}$ value of $0.75 \pm 0.07\text{‰}$, lying in the middle of the local isotopic variation (Fig. 2). Importantly, zooarchaeological data show that among the three most common herbivore taxa (reindeer, horse and bovid), at least two (reindeer and horse) show traces of soft part acquisition by Neanderthals. In the MixSIAR modelling (cf. Section 2 Materials and methods) we focus on the mean of the identified dietary end-members, i.e., bone of bovid and cervid (ruminant herbivores), bone of monogastric herbivores and European plants or AGB, with the latter indistinguishable from meat. Results for the Grotte du Bison Neanderthal suggest that the contribution of each potential food source was broadly similar (Fig. 3A), ranging from 20% of bovid bone to 30% of AGB or meat. This result is consistent with a Neanderthal individual who was not far from the top of the trophic chain, and also reflects the metabolic constraint that its diet cannot solely come from animal sources.

4.4. *Estimation of diet composition for Regourdou 1 Neanderthal*

The Regourdou 1 samples display an average $\delta^{44/42}\text{Ca}$ value of $-1.58 \pm 0.16\text{‰}$ (n=3), placing this Neanderthal individual at the lower end of local isotopic variability, among carnivores and out of the range of herbivores (Fig. 2). The results of the MixSIAR modelling

for Regourdou 1 Neanderthal suggest a preponderance of cervid bone consumption in the diet (51%; Fig. 3B). Bovid bone shows a modest contribution (29%), while monogastric bone and AGB (or meat) show a low contribution, 11% and 10%, respectively (Fig. 3B). The MixSIAR results, along with the observed consistency of the $\delta^{44/42}\text{Ca}$ values between cortical and trabecular bone, suggest a specialization in the frequent consumption of cervids and bovids. The diet of Regourdou 1 Neanderthal is in agreement with the traditional view drawn from nitrogen isotopic data (Balter et al., 2002; Henry et al., 2011; Wißing et al., 2016) or more recent compound specific analysis of nitrogen stable isotopes in individual amino acids (Naito et al. 2016, Jaouen et al. 2019).

4.5. *Estimation of diet composition for Regourdou 2 Neanderthal*

Regourdou 2 samples display an average $\delta^{44/42}\text{Ca}$ value of $0.79 \pm 0.04\text{‰}$ ($n=2$), placing this Neanderthal individual at the upper end of the local variability, among herbivores and out of the carnivore range (Fig. 2). The results of the MixSIAR modelling for Regourdou 2 Neanderthal suggest that the consumption of AGB (or meat) and bovid bone is predominantly providing, respectively, 38% and 35% of the diet (Fig. 3C). Bone of monogastric animals shows a medium contribution (19%), while cervid bone provides a low contribution (9%). This result is unexpected considering the previous studies on Neanderthal diet based on nitrogen isotopic data (Balter and Simon, 2006; Richards and Trinkaus, 2009; Naito et al., 2016; Wißing et al., 2016) or other isotope systems chemical proxies (e.g. Sr/Ca; Balter et al. 2001; $\delta^{66/64}\text{Zn}$; Jaouen et al. 2023), even if the AGB contribution is overestimated and instead reflects meat consumption. It suggests that animal resources contribute less to Regourdou 2 diet than plant resources, with a less extensive utilization of carcasses bone marrow exploitation. This result is even more surprising when one considers that Regourdou 1 and Regourdou 2 individuals are supposed to be attributed to the same sedimentary layer 4 (Madelaine et al., 2008), as this would

suggest that they may have been pene-contemporaries. Even if we cannot ascertain that they were contemporaries, they most probably evolved in similar environments (Fig. 1B and 1C).

4.6. *Dietary diversity among Neanderthals*

This study presents Ca isotope compositions for three Neanderthal individuals, showing they were probably occupying distinct trophic positions relative to the local fauna, thus suggesting different dietary strategies. This finding reconciles metabolic constraints (e.g., Cordain et al., 2000; Fiorenza et al., 2015), ethnographic studies (e.g., Speth and Spielmann, 1983; Speth, 2010), archaeological evidence (e.g., Henry et al., 2011) and geochemical results based on nitrogen isotopes (e.g., Balter and Simon, 2006; Richards and Trinkaus, 2009; Naito et al., 2016; Wißing et al., 2016) or other isotopes or geochemical proxies (e.g. Sr/Ca; Balter et al. 2001; $\delta^{66/64}\text{Zn}$; Jaouen et al. 2023). A Bayesian mixing model used to uncover probable vs improbable diet composition shows that we should consider bone and AGB (or meat) as potential dietary sources to match Neanderthal bone $\delta^{44/42}\text{Ca}$ values, at least for Grotte du Bison and Regourdou 2 individuals. Despite the similarity of the AGB and meat $\delta^{44/42}\text{Ca}$ values, the present study is the first to consider a vegetal component for paleodietary reconstructions based on Ca stable isotopes. Using an AGB $\delta^{44/42}\text{Ca}$ mean value of $-0.49 \pm 0.26\text{‰}$, it is possible to estimate a dietary plant fraction of ~10%, ~30%, and ~40% for Regourdou 1, Grotte du Bison, and Regourdou 2 individuals, respectively. Using a local living leaf $\delta^{44/42}\text{Ca}$ mean value of $-0.53 \pm 0.09\text{‰}$ and $-0.49 \pm 0.02\text{‰}$ for Grotte du Bison and Regourdou, respectively, does not change the overall picture, because these $\delta^{44/42}\text{Ca}$ values are similar to that of AGB (Fig. 2). However, when local present stem $\delta^{44/42}\text{Ca}$ values ($-0.89 \pm 0.13\text{‰}$ and $-0.79 \pm 0.08\text{‰}$ for Grotte du Bison and Regourdou, respectively; Fig. 2) are used as a proxy for root (Tacail et al., 2019, 2020), the dietary reconstruction is different for the three Neanderthal individuals (Fig. 4). The plant proportion increases to 20% for Regourdou 1

Neanderthal, while it decreases for the two other individuals, i.e., 8% and 13% for the Grotte du Bison and Regourdou 2 Neanderthals, respectively. These results show that whatever the plant $\delta^{44/42}\text{Ca}$ value (or that of meat), it is not possible to obtain matching proportions of dietary sources for the three studied Neanderthal individuals. Therefore, we conclude these three individuals had diverse dietary strategies.

Although bone balance is a complex process, trabecular bone is known to have a faster turnover rate than cortical bone (18%/year and 8%/year, respectively; Parfitt, 2002). The absence of a difference between trabecular and cortical bone for Regourdou 1 and Regourdou 2 suggests that the average diet, as measured in the $\delta^{44/42}\text{Ca}$ value, during the shortest bone lifetime ($0.18^{-1} = 5.5$ year for trabecular bone) is the same as during the longest bone lifetime ($0.08^{-1} = 12.5$ year for cortical bone). In other words, the similar trabecular and cortical bone $\delta^{44/42}\text{Ca}$ values for these two Neanderthals are indicative of a relatively stable diet with a duration of several years. Given that variability in bone turnover rate may be high, especially between the axial and appendicular skeleton (Parfitt, 2002), this conclusion remains preliminary. Nevertheless, the possibility to track dietary changes using small pieces of bone with contrasting turnover rates is now a distinct possibility given the low sample amounts needed for Ca isotope measurements.

Metabolic arguments mandate that Neanderthals could not have had a diet of 100% meat; their diet must have included fat. Animal fat is a highly sought-after resource for hunter-gatherer populations (Speth and Spielmann, 1983; Cordain et al., 2000; Speth, 2010; Morin, 2020a). In ungulates, fat is found as body fat directly beneath the skin or around organs, or as skeletal fat (Morin, 2020b). In winter, hunter-gatherers may have a special interest in skeletal fat because it is kept in reserve even when animals are in poor physical conditions (Morin, 2020a, 2020b). Skeletal fat is found in yellow marrow stored in the medullary cavity of long bones, and as bone grease in the spongy bone. However, the consumption of meat or yellow

marrow is insufficient to induce a negative isotopic shift of the dietary $\delta^{44/42}\text{Ca}$ value; this comes only with the presence of bone in the diet (Heuser et al., 2011; Martin et al., 2017; Dodat et al., 2021). How might this have happened? It could be the case that trabecular bone is present in the medullary cavity of long bones along with yellow marrow. The collection/recovery of yellow marrow does not require sophisticated techniques to break open long bones. Archaeologically, yellow marrow consumption is well-documented since at least the emergence of the genus *Homo* and persists through Mesolithic (Sahnouni et al., 2013). In this case, the ingestion of small amounts of bone would have been accidental but likely inevitable. In contrast, the consumption of bone grease requires more processing. Specifically, the epiphyses tend to be comminuted, with the resulting powder boiled to extract grease (Morin, 2020a, 2020b). The consumption of bone grease, as grease loaves or soup, could also result in the ingestion of a significant quantity of bone. In this case, the consumption of a bone-based food would have been voluntary. This is a provocative interpretation because boiling as a technique is thought by some to have only originated in the Upper Paleolithic (Speth, 2015; Morin and Soulier, 2017).

The current work suggests the existence of diverse diets among Neanderthals whatever their proportions of plant foods and/or fat. This is one of the first potential demonstration of substantial diversity in individual dietary behaviors among Neanderthals using stable isotopes, two of them from the same site. Our results concur with those on dental calculus (Henry et al. 2011; Weyrich et al. 2017; Hardy et al. 2022) suggesting that there is a greater heterogeneity in feeding strategies within or between Neanderthal groups than previously thought, particularly regarding the variability of plants source in the diet. Whether the differences between these dietary strategies were sociocultural, symbolic, seasonal, or personal in nature (or due to some unknown reason) remains an open question. These observations support the hypothesis that Neanderthals dietary strategies are substantially influenced by their surroundings and indicate

a great degree of ecological plasticity (Fiorenza et al. 2020; Rivals et al., 2022). The use of new isotopic methods enables us to broaden our investigation into the Neanderthal diet, which must be extended beyond isotopic stage 4.

Declaration of interests

The authors declare no competing interests.

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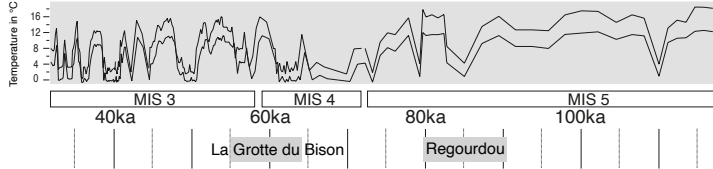
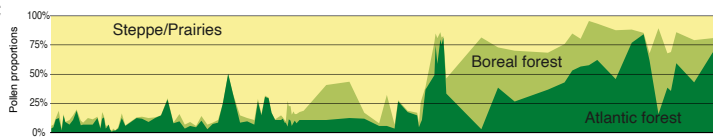
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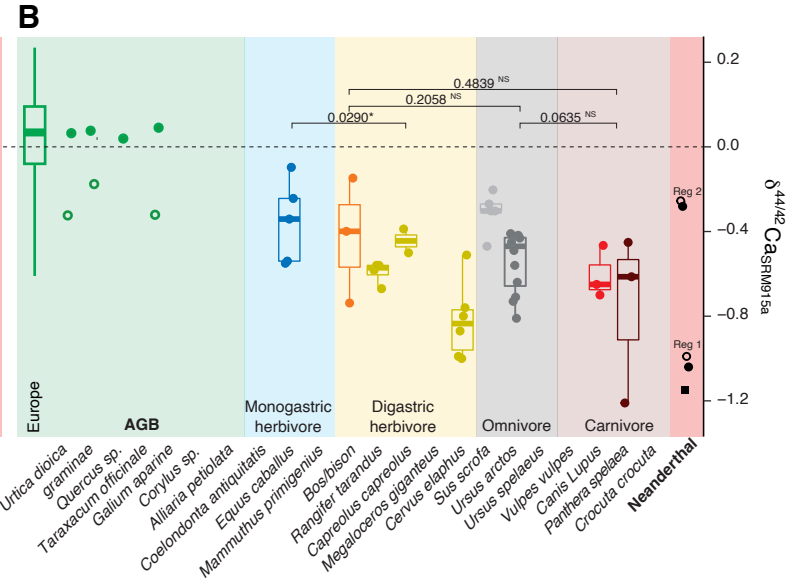
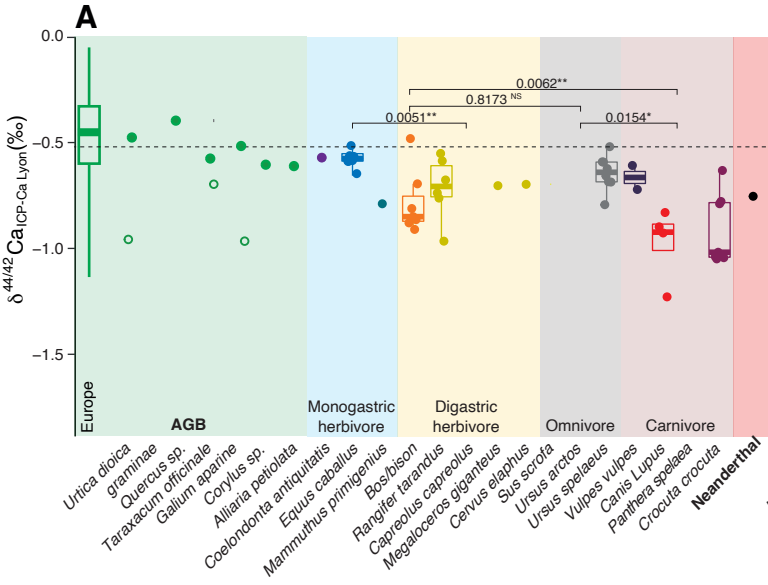
Figure 1. Correspondence between the different sites studied and palaeo-climatic and paleoenvironmental records of core MD04-2845 (Gascogne Bay) for the period 140–35 ka (Goñi et al., 2008; Discamps, 2011). A) Localization of the different sites; B) surface water temperature in summer and winter (in °C) and absolute chronology with the different sites studied. C) pollen proportions according to biotope type (expressed in %)

Figure 2. Box plot of species-specific distribution of $\delta^{44/42}\text{Ca}$ values at the Grotte du Bison and Regourdou. The dotted line gives the correspondence between $\delta^{44/42}\text{Ca}$ values relative to ICP-Ca Lyon and standard SRM915a. Open and filled symbols for vegetal samples stand for stem and leaf, respectively. Open and filled symbols for bone sample stand for spongy and cortical bone, respectively. For Regourdou 1 circle correspond to femur and square correspond to humerus sample. *P*-values of Wilcoxon tests are indicated with ‘NS’ if non-significant, with a single asterisk if $p < 0.05$, with a double asterisk if $p < 0.01$, and with a triple asterisk if $p < 0.001$. Abbreviation: AGB = aboveground biomass.

Figure 3. Violin plots representing diet proportion estimates for the three Neanderthal individuals: Grotte du Bison (A), Regourdou 1 (B) and Regourdou 2 (C) using $\delta^{44/42}\text{Ca}$ values of fossil bone and aboveground biomass (AGB) average from actual European plants or local leaf $\delta^{44/42}\text{Ca}$ values. Dots indicate the probable mean value.

Figure 4 Violin plots representing diet proportion estimates for the three Neanderthal individuals: Grotte du Bison (A), Regourdou 1 (B) and Regourdou 2 (C) using $\delta^{44/42}\text{Ca}$ values of fossil bone and local stem (as a proxy for root) $\delta^{44/42}\text{Ca}$ values. Dots indicate the probable mean value.

A**B****C**



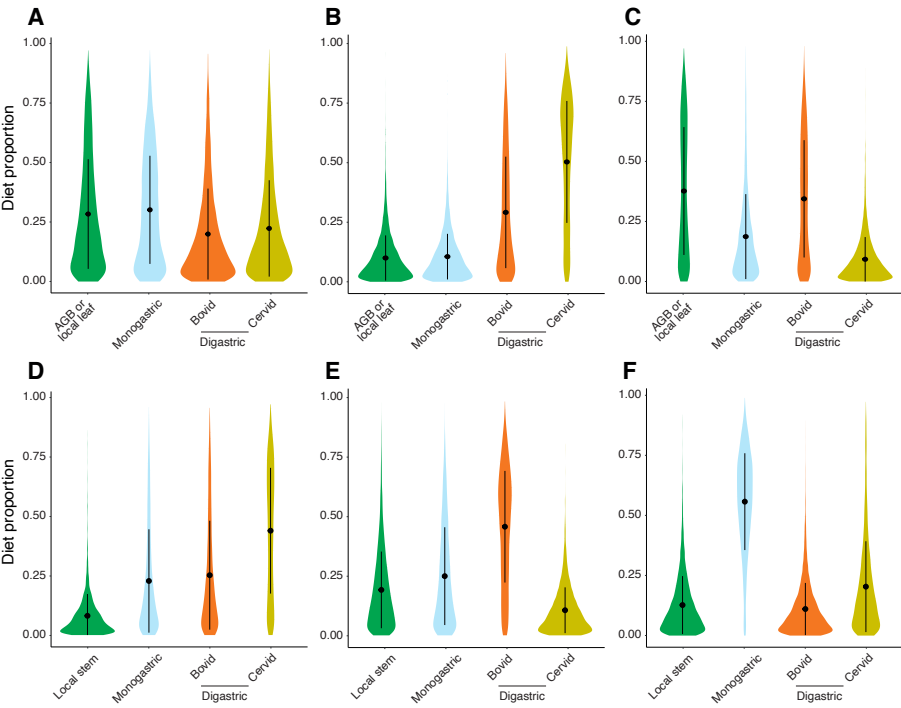


Table 1

Mean isotopic data and standard deviation used for the Bayesian mixing models for stable isotope analyses in R model grouped by sources and site share. The above ground biomass (AGB) value is the same for both sites.

Source	Site	Mean $\delta^{44/42}\text{Ca}$	SD $\delta^{44/42}\text{Ca}$	<i>n</i>
Bovid	Regourdou	-0.95	0.30	3
Cervid	Regourdou	-1.20	0.20	12
Monogastric	Regourdou	-0.87	0.19	5
AGB	Regourdou/Grotte du Bison	-0.49	0.26	44
Bovid	Grotte du Bison	-0.78	0.15	7
Cervid	Grotte du Bison	-0.71	0.13	8
Monogastric	Grotte du Bison	-0.60	0.08	8

Supplementary Online Material (SOM):

Diverse bone calcium isotope compositions in Neandertals indicates different dietary strategies

Pierre-Jean Dodat^{a,b,*}, Emmanuelle Albalat^a, Vincent Balter^a, Christine Couture-Veschambre^b, Maurice Hardy^c, Juliette Henrion^b, Trenton Holliday^{d,e}, Bruno Maureille^b

^a *Laboratoire de Géologie de Lyon : Terre, Planètes, Environnements. UMR 5276, CNRS, Ecole Normale supérieure de Lyon. 46 Allée d'Italie, 69342 Lyon Cedex 07, France*

^b *Univ. Bordeaux, CNRS, Ministry of Culture, PACEA UMR 5199, F-33600 Pessac France*

^c *CNRS, UMR 7041, Univ. Nanterre, Ministère de la Culture, ArScAn, 92000 Nanterre, France*

^d *Tulane University; Department of Anthropology, 101 Dinwiddie Hall, New Orleans, Louisiana 70118, USA*

^e *University of the Witwatersrand; Centre for the Exploration of the Deep Human Journey, Private Bag 3, Wits 2050, Republic of South Africa*

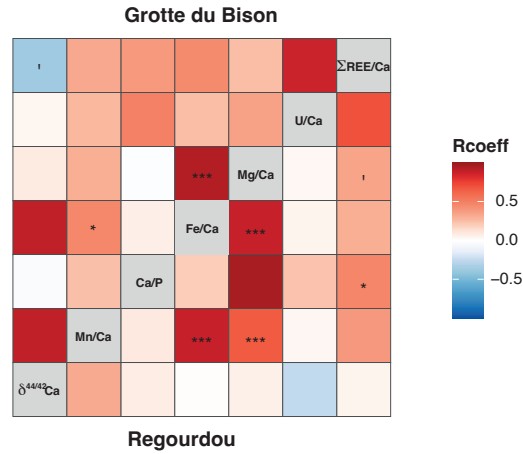
*** Corresponding author.**

E-mail address: pjdodat@naturalsciences.be (P.-J. Dodat).

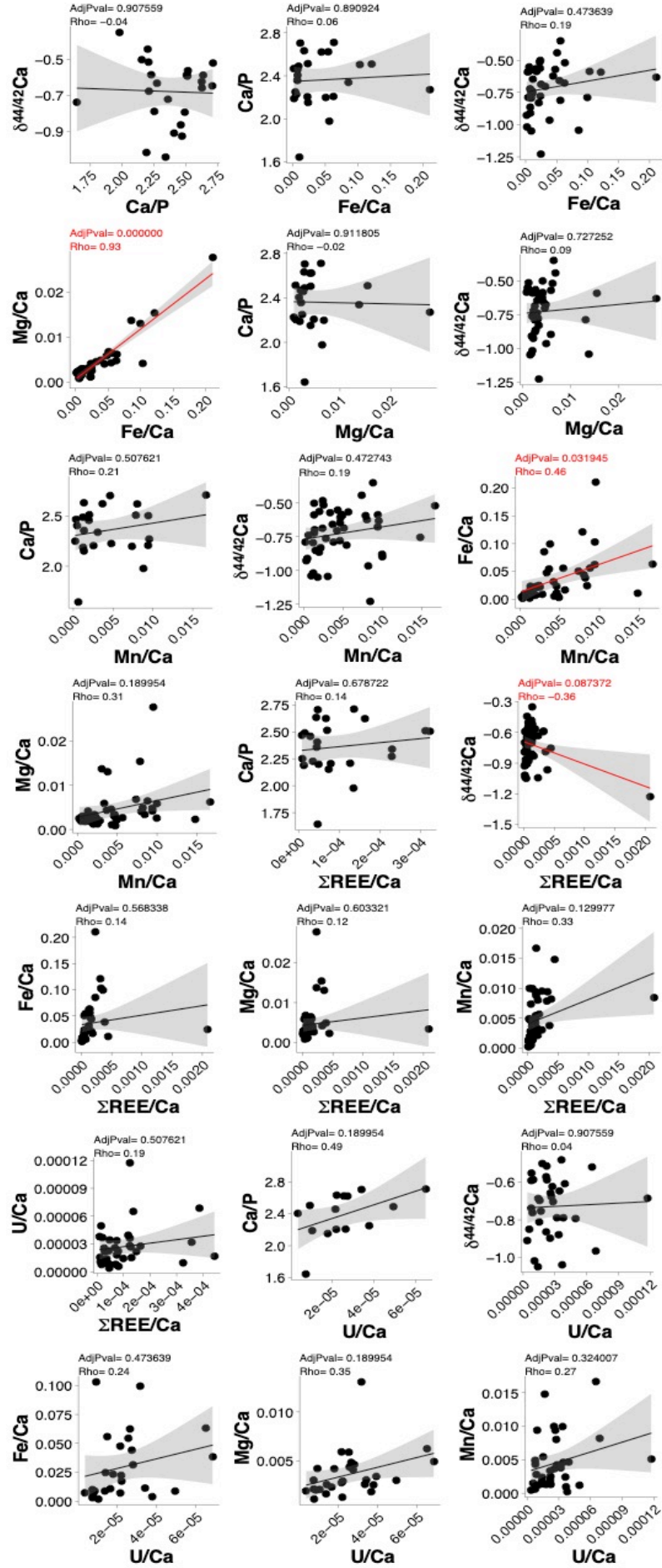
SOM S1

Commentary on the digested bone from Grotte du Bison

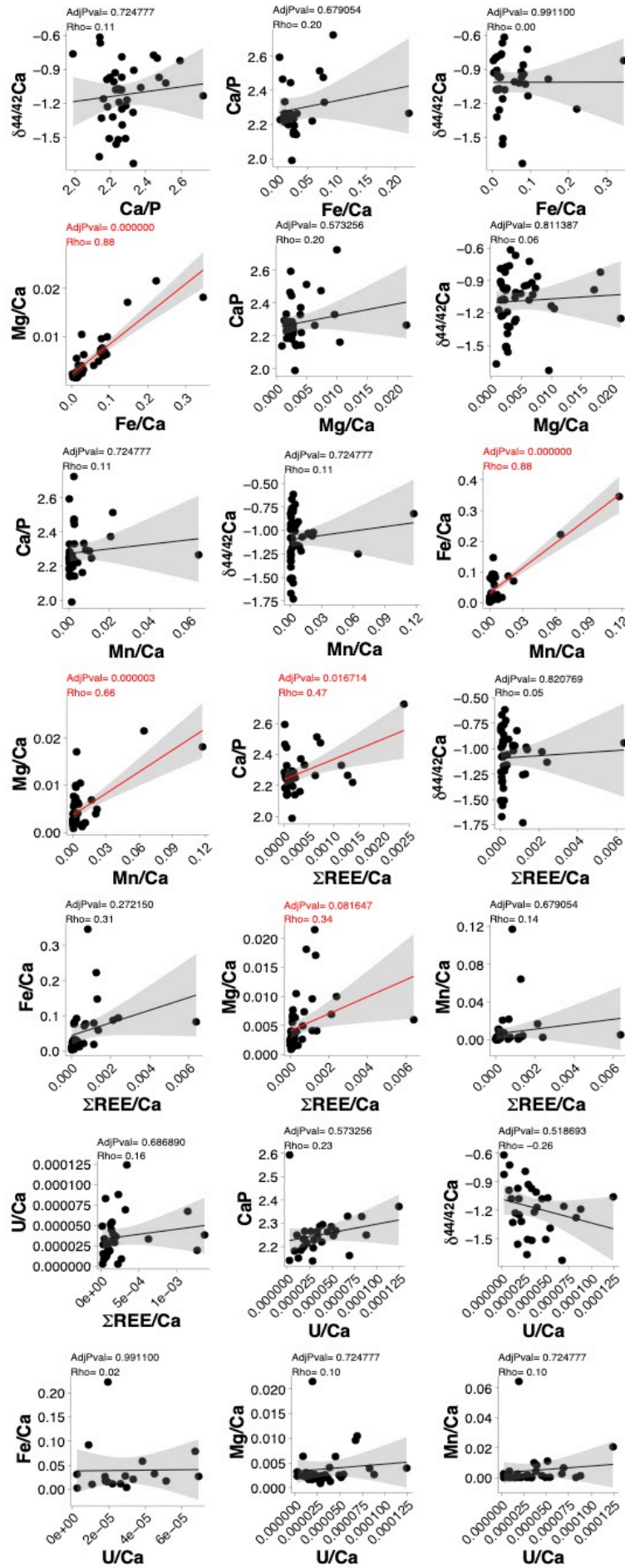
Several traces of digestion could be identified on the bone Arcy 2015 Bis J T14-12. The abnormal thinning of the cortical bone and a reduction of the bone edges are two elements allowing the identification of modification to this fossil piece due to the digestion of the bone by a carnivore. The Grotte du Bison site has a large amount of hyena remains and a carnivore/ungulate ratio suggesting that part of the accumulation of remains is due to hyena action. The consumption of bone by hyenas is a widely documented phenomenon, so we can rightly assume that the wolf sample presented above was ingested by a hyena during its occupation of the cave. Numerous other digested bones have been identified in the Grotte du Bison collection that were not collected for this study.



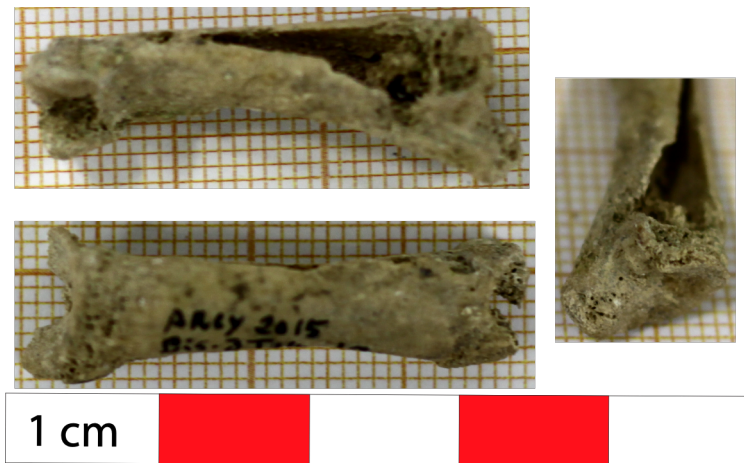
SOM Figure S1. Heatmap of the correlation coefficients (Rcoeff) between Ca-normalized elemental ratios and Ca isotopic compositions. Significant p -values after a Benjamini-Hochberg adjustment for multiple comparisons are indicated with a quotation mark if $p = 0.05$ – 0.1 , with a single asterisk if $p = 0.01$ – 0.05 , with a double asterisk if $p = 0.001$ – 0.01 , and with a triple asterisk if $p < 0.001$. The correlation matrix for Grotte du Bison is displayed on the top left part of the figure and the correlation matrix for Regourdou is displayed on the lower right part of the figure. Abbreviation: REE = rare earth elements.



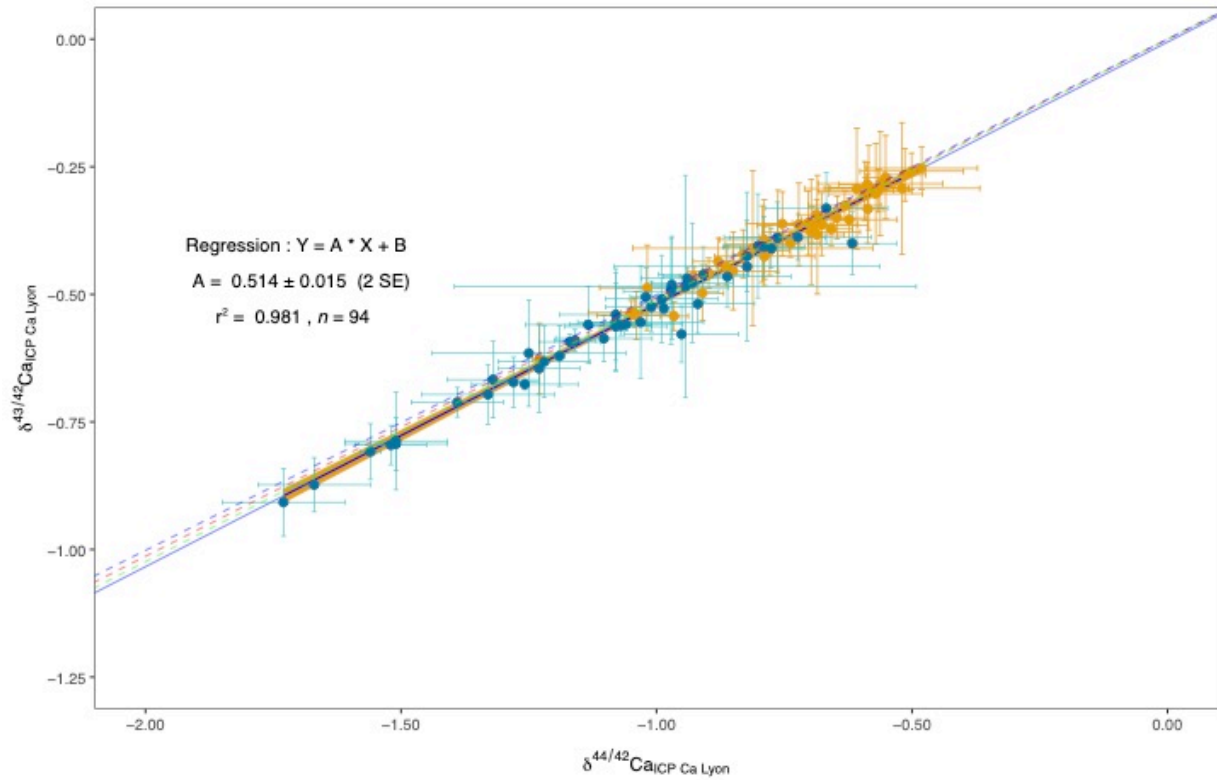
SOM Figure S2. Individual correlations between Ca-normalized elemental ratios and Ca isotopic compositions at Grotte du Bison. Significant adjusted p -values after a Benjamini-Hochberg correction (AdjPval) for multiple comparisons are indicated in the left corner. Correlations with significant adjusted p -values are highlighted in red.



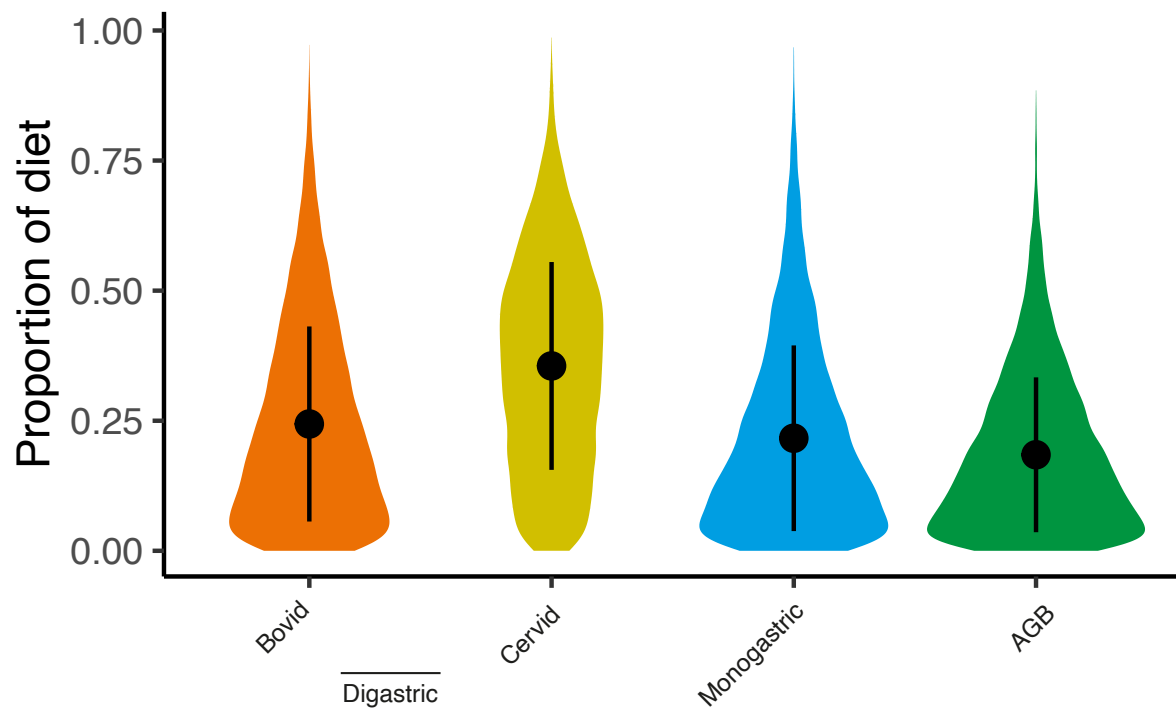
SOM Figure S3. Individual correlations between Ca-normalized elemental ratios and Ca isotopic compositions at Regourdou. Significant adjusted p -values after a Benjamini-Hochberg correction (AdjPval) for multiple comparisons are indicated in the left corner. Correlations with significant adjusted p -values are highlighted in red.



SOM Figure S4. Arcy 2015 BIS J T14 12 wolf bone, before sampling for Ca isotopes analysis



SOM Figure S5. Mass fractionation in three-isotope space of the samples analyzed in this study relative to the inductively coupled plasma measure of Ca in Lyon reference standard (ICP Ca Lyon). The blue line shows the linear regression of $\delta^{44/42}\text{Ca}$ as a function of $\delta^{43/42}\text{Ca}$ values (slope = 0.514 ± 0.015 ; 2SE; $r^2 = 0.981$; $n = 94$). The blue and yellow points are for Regourdou and the Grotte du Bison samples, respectively. The dotted lines represent the three theoretical lines describing a mass-dependent isotopic fractionation depending on the considered mass-dependent fractionation exponential (red), inverse (green) and power (blue) laws, respectively.



SOM Figure S6. Violin plots representing diet proportion estimates for the red deer of Regourdou using $\delta^{44/42}\text{Ca}$ values of fossil bone and AGB average from actual European plants or local leaf $\delta^{44/42}\text{Ca}$ values. Dots indicate the probable mean value.

SOM Table S1

Calcium isotope composition and element concentration in fossil bone and actual plant samples.

Site	Material	Field ID	Layers	MixSIAR	Common name	Latin name	Type	Age at death	Lab ID	n	$\delta^{44/42}\text{Ca}$ vs. ICP-Ca Lyon (‰)	± 2 SD (‰)	P (μg)	Mg (μg)	Ca (μg)	Fe (μg)	Mn (μg)	U (μg)	REE (μg)
Grotte du Bison	bone	Arcy 2016 BIS Jbis R6 24	BisJ	Monogastric	Woolly rhinoceros	<i>Coelodonta antiquitatis</i>	radius	Mature	B29	4	-0.57	0.09	—	0.24	41.1	1.96	0.138	0.0009	0.006
Grotte du Bison	bone	Arcy 2012 BIS J O10 29	BisJ	Monogastric	Horse	<i>Equus caballus</i>	metatarsal	Mature	B31	4	-0.59	0.06	38.8	0.30	102.2	1.79	0.135	0.0023	0.004
Grotte du Bison	bone	Arcy 2015 BIS J S6 83	BisJ	Monogastric	Horse	<i>Equus caballus</i>	mandible	Mature	B32	5	-0.56	0.12	30.4	0.09	76.3	1.77	0.153	—	0.005
Grotte du Bison	bone	Arcy 2014 BIS J S10 52	BisJ	Monogastric	Horse	<i>Equus caballus</i>	femur	Mature	B33	3	-0.51	0.04	227.5	0.63	501.7	11.28	1.264	0.0111	0.040
Grotte du Bison	bone	Arcy 2015 BIS J P8 48	BisJ	Monogastric	Horse	<i>Equus caballus</i>	phalanx	Mature	B37	5	-0.58	0.08	125.5	0.24	279.4	1.56	1.331	—	0.010
Grotte du Bison	bone	Arcy 2014 BIS J S10 12	BisJ	Monogastric	Horse	<i>Equus caballus</i>	humerus	Mature	B44	4	-0.57	0.03	—	0.07	25.3	0.43	0.143	—	0.005
Grotte du Bison	bone	Arcy 2014 BIS J S10 37	BisJ	Monogastric	Horse	<i>Equus caballus</i>	humerus	immature	B55	4	-0.65	0.06	41.4	0.34	111.9	1.29	0.517	0.0038	0.005
Grotte du Bison	bone	Arcy BIS ?? T17 47	BisJ	Monogastric	Mammoth	<i>Mammuthus primigenius</i>		Mature	B36	5	-0.79	0.09	171.4	0.97	385.6	1.58	0.086	0.0146	0.004
Grotte du Bison	bone	Arcy 1963 BIS J1 T15 2822	BisJ	Bovid	Bovid	<i>Bos/bison</i>	femur	Mature	B12	3	-0.88	0.05	—	0.12	46.5	—	0.463	0.0016	0.003
Grotte du Bison	bone	Arcy 2012 BISJ O11 15	BisJ	Bovid	Bovid	<i>Bos/bison</i>	metacarpal	Mature	B16	2	-0.48	0.11	—	—	5.7	—	0.014	0.0002	0.001
Grotte du Bison	bone	Arcy 2016 BIS J S6 11	BisJ	Bovid	Bovid	<i>Bos/bison</i>	metacarpal	Mature	B17	3	-0.81	0.23	—	—	27.0	1.51	0.147	0.0004	0.004
Grotte du Bison	bone	Arcy 2012 BIS J R8 2/Q8 2	BisJ	Bovid	Bovid	<i>Bos/bison</i>	phalanx	Mature	B18	2	-0.85	0.09	—	—	14.9	—	0.022	0.0001	0.001
Grotte du Bison	bone	Arcy 2013 BIS J S5 38	BisJ	Bovid	Bovid	<i>Bos/bison</i>	talus	Mature	B22	3	-0.91	0.04	74.2	0.34	178.4	1.33	0.083	0.0007	0.008
Grotte du Bison	bone	Arcy 2013 BIS J Q14 15	BisJ	Bovid	Bovid	<i>Bos/bison</i>	metatarsal	Mature	B28	3	-0.86	0.04	89.7	0.61	220.4	1.61	0.431	0.0048	0.006
Grotte du Bison	bone	Arcy 2014 BIS J P9 74	BisJ	Bovid	Bovid	<i>Bos/bison</i>	humerus	Mature	B52	2	-0.69	0.11	—	0.08	—	0.53	0.042	—	0.005
Grotte du Bison	bone	Arcy 2015 BIS J Q12 2	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metatarsal	Mature	B21	4	-0.74	0.06	768.4	3.81	1262.4	12.87	0.780	0.0096	0.060

Grotte du Bison	bone	Arcy 2015 BIS J Q12 20	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metatarsal	Mature	B23	2	-0.76	0.04	—	0.38	190.1	1.71	0.535	0.0017	0.008
Grotte du Bison	bone	Arcy 2015 BIS J P6 9	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metacarpal	Mature	B24	2	-0.55	0.04	—	0.42	393.4	2.22	1.699	0.0031	0.028
Grotte du Bison	bone	Arcy 2014 BIS J R8 41	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metatarsal	Mature	B53	4	-0.59	0.03	54.6	0.57	136.8	14.09	1.288	0.0013	0.044
Grotte du Bison	bone	Arcy 2014 BIS J S10 22	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metatarsal	Mature	B54	3	-0.97	0.03	—	0.05	9.5	0.37	0.078	0.0007	0.004
Grotte du Bison	bone	Arcy 2014 BIS J S10 5	BisJ	Cervid	Reindeer	<i>Rangifer tarandus</i>	metatarsal	Mature	B57	4	-0.68	0.07	161.2	1.72	356.0	22.24	3.347	0.0095	0.045
Grotte du Bison	bone	Arcy 2013 BIS I J R4	BisJ	Cervid	Megaloceros	<i>Megaloceros giganteus</i>	phalanx	Mature	B9	2	-0.7	0.03	—	1.05	227.9	7.20	0.964	0.0064	0.028
Grotte du Bison	bone	Arcy 2014 BIS J R3 3	BisJ	Cervid	Red deer	<i>Cervus elaphus</i>	metacarpal	Mature	B15	2	-0.7	0.1	—	—	20.6	—	0.029	0.0003	0.000
Grotte du Bison	bone	Arcy 2013 BIS J Q13 42	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	vertebra	Mature	B1	2	-0.59	0.07	—	0.72	343.1	1.12	1.682	0.0026	0.006
Grotte du Bison	bone	Arcy 2017 BIS J P10 41	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	hemi-mandible	Immature	B39	4	-0.59	0.09	59.6	2.31	149.7	18.13	1.177	—	0.047
Grotte du Bison	bone	Arcy 2011 BIS J O10 304	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	axis	Mature	B40	4	-0.79	0.07	47.8	0.36	119.1	1.06	0.142	0.0059	0.002
Grotte du Bison	bone	Arcy 2013 BIS J T11 123	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	rib	Mature	B46	4	-0.66	0.04	30.6	0.35	80.2	4.37	0.294	0.0021	0.005
Grotte du Bison	bone	Arcy 2015 BIS J R8 48	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	metapod	Mature	B58	4	-0.62	0.09	39.1	0.42	102.4	4.53	0.822	0.0028	0.017
Grotte du Bison	bone	Arcy 2014 BIS J Q14 27	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	fibula	Mature	B6	2	-0.69	0.05	—	—	6.6		0.033	0.0008	0.001
Grotte du Bison	bone	Arcy 2013 BIS J P6 3	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	metapod	Mature	B61	4	-0.52	0.15	38.9	0.66	105.5	6.67	1.761	0.0069	0.014
Grotte du Bison	bone	Arcy 2013 BIS J Q7 6	BisJ	Na	Cave bear	<i>Ursus spelaeus</i>	metapod	Mature	B7	2	-0.69	0.04	—	0.11	43.0	1.07	0.103	0.0006	0.004
Grotte du Bison	bone	Arcy 2015 BIS J S10 4	BisJ	Na	Fox	<i>Vulpes vulpes</i>	Right	Mature	B11	2	-0.61	0.1	—	0.10	29.5	—	0.137	0.0012	0.003
Grotte du Bison	bone	Arcy 2013 BIS J O11 8	BisJ	Na	Fox	<i>Vulpes vulpes</i>	mandible	Mature	B41	3	-0.72	0.07	75.7	0.41	178.3	1.28	0.238	—	0.008
Grotte du Bison	bone	Arcy 2015 BIS J Q10 17	BisJ	Na	Wolf	<i>Canis lupus</i>	radius	Mature	B19	2	-0.9	0.01	—	0.22	37.4	—	0.374	0.0010	0.001
Grotte du Bison	bone	Arcy 2015 BIS J T14 12	BisJ	Na	Wolf	<i>Canis lupus</i>	phalanx	Mature	B30	3	-0.5	0.1	345.8	3.11	744.1	17.51	0.987	0.0134	0.055
Grotte du Bison	bone	Arcy 2013 BIS J Q14	BisJ	Na	Wolf	<i>Canis lupus</i>	first phalanx	Mature	B34	3	-0.93	0.03	104.5	0.57	257.8	0.41	0.086	—	0.002

Grotte du Bison	bone	Arcy 2015 BIS J S5 7	BisJ	Na	Wolf	<i>Canis lupus</i>	radius	Mature	B35	3	-0.83	0.02	—	0.08	24.5	0.52	0.053	—	0.004
Grotte du Bison	bone	Arcy 2011 BIS J T11 19	BisJ	Na	Wolf	<i>Canis lupus</i>	first phalanx	Mature	B42	2	-1.23	0.01	—	0.03	7.8	0.19	0.066	—	0.016
Grotte du Bison	bone	Arcy 2015 BIS J S16 35	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	mandible	Mature	B10	3	-1.04	0.08	—	0.28	153.9	—	0.148	0.0057	0.003
Grotte du Bison	bone	Arcy 2015 BIS J Q11 1	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	tibia	Mature	B14	3	-1.05	0.08	—	0.45	280.4	2.53	0.498	0.0039	0.010
Grotte du Bison	bone	Arcy 2015 BIS J T15 1	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	metapod	Mature	B20	2	-1.02	0.09	157.1	0.71	343.9	0.71	0.419	0.0037	0.005
Grotte du Bison	bone	Arcy 2015 BIS J O4 48	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	mandible	Immature	B3	2	-0.79	0.1	—	0.27	20.6	2.05	0.078	0.0007	0.007
Grotte du Bison	bone	Arcy 2012 BIS J S13 1	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	metatarsal	Mature	B47	3	-0.78	0.04	—	0.18	56.2	1.33	0.259	—	0.003
Grotte du Bison	bone	Arcy 2014 BIS J S7 1	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	femur	Mature	B48	3	-0.63	0.07	101.8	6.41	231.2	48.67	2.203	—	0.053
Grotte du Bison	bone	Arcy 2012 BIS J P12 36	BisJ	Na	Hyena	<i>Crocutea crocuta</i>	metapod	Mature	B49	3	-1.04	0.03	203.3	6.54	475.5	40.61	1.451	—	0.110
Grotte du Bison	bone	Arcy 2019 BISJ R12-31(2)	BisJ	Na	Neandertal	<i>Homo neandertalensis</i>	Fibula	Mature	B25	3	-0.75	0.07	—	0.47	204.4	2.24	3.026	0.0034	0.090
Regourdou	bone	2580	5	Monogastric	Horse	<i>Equus caballus</i>	radius	Mature	R10	3	-1.07	0.06	48.4	0.23	108.8	1.89	1.217	0.0056	0.013
Regourdou	bone	3200 / L6-18	4	Monogastric	Horse	<i>Equus caballus</i>	mandible	Mature	R11	3	-1.06	0.11	23.9	0.23	56.8	—	1.174	0.0071	0.019
Regourdou	bone	Reg E3 24	/	Monogastric	Horse	<i>Equus caballus</i>	first phalanx	Mature	R36	5	-0.86	0.12	—	0.44	56.8	4.61	0.035	—	0.009
Regourdou	bone	Reg J5 13	/	Monogastric	Horse	<i>Equus caballus</i>	second phalanx	Mature	R37	4	-0.62	0.09	238.9	1.64	511.4	15.96	1.391	0.0013	0.113
Regourdou	bone	Reg I5 4	/	Monogastric	Horse	<i>Equus caballus</i>	left scapula	Mature	R38	3	-0.76	0.09	349.4	2.10	694.9	16.50	0.959	—	0.114
Regourdou	bone	Reg 4C 20 C4 6	4c	Bovid	Bovid	<i>Bos/bison</i>	first phalanx	Immature	R39	4	-0.92	0.11	—	0.21	30.6	2.33	0.070	—	0.004
Regourdou	bone	Reg 4C 20 C4 6 *	4c	Bovid	Bovid	<i>Bos/bison</i>	first phalanx	Mature	R40	3	-1.26	0.1	—	0.05	12.5	0.23	0.007	—	0.014
Regourdou	bone	Reg 2 K3 30 2154	2	Bovid	Bovid	<i>Bos/bison</i>	left tibia	Mature	R41	6	-0.67	0.12	241.3	2.09	517.2	13.64	0.702	—	0.034
Regourdou	bone	2970 / J5-3	2	Cervid	Reindeer	<i>Rangifer tarandus</i>	metapod	Mature	CA19	3	-1.1	0.09	—	—	—	—	—	—	—
Regourdou	bone	H7-3	2	Cervid	Reindeer	<i>Rangifer tarandus</i>	coxal	Mature	R06	4	-1.08	0.06	25.2	0.36	57.2	1.85	0.088	0.0026	0.008
Regourdou	bone	I7-11	2	Cervid	Reindeer	<i>Rangifer tarandus</i>	scapula	Mature	R07	4	-1.08	0.1	53.4	0.27	120.1	1.26	0.047	0.0013	0.006

Regourdou	bone	H7-7	2	Cervid	Reindeer	<i>Rangifer tarandus</i>	scapula	Mature	R08	3	-1.19	0.01	30.1	0.18	67.7	—	0.096	0.0060	0.015
Regourdou	bone	Reg 4 M5 14 3387	4	Cervid	Roe deer	<i>Capreolus capreolus</i>	right hemi-mandible	Mature	R47	4	-0.91	0.09	129.2	0.47	301.4	3.50	2.224	—	0.124
Regourdou	bone	Reg 4b I3 36 1700	4b	Cervid	Roe deer	<i>Capreolus capreolus</i>	left hemi-mandible	Mature	R48	4	-1.02	0.03	72.6	0.90	182.4	12.94	3.965	—	0.120
Regourdou	bone	2472	4	Cervid	Red deer	<i>Cervus elaphus</i>	tibia	Mature	R01	3	-1.51	0.1	38.7	0.23	88.6	—	0.026	0.0044	0.001
Regourdou	bone	H4-34	4	Cervid	Red deer	<i>Cervus elaphus</i>	tibia	Mature	R02	3	-1.39	0.09	44.2	0.27	100.2	—	0.038	0.0054	0.014
Regourdou	bone	J6-36	2	Cervid	Red deer	<i>Cervus elaphus</i>	radius	Mature	R03	3	-1.52	0.07	48.5	0.27	108.9	—	0.015	0.0037	0.005
Regourdou	bone	J6-43	2	Cervid	Red deer	<i>Cervus elaphus</i>	metatarsal	Mature	R04	3	-1.32	0.09	60.4	0.36	133.8	1.53	0.035	0.0030	0.012
Regourdou	bone	563 / F6-5	2	Cervid	Red deer	<i>Cervus elaphus</i>	femur	Mature	R05	4	-1.28	0.05	19.8	0.18	46.2	—	0.011	0.0038	0.003
Regourdou	bone	Reg 4 3204	4	Cervid	Red deer	<i>Cervus elaphus</i>	humerus	Mature	R45	5	-1.03	0.12	—	0.15	22.1	1.92	0.371	—	0.047
Regourdou	bone	I7-10	2	Na	Boar	<i>Sus scrofa</i>	femur	Mature	R09	3	-0.99	0.11	51.3	0.27	111.8	—	0.026	0.0009	0.004
Regourdou	bone	463 / F3 57	4	Na	Boar	<i>Sus scrofa</i>	humerus	Mature	R14	3	-0.79	0.08	50.9	0.18	115.4	1.35	0.125	0.0031	0.003
Regourdou	bone	Reg E3 101	/	Na	Boar	<i>Sus scrofa</i>	left hemi-mandible	Immature (6-10 m)	R49	5	-0.82	0.26	—	0.61	33.6	11.63	3.945	—	0.028
Regourdou	bone	Reg 4 291 F2 84	4	Na	Boar	<i>Sus scrofa</i>	ulna	Immature	R50	5	-0.72	0.14	—	0.48	75.3	6.93	0.334	0.0007	0.020
Regourdou	bone	Reg 2 1008 G5 12	2	Na	Boar	<i>Sus scrofa</i>	ulna	Mature ?	R51	4	-0.82	0.03	63.6	0.38	165.0	0.44	0.027	0.0004	0.003
Regourdou	bone	242 / F2-35	4	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R16	3	-0.93	0.08	36.8	0.14	82.0	0.33	0.034	0.0024	0.011
Regourdou	bone	3914 / E3-56	4	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R18	3	-0.97	0.11	38.1	0.23	86.3	1.80	0.044	0.0029	0.054
Regourdou	bone	3827 / D2-33	4	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R19	3	-0.97	0.04	40.6	0.18	89.3	1.58	0.141	0.0016	0.008
Regourdou	bone	3827 / D2-33	4	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R20	5	-1.25	0.19	24.9	1.22	56.5	12.56	3.631	0.0011	0.072
Regourdou	bone	397 / F3-44	4	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R22	4	-1.01	0.09	29.9	0.27	66.3	3.87	0.284	0.0026	0.091
Regourdou	bone	1037 / G5-42	2	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R23	4	-1.08	0.11	37.5	0.14	83.6	1.31	0.032	0.0016	0.009
Regourdou	bone	1644 / H6-60	5	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R24	2	-1.23	0.08	24.9	0.09	54.5	—	0.007	0.0008	0.001
Regourdou	bone	1644 / H6-60	5	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R25	3	-1.33	0.13	34.1	0.23	73.4	—	0.030	0.0009	0.005
Regourdou	bone	3441	7	Na	Brown bear	<i>Ursus arctos</i>	femur	Mature	R26	3	-1.16	0.04	31.8	0.72	68.8	1.85	0.458	0.0048	0.022
Regourdou	bone	ours sepulture	4	Na	Brown bear	<i>Ursus arctos</i>	tibia	Immature	R27	4	-0.94	0.09	—	—	—	—	0.094	0.0040	0.005
Regourdou	bone	E2-103 4C 4084	4	Na	Brown bear	<i>Ursus arctos</i>		Mature	R33	3	-0.94	0.45	—	0.42	69.7	5.75	0.360	—	0.445
Regourdou	bone	E2-103 4C 4084	4	Na	Brown bear	<i>Ursus arctos</i>	right ulna	Mature	R35	3	-0.95	0.11	—	0.07	13.1	0.18	0.008	—	0.002
Regourdou	bone	3455 / M6-8	4	Na	Wolf	<i>Canis lupus</i>	tibia	Mature	R13	3	-1.17	0.06	31.2	0.09	71.6	—	0.597	0.0028	0.011

Regourdou	bone	3969 / E3-109	4	Na	Wolf	<i>Canis lupus</i>	humerus	Mature	R15	4	-1.22	0.09	30.1	0.14	68.8	—	0.695	0.0025	0.013
Regourdou	bone	K3-69/2193	2	Na	Wolf	<i>Canis lupus</i>	hemi- mandible	Mature	R31	2	-0.99	—	—	0.15	8.7	1.28	0.029	—	0.011
Regourdou	bone	2636 / L4-12	2	Na	Cave lion	<i>Panthera spelaea</i>	radius	Mature	R12	3	-1.73	0.12	18.1	0.41	42.3	3.33	0.113	0.0028	0.049
Regourdou	bone	Reg L4 13	2	Na	Cave lion	<i>Panthera spelaea</i>	right talus	Mature	R42	4	-0.97	0.09	77.1	1.40	190.8	14.69	0.486	—	0.139
Regourdou	bone	Reg K4 6	2	Na	Cave lion	<i>Panthera spelaea</i>	left hemi- mandible	Mature	R43	5	-1.13	0.12	44.1	1.20	120.2	11.27	0.297	—	0.288
Regourdou	bone	REG 2	4	Na	Neandertal	<i>Homo neandertalensis</i>	calcaneus	Mature	Ma79	4	-0.78	0.06	54.5	0.33	133.1	2.86	0.356	—	0.007
Regourdou	bone	REG 2	4	Na	Neandertal	<i>Homo neandertalensis</i>	calcaneus	Mature	Ma80	4	-0.8	0.07	56.4	0.30	138.9	1.12	0.334	—	0.003
Regourdou	bone	REG 1	4	Na	Neandertal	<i>Homo neandertalensis</i>	humerus	Mature	R28	3	-1.67	0.11	24.5	0.05	52.3	—	0.022	0.0015	0.003
Regourdou	bone	REG 1	4	Na	Neandertal	<i>Homo neandertalensis</i>	femur	Mature	R29	3	-1.51	0.1	42.2	0.23	92.5	2.57	0.165	0.0027	0.016
Regourdou	bone	REG 1	4	Na	Neandertal	<i>Homo neandertalensis</i>	femur	Mature	R30	4	-1.56	0.02	36.5	0.23	81.4	2.16	0.210	0.0015	0.008
Grotte du Bison	vegetal				Garlic mustard	<i>Alliaria petiolata</i>	leaf	—	P42	3	-0.61	0.15	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Garlic mustard	<i>Alliaria petiolata</i>	stem	—	P43	3	-0.92	0.05	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Common nettle	<i>Urtica dioicas</i>	leaf	—	P35	4	-0.57	0.09	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Common nettle	<i>Urtica dioicas</i>	stem	—	P37	5	-0.96	0.07	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Common dandelion	<i>Taraxacum officinale</i>	leaf	—	P39	2	-0.39	0.06	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Common dandelion	<i>Taraxacum officinale</i>	stem	—	P36	5	-0.7	0.02	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Cleavers	<i>Galium aparine</i>	leaf	—	P41	2	-0.51	0.13	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Cleavers	<i>Galium aparine</i>	stem	—	P44	2	-0.97	0.07	—	—	—	—	—	—	—
Grotte du Bison	vegetal				Oak	<i>Quercus sp.</i>	leaf	—	P38	5	-0.47	0.09	—	—	—	—	—	—	—
Regourdou	vegetal				Grasses	<i>Gramineae</i>	leaf	—	P18	3	-0.44	0.08	—	—	—	—	—	—	—
Regourdou	vegetal				Grasses	<i>Gramineae</i>	stem	—	P2	2	-0.69	0.09	—	—	—	—	—	—	—
Regourdou	vegetal				Common nettle	<i>Urtica dioica</i>	leaf	—	P16	3	-0.45	0.01	—	—	—	—	—	—	—

Regourdou	vegetal	Common nettle	<i>Urtica dioica</i>	stem	—	P1	2	-0.84	0.02	—	—	—	—	—	—	—
Regourdou	vegetal	Common dandelion	<i>Taraxacum officinale</i>	leaf	—	P12	2	-0.43	0.09	—	—	—	—	—	—	—
Regourdou	vegetal	Common dandelion	<i>Taraxacum officinale</i>	stem	—	P10	2	-0.84	0.08	—	—	—	—	—	—	—
Grotte du Bison	vegetal	Hazel	<i>Corylus sp.</i>	leaf	—	P40	2	-0.6	0.03	—	—	—	—	—	—	—
Regourdou	vegetal	Oak	<i>Quercus sp.</i>	leaf	—	P5	3	-0.48	0.04	—	—	—	—	—	—	—

Abbreviations: ID = identification; MixSIAR = Bayesian mixing models for stable isotope analyses in R; REE = rare earth elements.

SOM Table S2

Compilation of the literature on plant Ca isotope compositions

Reference	Type	Family	Taxon	Organ	$\delta^{44/42}\text{Ca}$ vs ICP-Ca Lyon (‰)	± 2 SD (‰)
Christensen et al. (2018)	Grass/herb	Poaceae	<i>Triticeae</i>	Leaf	-0.58	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Root	-0.45	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Leaf	-0.33	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Root	-0.45	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Leaf	-0.44	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Root	-0.36	—
	Grass/herb	Poaceae	<i>Triticeae</i>	Leaf	-0.48	—
Chu et al. (2006)	Grass/herb	—	—	Above ground biomass	-0.61	0.12
	Grass/herb	—	—	Above ground biomass	-0.87	0.04
	Grass/herb	—	—	Above ground biomass	-0.78	0.08
	Grass/herb	—	—	Above ground biomass	-0.85	0.18
	Grass/herb	—	—	Above ground biomass	-1.13	0.36
	Grass/herb	—	—	Above ground biomass	-0.88	0.04
	Grass/herb	—	—	Above ground biomass	-1.07	0.03
	Grass/herb	—	—	Above ground biomass	-0.99	0.02
	Grass/herb	—	—	Above ground biomass	-0.54	0.02
	Grass/herb	—	—	Above ground biomass	-0.68	0.08
Hindshaw et al. (2013)	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Root	-0.63	0.07
	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Cortex	-0.69	0.07
	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Stele	-0.44	0.07
	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Stem	-0.57	0.07
	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Leaf	-0.11	0.07
	Grass/herb	Polygonaceae	<i>Rumex scutatus</i>	Flower	-0.12	0.07
	Grass/herb	Polygonaceae	<i>Oxyria digyna</i>	Leaf	-0.07	0.07
	Grass/herb	Polygonaceae	<i>Oxyria digyna</i>	Leaf	-0.05	0.07
	Grass/herb	Polygonaceae	<i>Oxyria digyna</i>	Leaf	-0.20	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Leaf	-0.51	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Leaf	-0.42	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Leaf	-0.42	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Leaf	-0.43	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Leaf	-0.45	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Flower	-0.56	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Flower	-0.60	0.07
	Grass/herb	Poaceae	<i>Agrostis</i>	Flower	-0.57	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.18	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.33	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.31	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.39	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.28	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.29	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.37	0.07
	Grass/herb	Asteraceae	<i>Leucanthemopsis alpina</i>	Above ground biomass	-0.36	0.07
Skulan et al (1999)	Grass/herb	Fabaceae	<i>Medicago sativa</i>	Above ground biomass	-0.25	—
	Grass/herb	Poaceae	<i>Festuca</i>	Above ground biomass	-0.55	—

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