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ABSTRACT

The prey choice of extinct cave lions *Panthera spelaea* was determined using bone collagen isotopic signatures in the Belgian Ardennes and the Swabian Jura between 40,000 and 25,000 years ago as well as in the Late-glacial of the northwestern Alp foreland and of the Paris Basin. More than 370 specimens of large carnivorous and herbivorous mammals from 25 sites coeval with cave lion were analyzed. The isotopic results point to an individualistic prey choice for cave lions, with some individuals more oriented on reindeer and others on young cave bears. The isotopic signatures and therefore dietary choice of cave lions did not overlap with those of cave hyenas, indicating competitive exclusion between the large predators. The most recent western European cave lions seem to have been consuming mainly reindeer until the local extirpation of this prey species, which coincides chronologically with their own extinction. This restricted prey choice may be involved in the extinction of this large predator in Western Europe.

1. Introduction

Determining the actual dietary preferences of extinct species is a difficult task even when closely related modern representatives are still extant. This is especially true when the environmental conditions, potential prey and competitor suite, as well as the genetic structure were different in the past than for the modern populations used for comparison. This is the case for cave lions,

considered sometimes as a subspecies of modern lions *Panthera leo spelaea* (e.g., Kurtén, 1985; Burger et al., 2004; Barnett et al., 2009), or treated as a distinct species, *Panthera spelaea* (e.g., Argant, 1996; Stuart and Lister, 2011). This paper follows the latter option in ranking the cave lion as a separate species. Investigations of ancient DNA have demonstrated a long genetic separation between the modern lions from subtropical Africa and Asia, and the Eurasian and American lions adapted to cold climates (Burger et al., 2004; Barnett et al., 2009). A similar conclusion was based on distinctive morphological characters from the skull and teeth (Sotnikova and Nikolskiy, 2006). Although modern lions have survived quite successfully until the advent of firearms, cave lions became extinct

in their whole distribution area by around 12,000 years ago (Stuart and Lister, 2011). Understanding the reasons behind this extinction implies a detailed knowledge of the ecology of this species, including its diet, more precisely the prey preferences in case of a predator such as the cave lion.

The main approaches used to infer prey preferences in extinct predators such as the cave lion are analogy with modern relatives and evidence of predation activity on preys in the fossil record. In the case of the cave lion, fortunately there is a very close modern relative abundantly studied for its dietary ecology (e.g., Breuer, 2005; Funston and Mills, 2006) and for competition with other large predators (Trinkel and Kastberger, 2005; Hayward, 2006). Some predators are also closely related to the ones formerly sharing the same environment with cave lions, such as cave hyenas *Crocuta crocuta spelaea* (e.g., Rohland et al., 2005), even if behavioural differences are to be expected between modern and Pleistocene hyenas, the latter being most probably a more active predator than modern hyenas (e.g., Baryshnikov, 1999). Since modern lions consume essentially large ungulates such as zebras and large antelopes but are unable to tackle adults of very large species such as elephants and rhinoceros, it is generally assumed that cave lions should have had a similar prey choice shifted to larger sized prey, as the average size of cave lions was larger than that of modern lions (e.g., Hemmer, 2004). This leads to the assumption that cave lions were primarily consuming horse and bison, as well as reindeer, muskoxen and young individuals of mammoths and woolly rhinoceros (e.g.. Guthrie, 1968; Turner, 2009; Stuart and Lister, 2011). Based on such an assumption, a link has been suggested between the decline of genetic diversity in bison around 45,000 years ago in North America and the decrease of genetic diversity that occurred in fossil lions around the same time, as cave lions were supposed to be preferentially feeding on this large herbivore (Barnett et al., 2009). However, extant lion populations exhibit important variations in their diet and prey choice, even within a given ecosystem, as documented in the Serengeti (Hopcraft et al., 2005). Although the habitats used by modern lions range from desert to closed woodland (Patterson, 2007), none of the modern lion populations dwells under ecological conditions even remotely comparable to the steppe-tundra of the late Pleistocene, making the ecological analogy between modern and fossil lions very difficult.

Another source of information is the direct predation traces left by cave lions on the fossil remains of their prey. Most spectacular are those found on the mummy of an Alaskan bison, bite marks and a tip of lion canine embedded in the carcass, showing clearly that cave lions happened to prey on bison (Guthrie, 1990). However, such evidence yields information about which prey species was consumed by cave lions, but does not provide quantitative results. In contrast, approaches such as stable isotopic tracking may provide such direct quantitative evidence at an individual level.

Based on the analysis of the faunal composition and taphonomical aspects of some upper Pleistocene cave deposits, some inferences have been made on possible antagonism between cave lions and cave hyenas (e.g.. Diedrich, 2008, 2009b). Here again, it is very difficult to infer quantitatively this type of ecological interaction between predators in the past with such evidence, while stable isotope approaches allow to test dietary competition between predators by comparing their signatures: different isotopic signatures indicate that the average source of proteins was different for both predators (e.g., Lavin et al., 2003; Zhao et al., 2004; Lewis et al., 2006; Mitani et al., 2009).

Finally, prehistoric cave paintings depicting cave lions together with potential prey species have sometimes been interpreted as reflecting naturalistic behaviour. For instance, in Chauvet Cave (Ardèche, France), a whole panel includes several lions and bisons that may represent a hunting event (Packer and Clottes, 2000). Such an interpretation implies that cave lions hunted cooperatively in pack as modern lions do in savanna environments, and that they hunted bison. However, there is no certainty in the meaning of such representations and, although anatomical details of such cave paintings are usually very accurate, the species association may have other meanings than predator−prey interactions. Even if such a hunting event actually happened, it is not clear how representative it would be in the predatory behaviour and the palaeobiology of cave lions in terms of occurrence in time and across the distribution range of the species.

The present paper aims at considering quantitatively how much of different prey species were consumed by individual cave lions, and to which extent competition with other large predators impacted on the dietary ecology of cave lions. It considers exemplary sites in North Western Europe, where cave lions co-occur with potential prey and competitors, during two different time periods, before and after the Last Glacial Maximum (LGM). Pre-Last Glacial Maximum (pre-LGM) assemblages of large mammals from sites in the Ardennes (Belgium) and the Swabian Jura (Southern Germany), dated between around 40,000 and 24,000 ^{14}C years ago, were used. These sites have yielded, besides cave lions, other predators that were potential competitors of the lions, such as leopards, cave hyenas, wolves, wolverines and brown bears, as well as a diverse assemblage of herbivores that represent the potential prey, such as reindeer, bison, horse, woolly rhinoceros and mammoth, as well as cave bears. Although cave bears belong to the order Carnivora, the isotopic data gathered for specimens from the studied sites clearly point to a vegetarian diet, ruling them out from dietary competition with lions (e.g., Bocherens et al., 1997; 2011; Münzel et al., 2008; Bocherens et al., in press). Predation of cave lions on cave bears has also been suggested based on taphonomical analyses (Weinstock, 1999; Diedrich, 2009b), which led to the inclusion of cave bears in the list of potential prey of cave lions. The sites dated from the late-glacial (post-LGM) considered here include some of the most recently dated cave lions, in the Paris basin (France) and in the French and Swabian Jura (France, Switzerland, Germany) (Stuart and Lister, 2007, 2011).

2. Material and methods

Faunal remains from 25 sites were studied in the present work. Five of these sites yielded cave lions and other mammalian species while the other sites provided additional specimens of species of coeval herbivores and carnivores in the same area (Fig. 1). Altogether, 375 individual carbon and nitrogen isotopic signatures are reported here, of which 33 from Scladina cave were previously published in Bocherens et al. (1997). Nine were published as "horse" from the Swabian Jura by Stevens and Hedges (2004), but the taxonomic attribution of several samples were actually woolly rhinoceros or reindeer and they have been corrected here. A total of 32 isotopic data for late-glacial reindeer from southern Germany were published in Drucker et al. (2011), and 40 isotopic data for cave bears from the Swabian Jura were published in Münzel et al. (in this issue), the rest being published here for the first time. Some of the studied specimens were directly dated by Accelerator Mass Spectrometry (AMS) radiocarbon, usually on the same collagen as that measured for stable isotope abundances.

The studied material was treated as four separated spatial and chronological units (Table 1, Fig. 1): the Ardennes (Belgium) before the Last Glacial Maximum (pre-LGM), between around 24,000 and 40,000 ^{14}C BP; the Swabian Jura (Germany) before the Last Glacial Maximum (pre-LGM), between around 26,000 and 40,000 ^{14}C BP; the Jura, or North-western Alpine foreland (France, Switzerland, Germany) after the Last Glacial Maximum (post-LGM), between
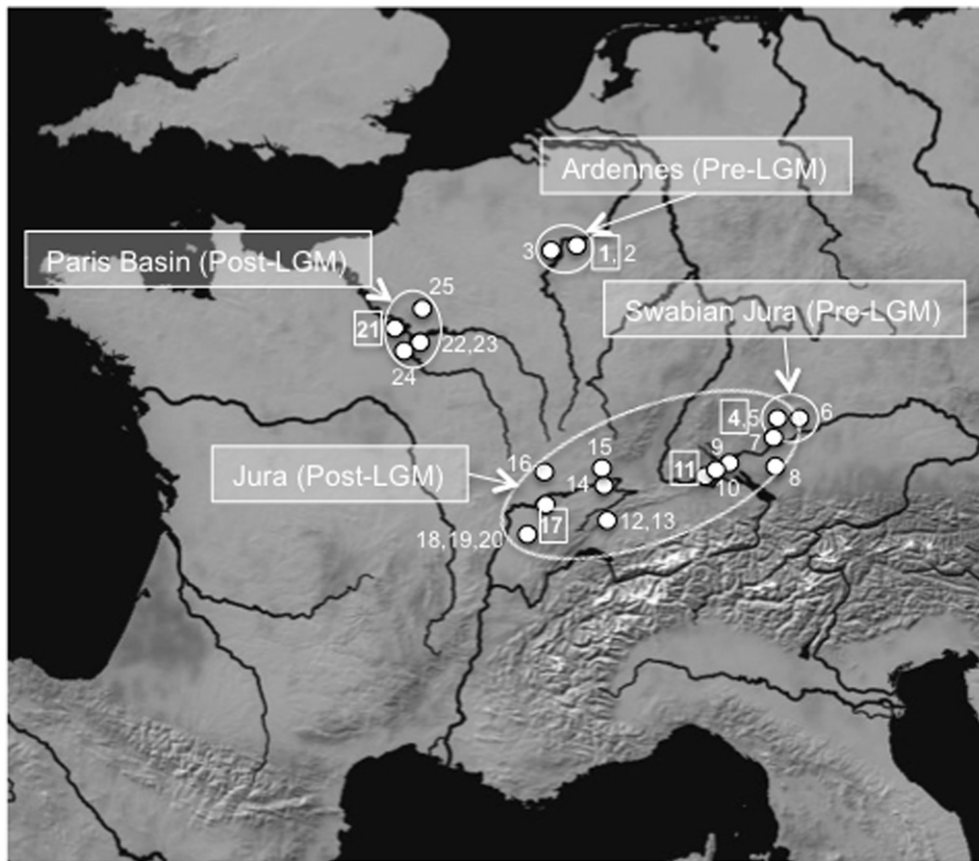
Fig. 1. Location map of studied sites (sites with cave lions are in italics and bold). Keys: 1-Goyet, 2-Scladina, 3-Freyr, 4-Hohle Fels, 5-Geissenklösterle, 6-Hohlenstein-Stadel, 7-Felsställe, 8-Schussenquelle, 9-Buttentalhöhle, 10-Peterfels, 11-Kesslerloch, 12-Champréveyres, 13-Monruz, 14-Rochedane, 15-Bavans, 16-Grotte de la Baume noire, 17-Ranchot, 18-Grotte du Chaumois-Boivin, 19-Grotte Grappin, 20-Grotte de Chaze II, 21-Le Closeau, 22-Tureau des Gardes, 23-Pincevent, 24-Etiolles, 25-Verberie.

around 14,000 and 12,000 ^{14}C BP; and the Paris Basin (France) after the Last Glacial Maximum (post-LGM), between around 13,000 and 12,000 ^{14}C BP. As the goal of this study is to compare the dietary ecology of cave lions during different time slots in different regions, no attempt was made to calibrate the radiocarbon dates. The radiocarbon dates were used as a means to verify contemporaneity in addition to the stratigraphic origin of the samples. This selection allows comparison of different palaeoecological situations for cave lions at the same time and to monitor their evolution before and after the LGM in North-western Europe.

2.1. Sites

A complete list of the sites and the number of specimens that they yielded for the present work is shown in Table 1.

Pre-LGM sites in Ardennes (Belgium): Two sites yielded almost all the samples included in the present study, Goyet and Scladina cave. Both are located close to the Meuse valley, 5 km apart, and have yielded rich assemblages of fossil mammals of Upper Pleistocene age (e.g., Dupont, 1873; Simonet, 1992; Germonpré and Sablin, 2001; Lamarque, 2003; Germonpré, 2004; Bourdillat, 2008). Goyet cave yielded bone material ranging in age from upper Pleistocene to late-glacial (e.g., Germonpré, 2004; Germonpré et al., 2009; Stevens et al., 2009), but only material that could be confidently related to the pre-LGM period was selected. At Goyet cave, several postcranial bones, each pertaining to a different individual, were analyzed: 6 cave lions, 6 cave hyenas, 2 wolves, 5 brown bears, 23 cave bears, 3 mammoths, 3 woolly rhinoceros, 4 horses, 5 large bovines and 6 reindeer (Table 1). Material from layers 40 and 1 A in

Scladina Cave was selected as these layers are coeval to the upper Pleistocene layers from Goyet that yielded the cave lions (Pirson et al., 2008). This site provided additional material from the same species already collected in Goyet, such as 6 hyenas, 1 wolf, 7 cave bears, 3 mammoths, 6 horses, 7 large bovines (Table 1). In addition, additional species from Scladina cave included 1 leopard, 2 chamois, 1 roe deer, 2 red deer, and 3 giant deer (Table 1). Finally, one directly radiocarbon dated wolverine from Freyr, a site near Hastière in the Meuse Valley excavated by Edouard Dupont in the 1860s, has been included in the study (Table 1).

Pre-LGM sites in the Swabian Jura (southern Germany): The four cave lions from the Swabian Jura come from Hohle Fels, a site from which 3 brown bears, 20 cave bears, and 1 horse were also analyzed (Table 1). The selected material comes from the lower levels that yielded Gravettian and Aurignacian prehistoric artefacts with radiocarbon dates ranging from around 40,000 to 25,000 BP (Conard and Bolus, 2003, 2008), or that were directly radiocarbon dated to this time interval (Table in appendix). Another cave located about 3−4 km away from Hohle Fels in the Ach Valley, Geißenklösterle, yielded additional material including 2 brown bears, 20 cave bears, 17 horses, 14 reindeer, and 2 chamois (Table 1). This material comes either from Gravettian and Aurignacian levels or was directly radiocarbon dated to the time interval 40,000 to 25,000 BP (Münzel and Conard, 2004; Münzel, in press). Finally, additional material was selected from the site of Hohlenstein-Stadel located in the Lone Valley about 50 km to the northeast (Hahn et al., 1985). This site yielded three additional species of the same period including 2 cave hyenas, 1 mammoth, and 1 woolly rhinoceros (Table 1). The chronological resolution of this material is

Table 1
Summary table of the sites from which material was selected, with information on chronology and sampled species. The taxonomic attribution was corrected for some samples previously published by Stevens and Hedges (2004).

Site (layer)	Location	Map	Age	Chronology	Carnivores	Herbivores	References
Goyet (A1, A2, A3, B4, B5)	Ardennes (Belgium)	1	28–40,000 BP	pre-LGM	lion (6), hyaena (6), wolf (2), brown bear (5)	mammoth (3), rhinoceros (3), horse (4), Bos/Bison (5), Reindeer (6), cave bear (23)	Germonpré (2004)
Scladina (40, 1A)	Ardennes (Belgium)	2	40,000 BP	pre-LGM	leopard (1), hyaena (6), wolf (1)	mammoth (3), rhinoceros (7), horse (6), Bos/Bison (8), chamois (2), roe deer (1), red deer (2), giant deer (3)	Bonjean (1998), Pirson et al. (2008), Lamarque (2003), Bourdillat (2008)
Freyr	Ardennes (Belgium)	3	32,000 BP	pre-LGM	wolverine (1)		
Hohle Fels	Swabian Jura (Germany)	4	25–35,000 BP	pre-LGM	lion (4), brown bear (3)	horse (1), cave bear (20)	Schiegl et al. (2003), Conard and Bolus (2008)
Geissenklösterle	Swabian Jura (Germany)	5	25–35,000 BP	pre-LGM	brown bear (2)	rhinoceros (1), horse (17), chamois (2), reindeer (14), cave bear (20)	Conard and Bolus (2008), Münzel (in press), Stevens and Hedges (2004)[a]
Hohlenstein-Stadel	Swabian Jura (Germany)	6	25–40,000 BP	pre-LGM	hyaena (2)	mammoth (1), rhinoceros (1)	Hahn et al. (1985), Conard and Bolus (2008)
Hohle Fels	Swabian Jura (Germany)	4	12,000 BP	post-LGM	brown bear (1)	reindeer (1)	Schiegl et al. (2003), Conard and Bolus (2008)
Geissenklösterle	Swabian Jura (Germany)	5	13,000 BP	post-LGM		reindeer (3)	Stevens and Hedges (2004)[b]
Felsställe	Swabian Jura (Germany)	7	~12,000 BP	post-LGM			Berke (1987), Kind (1987)
Schussenquelle	Swabian Jura (Germany)	8	13–12,000 BP	post-LGM	wolf (1), brown bear (2)	horse (1), reindeer (5), elk (2)	Schuler (1994)
Buttentalhöhle	Swabian Jura (Germany)	9	~12,000 BP	post-LGM	brown bear (1)		Peters (1936)
Petersfels	Swabian Jura (Germany)	10	~12,000 BP	post-LGM		reindeer (19)	Albrecht et al. (1983)
Kesslerloch	Swabian Jura (Switzerland)	11	14–12,000 BP	post-LGM	lion (2), wolf (2), wolverine (2), fox (1), lynx (1)	mammoth (2), rhinoceros (1), horse (5), Bos/Bison (3), reindeer (5), red deer (1), hare (17), ground squirrel (4)	Merk (1876), Napierala (2008)
Champréveyres	Swiss Jura (Switzerland)	12	13–12,000 BP	post-LGM		horse (2)	Leesch et al. (2004), Müller et al. (2006)
Monruz	Swiss Jura (Switzerland)	13	13–12,000 BP	post-LGM		horse (2)	Leesch et al. (2004), Müller et al. (2006)
Rochedane (D1)	French Jura (France)	14	~12,000 BP	post-LGM		reindeer (4), red deer (3)	Bridault & Chaix (2007), Drucker et al. (2009a)
Bavans	French Jura (France)	15	~12,000 BP	post-LGM		red deer (1)	David (1996), Cupillard (2003)
Grotte de la Baume Noire	French Jura (France)	16	13–12,000 BP	post-LGM		reindeer (1)	David (1996)
Ranchot	French Jura (France)	17	~12,000 BP	post-LGM	lion (1)	reindeer (1)	Cupillard and David (1995), Cupillard (2003)
Grotte du Chaumois-Boivin	French Jura (France)	18	13–12,000 BP	post-LGM		reindeer (1)	David (1996)
Grotte Grappin	French Jura (France)	19	14–12,000 BP	post-LGM		reindeer (1)	David (1996)
Grotte de Chaze II	French Jura (France)	20	~14,000 BP	post-LGM		rhinoceros (1)	Cupillard and Welté (2006)
Le Closeau	Paris Basin (France)	21	13–12,000 BP	post-LGM	lion (1), wolf (1)	horse (8), red deer (6), wild boar (1), hare (1)	Bodu and Mevel (2008)
Tureau-des-Gardes	Paris Basin (France)	22	13–12,000 BP	post-LGM	wolf (1)	horse (14), reindeer (6)	Alix et al. (1993), Bridault et al. (1997)
Pincevent (IV)	Paris Basin (France)	23	13–12,000 BP	post-LGM		horse (4), reindeer (8)	Leroi-Gourhan and Brézillon (1972)
Etiolles	Paris Basin (France)	24	13–12,000 BP	post-LGM		horse (2), reindeer (4)	Bridault et al. (2003), Olive (2004)
Verberie	Paris Basin (France)	25	13–12,000 BP	post-LGM		reindeer (3)	Audouze et al. (1981)

[a] Stands for samples that are woolly rhinoceros instead of horse.
[b] Stands for samples that are reindeer instead of horse.

not as good as for the two previous sites, but it comes roughly from the same time interval (Hahn et al., 1985; Beck, 1999; Gamble, 1999).

Post-LGM sites in the North-western Alpine foreland (French/Swiss/German Jura): the site of Kesslerloch, located near Thayngen in the Swiss canton of Schaffhausen, yielded a rich and diverse mammalian fauna associated with a Magdalenian prehistoric industry and dated from around 14,000 to 12,000 ^{14}C BP (Merk, 1876; Höneisen, 1986; Napierala, 2008). Besides 2 cave lion bones, other predators from this site were analyzed, including 2 wolves, 2 wolverines, 1 fox, and 1 lynx, as well as herbivores including 2 mammoths, 1 woolly rhinoceros, 5 horses, 3 bisons, 5 reindeer, 1 red deer, 17 hares, and 4 ground squirrels (Table 1). One radiocarbon dated cave lion tooth from Ranchot (northern Jura, France: Cupillard and David, 1995; Cupillard, 2003) was also analyzed for stable isotopes, together with a radiocarbon dated reindeer bone from the same site (Table 1). To complete the trophic reconstruction of the North-western Alpine foreland during the early late-glacial, additional faunal remains come from various sites in the Swabian and the northern French and Swiss Jura. The sites located in South-western Germany include Schussenquelle (Schuler, 1994), that provided 2 brown bears, 1 horse, 5 reindeer, and 2 elks; Buttentalhöhle (Peters, 1936), that provided one reindeer, Felsställe (Berke, 1987; Kind, 1987), that provided 3 reindeer, and Petersfels (Albrecht et al., 1983), from which 20 reindeer were analyzed in the present study (Table 1). The sites from the northern French Jura include Grotte Grappin in Arlay (David, 1996), that provided one reindeer, Grotte de Chaze II (Cupillard and Welté, 2006), that provided one woolly rhinoceros, Rochedane (Bridault and Chaix, 2007; Drucker et al., 2009a), that provided 4 reindeer and 3 red deer; Bavans (David, 1996; Cupillard, 2003) that yielded one red deer, Grotte de Chaumois-Boivin in Blois-sur-Seille (David, 1996) and Grotte de la Baume noire in Frétigney (David, 1996), each site provided one reindeer each for the present study. Finally, two additional horses were collected from each site of Champréveyres and Monruz in the northern Swiss Jura (Leesch et al., 2004; Müller et al., 2006) (Table 1). Although these sites cover a rather large area, the results are considered as belonging to one palaeoecological unit, as a previous study found very homogenous isotopic signatures across this range at this period (Drucker et al., 2009b).

Post-LGM sites in the Paris Basin: Le Closeau yielded one directly radiocarbon dated cave lion, in addition to coeval species (1 wolf, 8 horses, 6 red deer, 1 boar, 1 hare) (Bodu and Mevel, 2008). Additional material from Tureau-des-Gardes (1 wolf, 14 horses, 6 reindeer), Pincevent (4 horses, 8 reindeer), Etiolles (2 horses, 4 reindeer), and Verberie (3 reindeer) were used to complete the trophic reconstruction (Table 1) (Leroi-Gourhan and Brézillon, 1972; Audouze et al., 1981; Alix et al., 1993; Bridault et al., 1997, 2003; Olive, 2004).

2.2. Material

For carnivores, sampling was performed on bone as much as possible, and dentine was avoided unless it was the only material available. Previous investigations have shown systematic differences in carbon and nitrogen isotopic abundances between collagen from bone and dentine of the same individual, in recent and fossil samples (e.g., Bocherens et al., 1994; Fizet et al., 1995; Bocherens, 2000). In a few cases, only tooth material was available, for instance for the cave lion from Ranchot, the hyenas from Hohlenstein-Stadel (Swabian Jura), the leopard and some deer from Scladina cave (Ardennes), (Table in appendix). In the case of carnivores, a correction was performed using known differences between δ^{13}C and δ^{15}N values of dentine and bone in the same species or a closely related taxon. The values measured on 9 bone–dentine pairs from different individuals of cave hyenas in Scladina cave and Kent's Cavern (Bocherens et al., 1995, 1997) yielded an average difference between dentine and bone of 0.34 ± 0.54 and 1.08 ± 0.52 for δ^{13}C and δ^{15}N, respectively (Table 1 in appendix). For the deer species, dentine δ^{15}N values were not taken into account in the calculation of average isotopic values (Table 2).

2.3. Methods

In the case of isotopic data not already published, collagen extraction was performed following Bocherens et al. (1997). The elemental and isotopic measurements were performed at the Geochemical unit of the Geoscience Faculty at the University of Tübingen (Germany), using an elemental analyser NC 2500 connected to a Thermo Quest Delta + XL mass spectrometer. The isotopic ratios are expressed using the "δ" (delta) value as follows: $\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{reference} - 1] \times 1000 \, (\text{‰})$ and $\delta^{15}N = [(^{15}N/^{14}N)_{sample}/(^{15}N/^{14}N)_{reference} - 1] \times 1000 \, (\text{‰})$, with the international reference being V-PDB for δ^{13}C values and atmospheric nitrogen (AIR) for δ^{15}N values. Samples were calibrated to δ^{13}C values of USGS24 ($\delta^{13}C = -16.00\text{‰}$) and to δ^{15}N values of IAEA 305A ($\delta^{15}N = 39.80\text{‰}$). The reproducibility was $\pm 0.1\text{‰}$ for δ^{13}C measurements and $\pm 0.2\text{‰}$ for δ^{15}N measurements, based on multiple analysis of purified collagen from modern bones.

The reliability of the isotopic signatures of the collagen extracts was addressed using their chemical composition. Only extracts with %C, %N, and C/N similar to those of collagen extracted from fresh bone should be considered reliable for isotopic measurements. Several studies have shown that collagen with atomic C/N ratios lower than 2.9 or higher than 3.6 are altered or contaminated, and should be discarded (DeNiro, 1985; Ambrose, 1990). Extracts with $2.9 \leq C/N \leq 3.6$ and %N < 5% may also be problematic (Ambrose, 1990) and were excluded from further palaeobiological interpretations as well.

The reconstruction of the average prey isotopic signatures for predators was performed using the range of isotopic fractionation established by Bocherens and Drucker (2003) between the collagen of prey and predator, i.e. from $+0.8\text{‰}$ to $+1.3\text{‰}$ and from $+3\text{‰}$ to $+5\text{‰}$ for δ^{13}C and δ^{15}N, respectively. This mode of calculation yields a rectangle that can be graphically compared with the actual average isotopic values of coeval potential prey species. When this rectangle falls among the most extreme values of prey species, this means that this prey is obligatory in the diet. In contrast, when the rectangle falls in the centre of the area represented by the different prey species, it means either that the prey located in the middle of the distribution was consumed, or that a mixture of prey with more contrasted isotopic values was consumed.

3. Results and discussion

In the Ardennes and the Swabian Jura during the pre-LGM period, around 40,000 to 24,000 ^{14}C BP, a similar pattern of δ^{13}C and δ^{15}N values was exhibited by ungulates: reindeer presented the least negative δ^{13}C values and rather low δ^{15}N values, while woolly mammoth and woolly rhinoceros exhibited the highest δ^{15}N values of all herbivores and mammoth the most negative δ^{13}C values. Horses were relatively low in δ^{13}C values and their δ^{15}N values were variable. When present, large bovines (*Bos* or *Bison*) had average isotopic values that made them difficult to distinguish from the rest of the ungulates such as horses and rhinoceros, but that were clearly different from those of mammoth and reindeer. The isotopic pattern seen between herbivorous species confirms the results presented previously and is most likely due to different dietary choice among the plants available in the steppe tundra (Bocherens et al., 1997; Bocherens, 2003; Fox-Dobbs et al., 2008).

Table 2

Summary table of the isotopic results for each species in each chronological/spatial unit. The "bone equivalent" isotopic values were calculated by substracting 0.34‰ and 1.08‰ for δ^{13}C and δ^{15}N, respectively (se text and Table S1 in supplementary data).

Species	Region	Age	n	δ^{13}C: min → max (av ± sd)	δ^{15}N: min → max (av ± sd)	Remark
Cave lion *Panthera spelaea*	Ardennes	pre-LGM	6	−20.7 → −18.5(−19.2 ± 0.7)	6.3 → 9.6 (8.2 ± 1.1)	
Leopard *Panthera pardus*	Ardennes	pre-LGM	1	−19.1(−19.4)	11.5 (10.1)	"Bone equivalent" in brackets
Cave hyaena *Crocuta crocuta spelaea*	Ardennes	pre-LGM	12	−20.2 → −19.2(−19.6 ± 0.3)	7.7 → 10.1 (9.2 ± 0.7)	
Wolf *Canis lupus*	Ardennes	pre-LGM	3	−20.4 → −18.8(−19.4 ± 0.7)	6.6 → 7.2 (6.8 ± 0.3)	
Wolferine *Gulo gulo*	Ardennes	pre-LGM	1	−19.6	7.8	
Brown bear *Ursus arctos*	Ardennes	pre-LGM	5	−20.3 → −19.1(−19.8 ± 0.4)	4.0 → 9.0 (6.5 ± 2.1)	
Cave bear *Ursus spelaeus*	Ardennes	pre-LGM	30	−22.3 → −20.8(−21.7 ± 0.5)	2.6 → 6.1 (4.3 ± 1.1)	
Mammoth *Mammuthus primigenius*	Ardennes	pre-LGM	6	−21.6 → −20.7(−21.3 ± 0.4)	6.7 → 9.4 (8.0 ± 0.9)	
Woolly rhinoceros *Coelodonta antiquitatis*	Ardennes	pre-LGM	10	−21.1 → −20.0(−20.6 ± 0.4)	4.3 → 7.5 (5.8 ± 0.9)	
Horse *Equus ferus*	Ardennes	pre-LGM	10	−21.9 → −20.5(−21.2 ± 0.5)	4.8 → 7.0 (5.8 ± 0.8)	
Large bovine *Bos/Bison*	Ardennes	pre-LGM	13	−20.8 → −19.8(−20.3 ± 0.3)	3.8 → 5.7 (4.7 ± 0.6)	
Chamois *Rupicapra rupicapra*	Ardennes	pre-LGM	2(1)	−21.1 → −19.5(−20.3 ± 0.3)	5.1 → *6.3 (5.1)	*Measured on tooth
Reindeer *Rangifer tarandus*	Ardennes	pre-LGM	6	−19.6 → −18.3(−18.7 ± 0.4)	2.6 → 4.5 (3.5 ± 0.6)	
Roe deer *Capreolus capreolus*	Ardennes	pre-LGM	1	−19.6	4.3	
Red deer *Cervus elaphus*	Ardennes	pre-LGM	2(1)	−19.9 → −19.4	2.3 → *4.5 (2.3)	*Measured on tooth
Giant deer *Megaloceros giganteus*	Ardennes	pre-LGM	3(1)	−20.2 → −19.7(−20.0 ± 0.2)	4.0 → *5.9 (4.0)	*Measured on tooth
Cervids except reindeer	Ardennes	pre-LGM	6(3)	−20.2 → −19.4(−19.8 ± 0.3)	2.3 → 4.3 (3.5 ± 0.9)	
Cave lion *Panthera spelaea*	Swabian Jura	pre-LGM	4	−20.7 → −17.5(−18.8 ± 1.2)	7.9 → 10.2 (8.7 ± 0.9)	
Cave hyaena *Crocuta crocuta spelaea*	Swabian Jura	pre-LGM	2	*−20.0 → *−19.7 (−20.2 ± 0.2)	*10.5 → *11.3 (9.8 ± 0.4)	"Bone equivalent" in brackets
Brown bear *Ursus arctos*	Swabian Jura	pre-LGM	5	−19.5 → −19.3(−19.4 ± 0.1)	7.3 → 9.6 (8.4 ± 0.8)	
Cave bear *Ursus spelaeus/U. ingressus*	Swabian Jura	pre-LGM	40	−21.3 → −20.3(−20.9 ± 0.3)	1.1 → 4.8 (3.2 ± 0.9)	
Mammoth *Mammuthus primigenius*	Swabian Jura	pre-LGM	1	−21.4	7.4	
Woolly rhinoceros *Coelodonta antiquitatis*	Swabian Jura	pre-LGM	2	−19.7 → −19.3(−19.5 ± 0.2)	6.1 → 6.8 (6.4 ± 0.4)	
Horse *Equus ferus*	Swabian Jura	pre-LGM	24	−21.8 → −19.8(−20.9 ± 0.5)	3.2 → 9.3 (6.2 ± 1.8)	
Chamois *Rupicapra rupicapra*	Swabian Jura	pre-LGM	2	−20.1 → −19.3(−19.7 ± 0.4)	2.6 → 3.2 (2.9 ± 0.3)	
Reindeer *Rangifer tarandus*	Swabian Jura	pre-LGM	15	−19.5 → −18.6(−19.0 ± 0.3)	1.0 → 4.7 (3.6 ± 1.0)	
Cave lion *Panthera spelaea*	Jura	post-LGM	3	−18.8 → *−18.4(−18.7 ± 0.1)	5.4 → *7.0 (5.6 ± 0.2)	"Bone equivalent" in brackets
Wolf *Canis lupus*	Jura	post-LGM	3	−20.3 → −19.0(−19.5 ± 0.6)	5.7 → 6.4 (6.0 ± 0.3)	
Wolferine *Gulo gulo*	Jura	post-LGM	2	−20.2 → −20.1(−20.2 ± 0.1)	5.2 → 7.1 (6.2 ± 1.0)	
Fox *Vulpes vulpes*	Jura	post-LGM	1	−19.6	4.7	
Lynx *Lynx lynx*	Jura	post-LGM	1	−19.4	4.2	
Brown bear *Ursus arctos*	Jura	post-LGM	4	−20.6 → −18.7(−19.7 ± 0.7)	2.8 → 4.7 (3.7 ± 0.7)	
Mammoth *Mammuthus primigenius*	Jura	post-LGM	2	−21.3 → −20.5(−20.9 ± 0.4)	5.0 → 6.4 (5.7 ± 0.7)	
Woolly rhinoceros *Coelodonta antiquitatis*	Jura	post-LGM	2	−20.3 → −19.9(−20.1 ± 0.2)	2.1 → 5.3 (3.7 ± 1.6)	
Horse *Equus ferus*	Jura	post-LGM	10	−21.2 → −19.8(−20.4 ± 0.4)	0.6 → 4.5 (1.8 ± 1.0)	
Large bovine *Bos/Bison*	Jura	post-LGM	3	−20.3 → −19.8(−20.0 ± 0.2)	2.2 → 2.4 (2.3 ± 0.1)	
Reindeer *Rangifer tarandus*	Jura	post-LGM	44	−20.3 → −19.1(−19.7 ± 0.3)	0.1 → 3.9 (2.2 ± 0.7)	
Red deer *Cervus elaphus*	Jura	post-LGM	5	−20.8 → −19.9(−20.4 ± 0.3)	0.8 → 2.4 (1.9 ± 0.6)	
Elk *Alces alces*	Jura	post-LGM	2	−20.2 → −19.8(−20.0 ± 0.2)	2.9 → 3.0 (3.0 ± 0.1)	
Hare *Lepus timidus*	Jura	post-LGM	17	−21.4 → −19.7(−20.4 ± 0.4)	−0.3 → 2.3(0.9 ± 0.6)	
Ground squirrel *Spermophilus rufescens*	Jura	post-LGM	4	−21.0 → −20.3(−20.7 ± 0.2)	1.7 → 2.5 (2.1 ± 0.3)	
Cave lion *Panthera spelaea*	Paris basin	post-LGM	1	−18.8	6.6	
Wolf *Canis lupus*	Paris basin	post-LGM	2	−20.6 → −19.9(−20.3 ± 0.4)	5.0 → 7.3 (6.2 ± 1.2)	
Horse *Equus ferus*	Paris basin	post-LGM	28	−21.7 → −20.3(−20.9 ± 0.4)	1.8 → 5.4 (3.0 ± 0.8)	
Reindeer *Rangifer tarandus*	Paris basin	post-LGM	21	−20.3 → −19.3(−19.8 ± 0.3)	1.6 → 3.9 (2.8 ± 0.5)	
Red deer *Cervus elaphus*	Paris basin	post-LGM	6	−20.5 → −20.1(−20.3 ± 0.2)	2.8 → 4.0 (2.8 ± 0.5)	
Boar *Sus scrofa*	Paris basin	post-LGM	1	−20.3	4.9	
Hare *Lepus timidus*	Paris basin	post-LGM	1	−21.3	0.9	

*Means measured on tooth.

This clear pattern of isotopic signatures between potential prey allows establishment of prey preferences in cave lions and coeval predators. Predators reflect, with a stable isotopic fractionation, the carbon and nitrogen isotopic signatures of their average prey (Bocherens and Drucker, 2003; Fox-Dobbs et al., 2007).

In the Ardennes, cave lions exhibited the most widespread isotopic values of all analyzed carnivores. The range of δ^{13}C values was almost 2‰ and the range of δ^{15}N values more than 3‰ (Table 2). Hyenas exhibited a smaller range of δ^{13}C and δ^{15}N values although twice as many samples were analyzed, leading to a much smaller

standard-deviation than for cave lions (Table 2). Some of this clustering of data may be due to the scavenging of prey killed by other predators by hyenas, but since cave hyenas were more active predators than modern ones (Baryshnikov, 1999), this should reflect mainly a similar prey choice for the analyzed specimens. Most of the predator species exhibited individual δ^{13}C and δ^{15}N values that overlapped with the area covered by the isotopic values of hyenas, in particular leopard, wolverine, and the brown bears with the highest δ^{15}N values (Fig. 2). In contrast, lions and wolves seemed to scatter around the area occupied by hyenas and other carnivorous species,
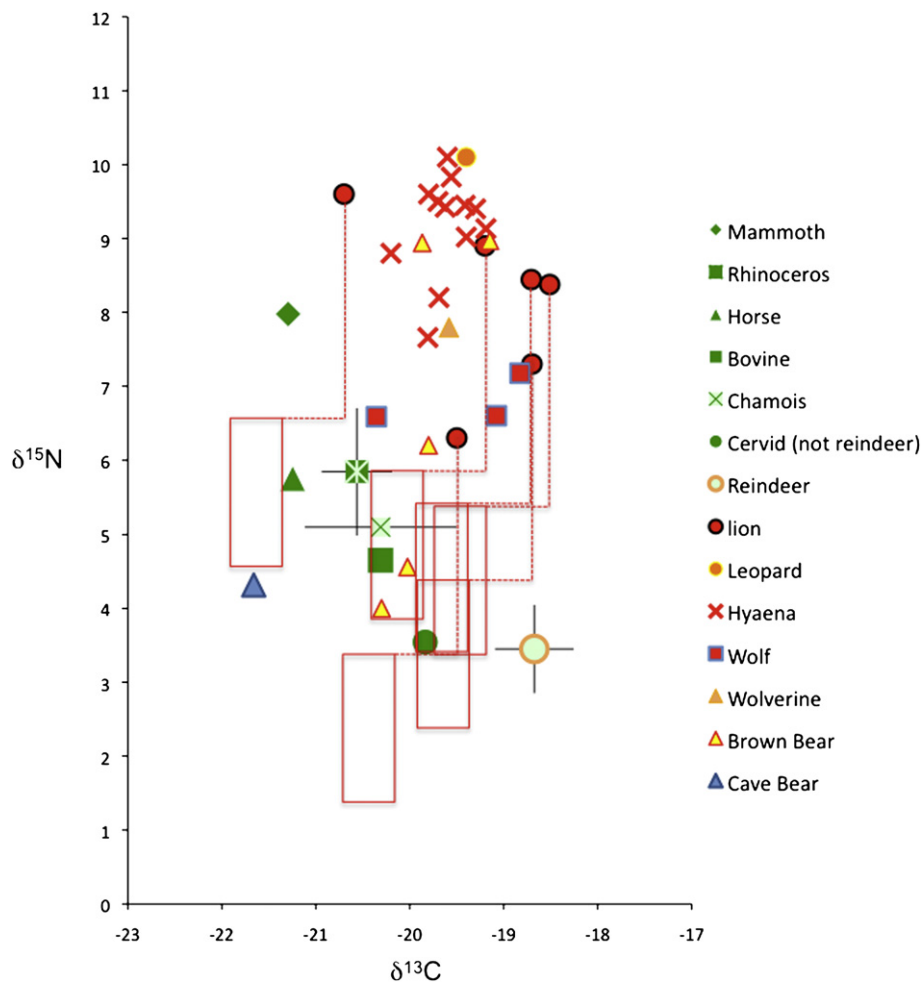
Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ values of collagen from herbivores (average $\pm$ 1 standard-deviation) and carnivores (individuals values) in Ardennes during pre-LGM times ($\sim 28-40,000$ [14]C BP). The rectangles stand for the range of average $\delta^{13}C$ and $\delta^{15}N$ values of prey bone collagen for each analyzed lion.

with either less negative or more negative $\delta^{13}C$ values or less positive $\delta^{15}N$ values (Fig. 2). Only one lion specimen fell in the area of the graph occupied by hyenas and brown bears. This specimen was directly radiocarbon dated and is one of the youngest specimens in Belgium, with an age of 24,470 $\pm$ 210 ^{14}C BP. As the youngest dated cave hyenas are 27,000 years old in Belgium (Germonpré, 1997), this would mean that this cave lion individual lived after the extirpation of cave hyenas and that cave lions could shift their diet to include prey that were previously mostly consumed by hyenas only after this predator was absent. This supports further the hypothesis of a competitive displacement of cave lions by cave hyenas. In combination with evidence for fights between cave hyenas and cave lions and that cave hyenas sometimes consumed carcasses of lions during the Late Pleistocene (e.g., Diedrich, 2008, 2009a), this indicates that lions were at a disadvantage in the competition with hyenas. This could be linked to the solitary habits of cave lions in contrast with the clan behaviour of cave hyenas. This is in contrast with modern spotted hyenas and lions in Africa, where both predator species exhibit a large overlap in the prey choice (Hayward, 2006). Modern lions, even if they are smaller than the Pleistocene ones, may resist better the competition with spotted hyenas thanks to their collective behaviour. In contrast, carnivorous brown bears could sustain dietary competition with hyenas using overlapping prey items as Pleistocene brown bears were even larger than modern ones (e.g., Baryshnikov and Boeskorov, 2004) and therefore much larger than

hyenas, while leopard could use food caching to protect their prey from competing hyenas, as they do nowadays for instance when they are in competition with tigers (e.g., Seidensticker, 1976).

In agreement with the scattering of $\delta^{13}C$ and $\delta^{15}N$ values of lion bone collagen, the reconstructed range of isotopic values of their prey collagen was also scattered, falling either in between the average isotopic values of reindeer and other cervids, overlapping the average isotopic values of large bovines and chamois, being lower than those of any of the analyzed large herbivores, or overlapping the standard-deviation of horse and cave bears (Fig. 2). When the reconstructed isotopic ranges fell close to the extreme ranges measured for potential prey, this could be interpreted as the fact that the prey with the most extreme isotopic values was compulsory in the diet. This was the case for reindeer for the lions with the least negative $\delta^{13}C$ values, and for cave bears and horse for the lions with the most negative $\delta^{13}C$ values. The other cases could have incorporated various amounts of different prey, many different mixtures could end up in the same isotopic range of values. The case of the lion with seemingly low $\delta^{15}N$ values could mean that some prey species with unusually low $\delta^{15}N$ values have been missed. Small game species such as rodents and lagomorphs could be this missing prey, as they usually exhibit lower $\delta^{15}N$ than coeval ungulates, as shown for late-glacial sites in South-western France (Drucker, 2001) and for Kesslerloch and Le Closeau (Table 2). However, such a prey choice would be very different from the

feeding habits of modern lions, as they tend to prefer prey species at least as heavy as themselves, or even heavier when they hunt collectively (Hayward and Kerley, 2005). Nevertheless, lions from Cameroon were shown to include some rodents in their diet, although in proportions lower than 10% (Breuer, 2005). Another possibility to explain this low $\delta^{15}N$ value is that this lion specimen could be younger than thought and of post-LGM age, as its $\delta^{15}N$ value was similar to those measured for post-LGM lions in the Jura and the Paris Basin (see below), and since some bones from Goyet cave were directly dated to this period (e.g., Germonpré et al., 2009; Stevens et al., 2009). Further radiocarbon dating will help to solve this uncertainty.

In the pre-LGM Swabian Jura, the isotopic values of lions were also scattered, especially their $\delta^{13}C$ values ranging from $-20.7‰$ to $-17.5‰$ (average $= -18.8 \pm 1.2‰$, Table 2, Fig. 3). This is in contrast with the $\delta^{13}C$ values of hyenas and brown bears, which have a range of $0.3-0.2‰$, respectively (Table 2, Fig. 3). As in the Ardennes, the isotopic values of the lion seemed to fall outside the range of those of other predators such as hyenas and brown bears.

When the average isotopic values of the possible preys were reconstructed, two lions fell on or close to the isotopic values of reindeer, one fell on the isotopic value of woolly rhinoceros, and the last one in an area close to the range exhibited by horses and cave bears, but with slightly lower $\delta^{13}C$ and higher $\delta^{15}N$ than the average value for adult cave bears (Fig. 3). Predation of juvenile black rhinoceros by modern lions in Africa has been reported (e.g., Elliot, 1987; Brain et al., 1999; Plotz and Linklater, 2009), and therefore such a prey preference seems possible for cave lions. In the case of the cave lion with an average prey falling close to the adult cave bear value, young cave bears typically exhibit more negative $\delta^{13}C$ values and more positive $\delta^{15}N$ values than their adult counterparts (e.g., Bocherens et al., 1994; Nelson et al., 1998; Bocherens, 2004; Pérez-Rama et al., 2011), the consumption of such a prey in addition to horse could explain the observed pattern for this lion.

The fauna from the post-LGM exhibited a similar pattern between the Jura and the Paris Basin, with reindeer having the least negative $\delta^{13}C$ values and horse having the most negative one (Table 2, Figs. 4 and 5). When present, mammoth exhibited the
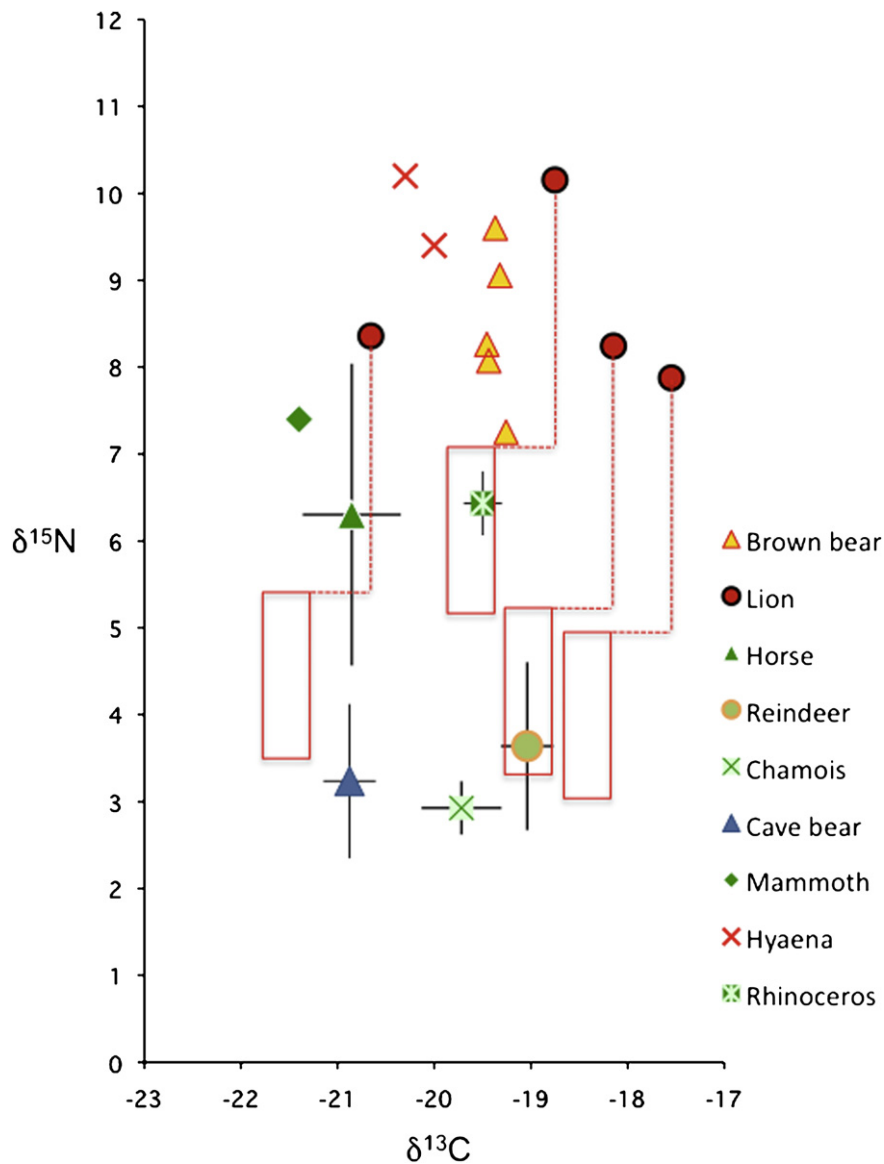

Fig. 3. $\delta^{13}C$ and $\delta^{15}N$ values of collagen from herbivores (average $\pm$ 1 standard-deviation) and carnivores (individuals values) in the Swabian Jura during pre-LGM times ($\sim 28-40,000$ 14C BP). The rectangles stand for the range of average $\delta^{13}C$ and $\delta^{15}N$ values of prey bone collagen for each analyzed lion.

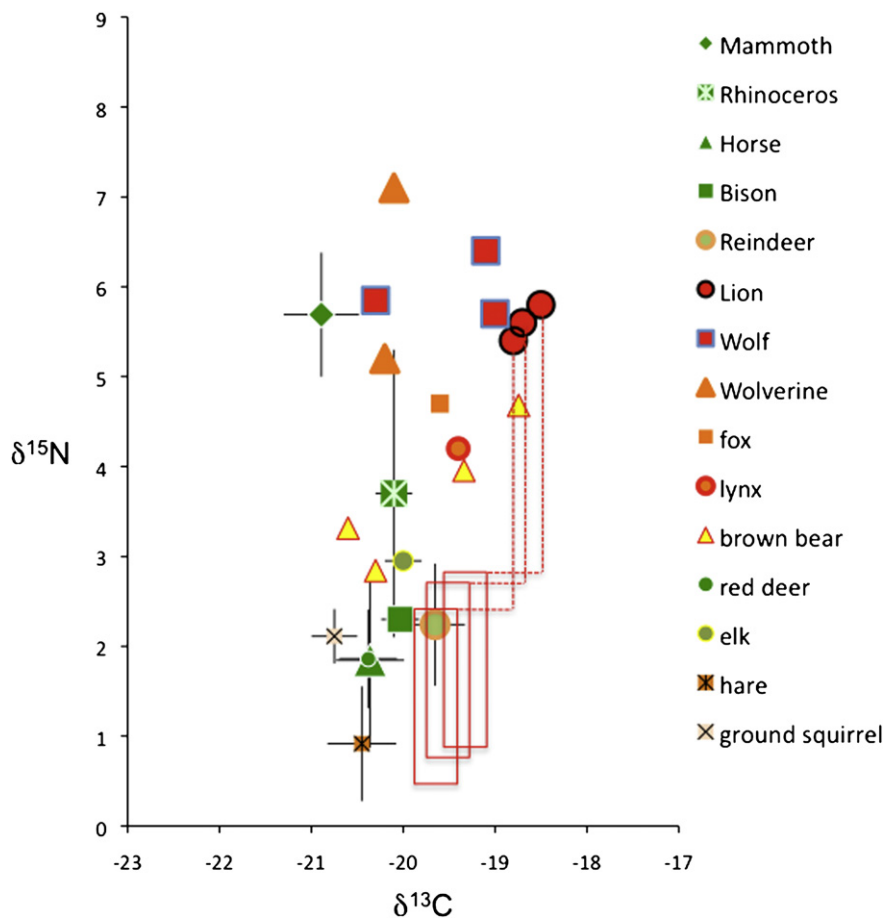**Fig. 4.** δ^{13}C and δ^{15}N values of collagen from herbivores (average $\pm$ 1 standard-deviation) and carnivores (individuals values) in the Jura northern Alpine foreland during post-LGM times ($\sim$14–12,000 ^{14}C BP). The rectangles stand for the range of average δ^{13}C and δ^{15}N values of prey bone collagen for each analyzed lion.

highest δ^{15}N values of all herbivores (Fig. 4). For each species present before and after the LGM, the average δ^{15}N values dropped by 2–3‰ (Table 2), a trend already noted by previous studies (e.g., Stevens and Hedges, 2004; Richards and Hedges, 2003). Among the predators, lions systematically exhibited the highest δ^{13}C values in comparison with wolves and wolverines, and the reconstructed average isotopic value of their prey fell on or close to the average isotopic value of reindeer. Interestingly, post-LGM brown bears exhibit δ^{15}N values similar to those of herbivores and differ from pre-LGM brown bears that were more strongly carnivorous.

The results of the present work strongly support the hypothesis that cave lions had an individualistic predatory behaviour. The scattering of their isotopic values suggests that different individuals were consuming prey with contrasting isotopic signature on a regular basis. This is in agreement with previous palaeobiological reconstructions based on the poor development of mane in male cave lions as documented by prehistoric parietal art that would indicate solitary hunting behaviour or hunting by breeding pairs of lion and lioness (Guthrie, 1990), although the relationship between mane development and social behaviour of lion is contested by others (e.g., Yamaguchi et al., 2004). In addition, the prey choice made by cave lions seem to be in favour of prey rarely consumed by other coeval predators, especially cave hyenas. When cave hyenas were present in the environment of cave lions in Ardennes as well as in the Swabian Jura, cave lions seem to have relied heavily either on reindeer or on cave bear cubs, with strong individual preferences. At Goyet, the remains of first spring bear cubs are the ones that were especially damaged by carnivores. It is possible that the

carnivores, and this study strongly suggests that they were cave lions, took advantage of the fact that the bear mothers left their young alone for a while, just as recent brown bears do (e.g., Couturier, 1954), when they were looking for food at the end of the winter rest (Germonpré and Sablin, 2001). The fact that the only cave lion from the Ardennes during the pre-LGM period that had δ^{13}C and δ^{15}N values overlapping those of the cave hyenas was actually post-dating the extirpation of cave hyenas further supports this view.

The possibility that some cave lions consumed high proportion of cave bears, especially young ones, is supported by the present study. Predation by cave lion has been suggested previously as a mortality cause of cave bear yearlings (e.g., Weinstock, 1999) and even the habit of cave bears to hibernated deep into cave system has been suggested to be a defence against predation by cave lions, among others (Diedrich, 2009b). The fact that the bone collagen of some individuals of cave lions was strongly influenced by the isotopic signature of young cave bears and that this tissue records an average of the food consumed during several years suggests that consumption of young cave bear may not have been accidental but was rather performed on a regular basis by some cave lions. Among modern lions, some individual dietary specialization on unusual prey has been documented, for instance the so-called "man-eaters from Tsavo", and were found especially in case of prey scarcity and in individuals suffering from craniodental infirmities (Yeakel et al., 2009).

In contrast, the hypothesis that cave lions hunted juvenile megaherbivores such as mammoth calves is not supported by the
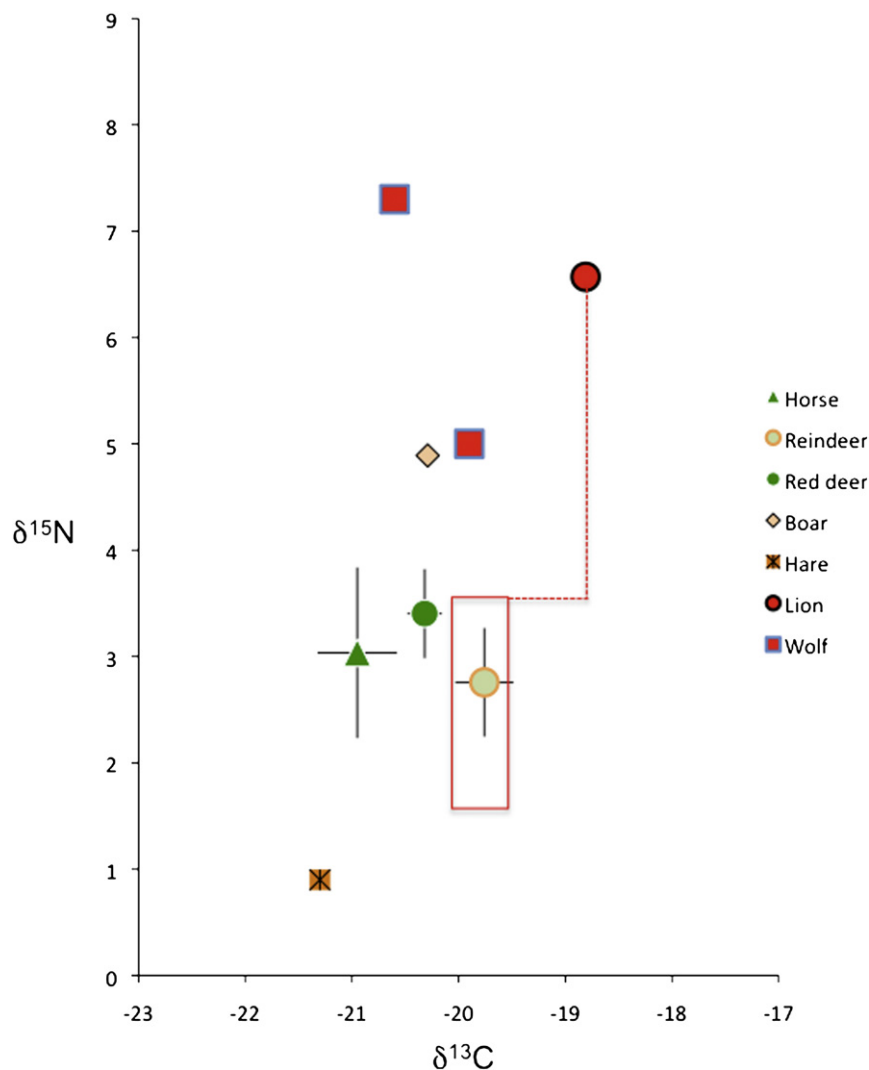
Fig. 5. $\delta^{13}C$ and $\delta^{15}N$ values of collagen from herbivores (average $\pm$ 1 standard-deviation) and carnivores (individuals values) in the Paris basin during post-LGM times ($\sim$ 14−12,000 ^{14}C BP). The rectangles stand for the range of average $\delta^{13}C$ and $\delta^{15}N$ values of prey bone collagen for the analyzed lion.

present study. Adult mammoths exhibit very high $\delta^{15}N$ and low $\delta^{13}C$ values in comparison with coeval herbivores (Bocherens, 2003, Figs. 2−4 in the present work), and young individuals suckling their mother's milk had even higher $\delta^{15}N$ values (Rountrey et al., 2007). One isotopic measurement made on a mammoth deciduous tooth from Spy (Belgium) was very high in $\delta^{15}N$, higher than the $\delta^{15}N$ values of coeval adult mammoths and even higher than the $\delta^{15}N$ values of coeval predators including cave lions (Bocherens et al., in press). Such an isotopic difference precludes young mammoths to be a regular prey of any of the analyzed cave lions. Although predation on some juvenile weaned elephants has been reported for some modern lion populations, for instance in the Savuti area of the Chobe National Park (Bostwana) (Power and Compion, 2009), such a predatory behavior needed coordinated hunting from large prides including up to 30 individuals. Collective hunting behavior is not supported for cave lions by the present work, therefore limiting their access to very large prey such as mammoths.

The isotopic signatures of cave lions from the post-LGM period do not overlap with those of contemporary wolves, possibly indicating competitive exclusion of the solitary predator (cave lion) by smaller but gregarious ones (wolf). In contrast with pre-LGM context, brown bear is not any more in dietary competition with cave lions as the late-glacial brown bears have shifted their diet to

a more vegetarian one, maybe in reaction to the extinction of the vegetarian cave bears that vacated an ecological niche for them (Döppes et al., 2008). Other factors could have changed the rules of competition between predators before and after the LGM in western Europe, such as the abundance of available prey and the disappearance of some of the large predators, such as hyena and leopard.

The isotopic data of cave lions post-dating the Last Glacial Maximum seem to be less variable than those of cave lions pre-dating the Last Glacial Maximum and point to the obligatory consumption of reindeer. This apparent restriction in prey choice after the LGM may be driven by a reduction of genetic diversity, or purely by ecological changes. As there is no ancient DNA data on the samples used in the present isotopic study, the first possibility cannot be directly tested at present. Barnett et al. (2009) documented a decrease of the genetic diversity of cave lion sometime around 45,000 years ago, a decline that was attributed to parallel demographic decline of bison. However, this scenario may have to be changed as the present study suggests that bison was not the preferred prey of cave lions in North-western Europe. In other regions, few other isotopic studies dealing with cave lions included coeval potential prey. In Eastern Europe, a Gravettian site in the Czech Republic, Milovice, dated to around 22,000 years ago, yielded

cave lions that exhibited $\delta^{13}C$ and $\delta^{15}N$ values indicating high consumption of reindeer (Péan, 2001). In eastern Beringia, a territory corresponding to modern Alaska and Yukon, cave lions seem not to have relied heavily on reindeer as this prey seems to have preferentially consumed by giant short-faced bears (Fox-Dobbs et al., 2008). It seems therefore that further isotopic investigations of cave lions through time and across their distribution range will greatly improve understanding of the carnivore guild during the late Pleistocene and the extinction episode of the final Pleistocene.

It would be interesting to investigate whether there was a coincidence between genetic impoverishment and reduction of the dietary breadth that would support a scenario of decreasing flexibility for cave lion prior to its extinction. The focus of the last western European cave lions on reindeer was possibly driven by the relative abundance of this prey species during the Last Glacial Maximum (Delpech, 1999), and could explain partially why this large predator survived this climatic episode while others such as cave hyena failed to do so. However, in the context of the late-glacial warming and the final extirpation of reindeer in the investigated area around 12,000 years ago (Bridault et al., 2000), this focused predation on reindeer was certainly a disadvantage for long-term survival of cave lions. Since prehistoric human populations expanded northward at the same time and could exploit other dietary resources in addition to reindeer, such a specialization on reindeer was certainly detrimental for cave lions. A striking example is the case of Le Closeau site in the Paris Basin, where the fauna hunted by prehistoric humans include mainly red deer and horse but no reindeer, whereas the isotopic signature of the cave lion found in the same site points to a very high proportion of reindeer in the diet.

4. Conclusion

The carbon and nitrogen isotopic signatures of bone collagen from the pre-LGM sites pointed to a large scatter of the individual data reflecting individualistic predatory behaviour with long lasting prey preferences, with some individuals strongly oriented on reindeer and others possibly on juvenile cave bears. In the post-LGM sites, the isotopic data point to a preference on reindeer for cave lion. It appears that cave lion was the most reindeer oriented large predator during the late Pleistocene in North-western Europe, and that this prey preference was still strongly established until the extirpation of the species, which seems therefore to coincide chronologically with the extirpation of reindeer notably in the region.

Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.quaint.2011.02.023.

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