

13. ISOTOPIC INSIGHTS ON ECOLOGICAL INTERACTIONS BETWEEN HUMANS AND WOOLLY MAMMOTHS DURING THE MIDDLE AND UPPER PALAEOLITHIC IN EUROPE

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ABSTRACT

Carbon and nitrogen isotopic composition of bone collagen in woolly mammoths, coeval herbivores and predators, as well as hominins, allow researchers to quantify the proportion of meat consumed by late Neanderthals and early modern humans in Europe. The proportions of consumed mammoth meat were found to be very high for late Neanderthals in sites from western France and Belgium between 45 and 40 ka, and for early modern humans from Belgium, Czech Republic, Crimea and western Russia, between 40 and 30 ka. A possible contribution of freshwater resources was excluded in Belgium and Crimea using a novel approach based on single compound amino acid nitrogen isotopes and confirmed that mammoth consumption was the source of the high nitrogen isotopic ratio of ancient hominins in these sites. The impact of

mammoth hunting on the Late Pleistocene ecosystems could be detected by a shift of isotopic values of horses onto those found for mammoth, suggesting that horses could use part of the ecological niche of mammoth probably due to a decrease of the proboscidean population. Moreover, isotopic tracking of predator diet suggests that the mammoth carcasses left by humans were also exploited by scavengers, such as fox, wolf and brown bear. Therefore, stable isotopic tracking is a very useful approach to decipher the trophic interaction between hominins and mammoths and their possible ecological consequences.

13.1 INTRODUCTION

The discovery that prehistoric humans and mammoths lived at the same time was a shock for early



scholars during the 19th century (Cohen, 1994). If artifacts made of mammoth bones or ivory could have been made using raw material from long dead ones, the engravings of mammoths with anatomical details clearly demonstrated the contemporaneity of both taxa as this could be done only by observing living mammoths. However, the coexistence of prehistoric humans and mammoths does not tell us how they interacted ecologically.

Extant elephants, the closest relatives of woolly mammoths and with a similar size, are immune from predatory pressure, except from human hunters. Today the hunting of elephants with guns takes dramatic proportions to the point of threatening the species to become extinct (e.g., Douglas-Hamilton, 1987; Thouless et al., 2016). However, recent hunter-gatherer without modern weapons can also kill elephants (see review in Agam and Barkai 2018; Ichikawa, this volume; Lewis, this volume). Did prehistoric people also do it? Archaeological evidence demonstrates that ancient elephants and mammoths were being butchered already hundreds of thousand years ago, implying that prehistoric people must have consumed elephant and mammoth meat for a long time. Active hunting is more difficult to demonstrate, but some convincing evidence has been described (e.g., Nikolskiy and Pitulko, 2013; Metcalfe, 2017; Sinitsyn et al., 2019; Wojtal et al., 2019). Even in such cases, the amount of mammoth meat consumption by humans is very difficult to evaluate. Still, active hunting is a crucial topic, because the intensity of mammoth exploitation has an impact on the demography and ecology of the hunted populations, or even the whole species, and could have contributed to their extinction.

In this contribution, we review how using stable isotope palaeoecological tracking can contribute to quantifying mammoth meat consumption by late Neanderthals and early Upper Palaeolithic modern humans in Europe. Moreover, we evaluate the possible ecological impact of mammoth hunting by humans.

13.2 PRINCIPLE OF ISOTOPIC TRACKING OF PREY CONSUMPTION AND APPLICATION TO MAMMOTH AND OTHER EXTINCT PROBOSCIDEANS

Animals obtain the carbon and nitrogen atoms needed for their metabolism from their food. These two major chemical elements of life can be found under two forms with slightly different atomic weights, called isotopes. The relative abundance of the isotopes of a given element varies slightly in different food categories, due to small differences in the speed of chemical reaction and the strength of chemical bonds between the isotopes of a given element. The differences between isotopic abundances in natural products are extremely small and therefore, in order to be measured accurately, they need to be compared to those of an international standard, under the conventional notation delta as follows:

$$\delta^{13}\text{C} = [((^{13}\text{C}/^{12}\text{C}_{\text{sample}})/(^{13}\text{C}/^{12}\text{C}_{\text{standard}})) - 1] \times 1000,$$

where standard is V-PDB;

$$\delta^{15}\text{N} = [((^{15}\text{N}/^{14}\text{N}_{\text{sample}})/(^{15}\text{N}/^{14}\text{N}_{\text{standard}})) - 1] \times 1000, \text{ where standard is AIR.}$$

Typically, the tissues of an animal are enriched in the heavy isotope of carbon and nitrogen, and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are higher than those of their average food. As we are dealing with meat eaters and comparing the bone collagen of predators and their potential prey, we will consider only the differences between collagen isotopic abundances of the prey and of the predator in the rest of this chapter. Using the results of feeding experiments on captive animals and measurements performed on animals from field studies, the difference between the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ values of a predator compared to those of its average prey is $+1.1 \pm 0.2 \text{ ‰}$ and $+3.8 \pm 1.1 \text{ ‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Bocherens and Drucker, 2003; Drucker et al., 2017; Krajcarz et al., 2018). In large mammals, bone collagen averages the isotopic composition of several years of life of an individual (e.g., Hedges et al., 2007). Therefore, predators feeding preferentially on prey with dis-

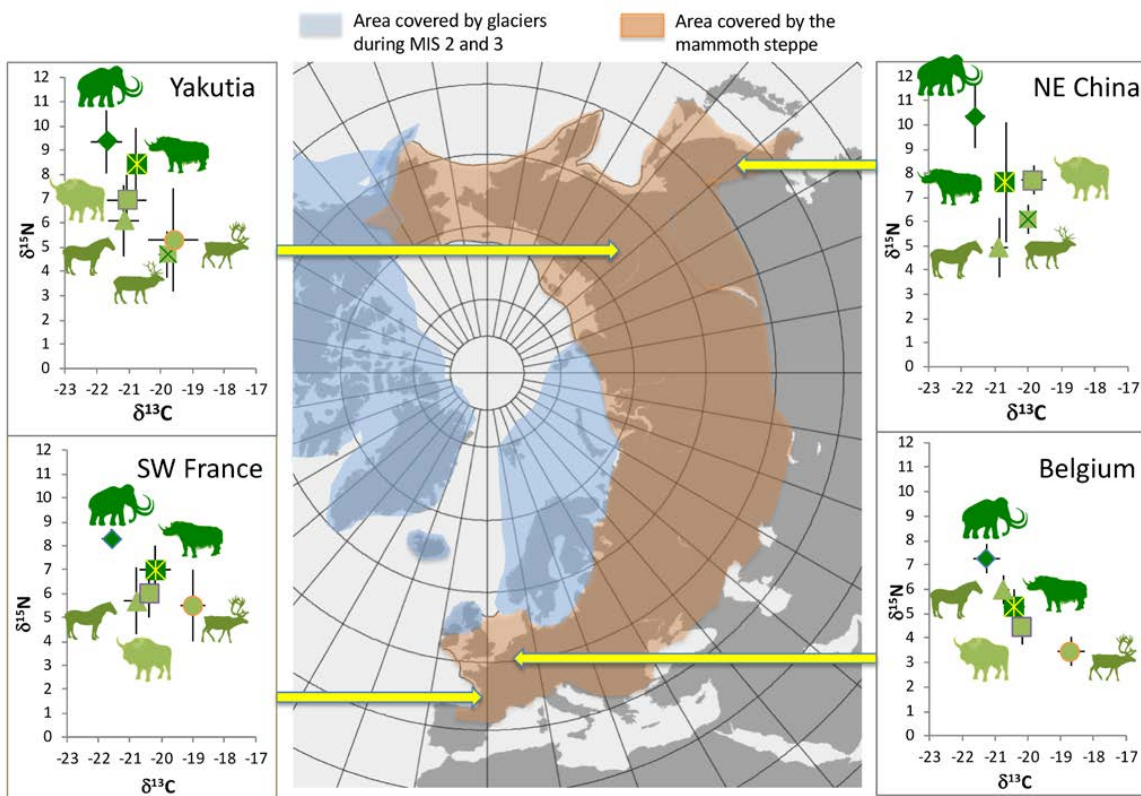


Figure 13.1: Examples of carbon and nitrogen isotopic composition of the main large herbivores coexisting with mammoths in Eurasia. Data for NE China are from Ma et al. (2017); for Yakutia from Bocherens et al. (1996), Iacumin et al. (2010), Szpak et al. (2010), Kirillova et al. (2015), Arppe et al. (2019); for Belgium from Bocherens et al. (2011); for SW France from Bocherens et al. (2005). Map modified from Jürgensen et al. (2017).

tinct $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to their specific habitat and diet composition will also exhibit isotopic differences, and it will be possible to evaluate the relative contribution of different potential prey in their average diet in modern (e.g., Yeakel et al. 2009, 2013; Adams et al., 2010; Dalerum et al., 2012) and ancient contexts (e.g., Bocherens et al., 2005; Bocherens, 2015). With the use of stable isotope mixing models it is possible to evaluate quantitatively the proportions of different categories of consumed proteins (i.e., prey), if they present different isotopic abundances. In contexts with a reasonably complete knowledge of the available prey and their isotopic values, using such approaches yields results that allow the comparison of different predators with human hunter-gatherers, and prehistoric sites of different geographic and chronological settings.

In the context of Late Pleistocene glacial terres-

trial ecosystems in Eurasia, the isotopic signatures of mammoth bone are distinctive compared to those of other large herbivores and potential prey of prehistoric humans (Bocherens et al., 1996; Bocherens, 2003; 2015). Mammoths exhibit $\delta^{13}\text{C}$ values in the low range of coeval herbivores and $\delta^{15}\text{N}$ values significantly higher than all other large herbivores (review in Bocherens, 2015), and also than small herbivores (Baumann et al., 2020). This pattern is consistent all over the geographical distribution of the woolly mammoth, from Western Europe to eastern Siberia, northeastern China and northwestern North America (e.g., Bocherens et al., 1996, 1997; Fox-Dobbs et al., 2008; Bocherens, 2015; Kirillova et al., 2015; Ma et al., 2017) (Fig. 13.1). It is also consistent in time over the period from the early Late Pleistocene until the Holocene in Wrangel Island (Arppe et al., 2019). This isotopic difference is most probably due to the consumption

of dry mature grass by mammoths, because this kind of plant food has higher $\delta^{15}\text{N}$ values than other grasses and browse consumed by the other herbivores (Bocherens, 2003; Bocherens et al., 2015). In few cases, some horses can show isotopic values overlapping with those of mammoths (Drucker et al., 2015; Wißing et al., 2019), but this is a rare occurrence and the ecological possible meaning of this pattern will be discussed later in this paper. When significant ecological disturbance took place, as in the case of the Late glacial mammoths from the Russian-Ukrainian Plains (Drucker et al., 2018) and of the Holocene mammoths from Saint-Paul Island (Graham et al., 2016), the isotopic values of the mammoths diverged from the usual pattern and can be used as a tracer of breaking down of the optimal mammoth ecosystem.

Most isotopic results on collagen from Pleistocene proboscideans are from woolly mammoth, due to its younger geological age than other extinct proboscideans and the favorable cold climatic conditions for organic matter preservation. A notable exception is the site of Schöningen in northern Germany, where straight-tusked elephants (*Palaeoloxodon antiquus*) that lived before 300,000 years under temperate climatic conditions, were preserved in organic rich sediment and yielded well-preserved collagen in their bones. They also exhibited the distinct nitrogen isotopic signature of woolly mammoths compared to coeval large herbivores (Kuitens et al., 2015), allowing potentially the quantification of the consumption of straight-tusked elephant meat by predators, here large felids (*Panthera*, *Homotherium*), as no human remains have been found to date in this Middle Pleistocene site.

13.3 PROPORTION OF MAMMOTH MEAT CONSUMPTION BY PREHISTORIC HUNTER-GATHERERS

Several recent publications yielded isotopic values on prehistoric hunter-gatherers and associated fauna that allow to evaluate the proportions of

mammoth meat consumed in sites following an increasing chronological depth. We will first consider Central European sites, where woolly mammoth (*Mammuthus primigenius*) remains are very abundant (the Moravian sites of Předmostí, Dolní Věstonice II and Pavlov I), then older Upper Palaeolithic sites in Eastern Europe (Buran-Kaya III in Crimea and Kostenki in Russia), and finally sites with late Neanderthals in Western Europe (Saint-Césaire in France, as well as Goyet and Spy in Belgium).

13.3.1. CENTRAL EUROPEAN UPPER PALAEOLITHIC

The Gravettian sites from the Lower Austrian-Moravian-South Polish corridor have yielded huge amounts of mammoth bones associated with abundant archaeological material, including human skeletal remains with clear indication of mammoth hunting (e.g., Musil, 2010; Wilczynski et al., 2019). In this context, an isotopic investigation of the mammal fauna, including one human bone from Předmostí (Bocherens et al., 2015), combined with the newly published isotopic results on Gravettian humans from Dolní Věstonice II and Pavlov I (Fewlass et al., 2019), clearly demonstrated that all the analyzed humans consumed high amounts of mammoth meat, accounting for ~60% of the protein source in the average human diet (Bocherens et al., 2015) (Figs. 13.2, 13.3). This is in great contrast with the prey proportions deduced from the isotopic results obtained on animal predators, with only wolves showing a high mammoth consumption similar to humans, and some scavengers, such as brown bears, wolverines and polar foxes also exhibiting higher than usual mammoth consumption in this site (Bocherens et al., 2015).

Such a high consumption of mammoth meat is not surprising, in view of the huge amount of mammoth bones accumulated and the evidence for mammoth hunting found in these sites, taking place in all seasons (Musil, 2010; Wojtal et al.,

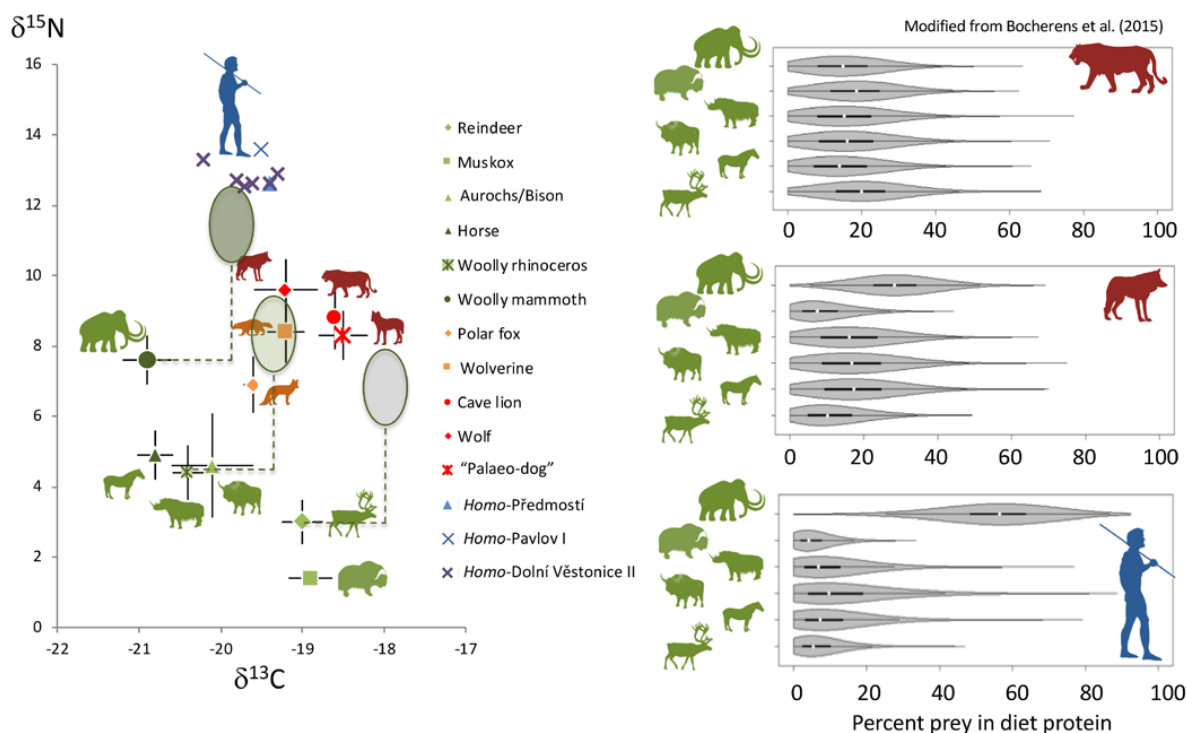


Figure 13.2: On the left, scatter-plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen from herbivores, predators and humans in the Moravian plain sites Předmostí, Dolní Věstonice II and Pavlov I (data from Bocherens et al., 2015 and Fewlass et al., 2019). The ellipses show the projected range of isotopic values for predators of the main prey species. On the right, results of the Bayesian mixing model SIAR showing the proportions of different prey for cave lion, wolf and humans from Předmostí (modified from Bocherens et al., 2015).

2016; Wilczyński et al., 2019; Germonpré et al., this volume). The fact that some scavengers had access to significant amounts of mammoth meat suggests that the carcasses provided not only food resources to humans, but also subsidies for some predators.

13.3.2. EASTERN EUROPEAN EARLY UPPER PALAEOLITHIC

CRIMEA | In the early Upper Palaeolithic site of Buran-Kaya III, an isotopic investigation of humans and coeval fauna also indicated that mammoth was consumed in high proportion by humans (Fig. 13.3; Drucker et al., 2017). This result is more surprising than in central Europe since no mammoth bone was found at the Crimean site. This could be due to the fact that this site corresponds to a hunting station of saiga antelopes

during their seasonal migration, therefore representing a small chronological snapshot on human activity that does not reflect the average subsistence strategy of the studied individuals (Crépin et al., 2014). This case study demonstrated how important are the isotopic investigations for reconstructing the contribution of different prey species, especially proboscideans, to prehistoric human diet, in particular when the faunal assemblages correspond to a specialized function of a site. However, these faunal remains provide material to establish the isotopic baselines needed for the interpretation of the isotopic data measured on human specimens.

KOSTENKI | A series of sites dated to the early Upper Palaeolithic (42–30 ka) in western Russia are also dominated by mammoth remains and yielded additionally human bones (Hoffecker et al., 2010; Bessudnov, 2019; Germonpré et al., this volume). Isotopic values of human, wolves and horses have

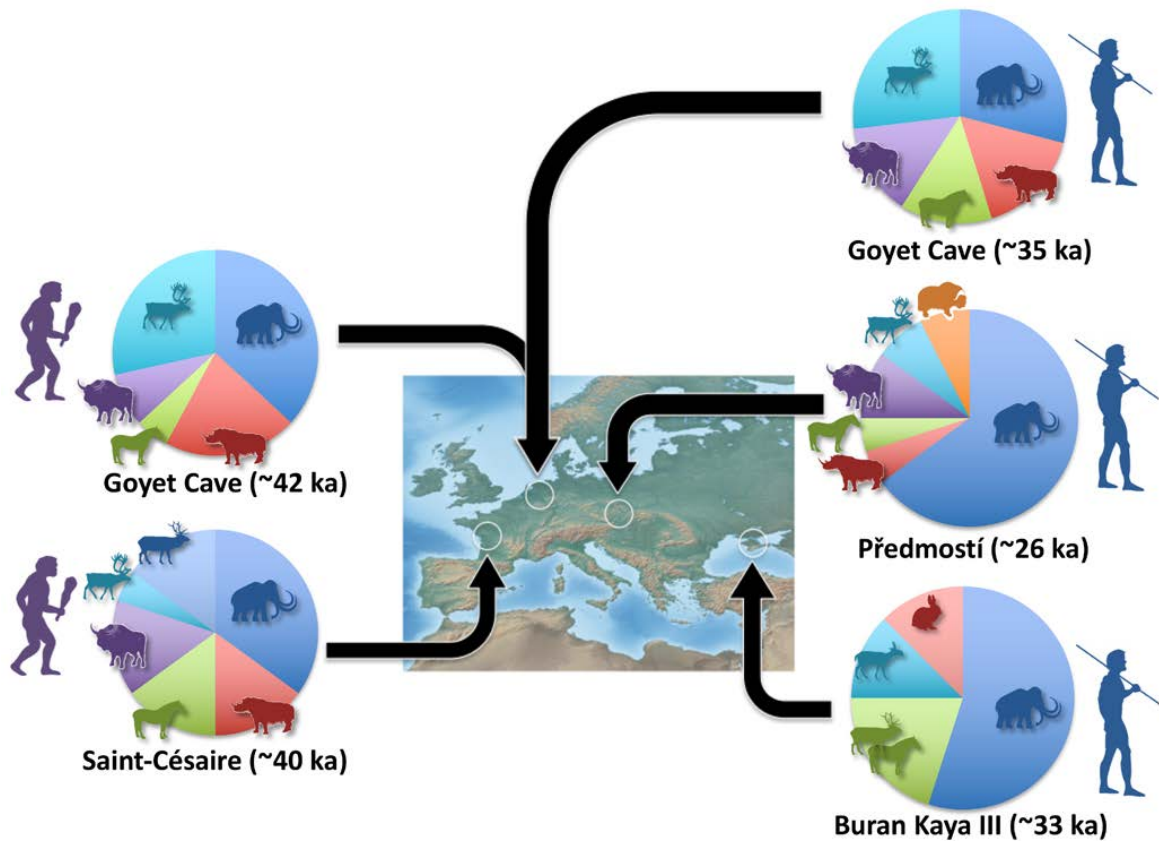


Figure 13.3: Proportion of prey consumption based on carbon and nitrogen isotopic composition of hominins and coeval herbivores in late Neanderthals and early modern humans. Map taken from Natural Earth (naturalearthdata.com). Data are from Wißing et al. (2016, 2019) for Goyet cave, from Bocherens et al. (2005) for Saint-Césaire, from Bocherens et al. (2015) for Předmostí, and from Drucker et al. (2017) for Buran Kaya III.

been measured (Richards et al., 2001; Dinnis et al., 2019), and they are similar to those from Buran-Kaya III (Drucker et al., 2017). Even if the isotopic abundances of mammoth bones have not been analyzed in this site, it is likely that here again, mammoth was high on the menu of humans, due to the similarity of all the other species with those from the Buran-Kaya site in Crimea (Drucker et al., 2017).

13.3.3. WESTERN EUROPEAN LATE NEANDERTHALS AND EARLY MODERN HUMANS

The sites of Spy and Goyet (Belgium) have yielded numerous remains of late Neanderthals, as well as

some early modern humans (Semal et al., 2009; Posth et al., 2016; Rougier et al., 2016). In these sites, an abundant mammalian fauna has been also recovered, as well as in the nearby contemporary site of Scladina (Simonet, 1992; Bocherens et al., 1997), providing the possibility to reconstruct the diet of late Neanderthals, early modern humans and animal predators in the same region (Wißing et al., 2016, 2019). Both sites, Spy and Goyet, have yielded mammoth remains (Germonpré et al., 2014; this volume), and a seasonality investigation based on dental wear of mammoth deciduous premolars indicates that mammoths were hunted during all seasons at both sites (Germonpré et al., this volume). The isotopic results clearly indicate a high amount of mammoth ~40% in the protein part of the diet of all Neanderthals, from Spy as

well as from Goyet, and also in similar amounts in the diet of early modern humans from Goyet (Fig. 13.2).

The site of Saint-Césaire (Charentes-Maritime, France) yielded one of the most recent Neanderthals in Europe associated to a Chatelperonnian (early Upper Palaeolithic) context (Lévêque and Vandermeersch, 1980; Hublin et al., 2012). This hominin specimen was investigated, together with associated mammals, and yielded results indicating a high amount of mammoth ~30 to 40% (Fig. 13.2; Bocherens et al., 2005; Wißing et al., 2019). The $\delta^{15}\text{N}$ values of the Neanderthal specimen are much higher than those measured on hyenas, showing that this scavenger had much less access to mammoth meat, and therefore the hominin had prime access and was most likely the one killing mammoths rather than scavenging them (Bocherens et al., 2005).

13.4 MAMMOTH OR FISH? CONTRIBUTION OF SINGLE COMPOUND AMINO ACID NITROGEN ISOTOPES

In Western Europe, Neanderthals from Saint-Césaire, Spy and Goyet as well as early modern humans from Goyet, present bone collagen carbon and nitrogen isotopic abundances that are in a similar position compared to those of coeval herbivores and predators than in the Central and Eastern European sites of Předmostí and Buran-Kaya III. When the possible contribution of each large herbivore in the diet of hominins and predators is evaluated, using Bayesian mixing models, mammoth always comes out as the most important contributor to the protein part of the diet. Besides mammoth, one other possible food resource could account for such an isotopic pattern in hominin collagen: freshwater fish. Freshwater fish also typically exhibit lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values than the meat of terrestrial herbivores except mammoth (e.g., Drucker and Bocherens, 2004). Mammoth is much more often found in Mid-

dle Palaeolithic and early Upper Palaeolithic sites than fish, but it cannot be totally excluded and this could be the source of an uncertainty in the diet reconstruction leading to an overestimation of mammoth consumption. Fortunately, a new approach allows sorting out this uncertainty: the single compound amino acid nitrogen isotope analysis (Naito et al., 2016).

This approach takes advantage of the difference of nitrogen isotopic fractionation between source amino acids that cannot be synthesized by an organism (such as phenylalanine), and remain essentially unchanged along the food chain and the trophic amino acids that can be synthesized by an organism with a significant fractionation (such as glutamic acid). Moreover, the nitrogen isotopic values of these amino acids are clearly different in terrestrial and aquatic foodwebs (e.g., Naito et al., 2013). When both types of amino acids are retrieved from the same collagen molecule, the isotopic difference between them allows distinguishing clearly the origin of the protein part of the food, from a terrestrial or an aquatic foodweb (e.g., Naito et al., 2013). Because this methodology is more technologically challenging than the isotopic measurements on bulk collagen, it has been applied so far to few adult hominin specimens, i.e. the Neanderthals from Spy (Naito et al., 2016) and the early Upper Palaeolithic modern humans from Buran Kaya III (Drucker et al., 2017). In both cases, the results indicate clearly a purely terrestrial diet, excluding fish and other freshwater resources as the possible reason for the high $\delta^{15}\text{N}$ values. This conclusion can very likely also apply to the other sites considered above.

13.5 POSSIBLE ECOLOGICAL IMPACT OF MAMMOTH HUNTING ON LATE PLEISTOCENE ECOSYSTEMS

With such a high consumption of mammoth meat by late Neanderthals and early modern humans in Europe, the question arises whether this killing of mammoths had a significant impact on

the mammoth populations (e.g., Brook and Bowman, 2004; Haynes, 2018), and possibly through a trophic cascade effect on the whole ecosystem (e.g., Malhi et al., 2016; Smith et al., 2019). First, it is necessary to see if human predation on mammoth was something unique or merely replacing predation by animal predators, and second if there is evidence of ecological disturbances that can be linked to a depletion of mammoth populations.

So far, isotopic tracking of Late Pleistocene animal predator diet has failed to demonstrate a high level of predation on proboscideans (e.g., Bocherens et al., 2005, 2015; Bocherens, 2015), even for the morphologically derived saber-toothed felids, such as *Smilodon* and *Homotherium*, for which proboscidean specialized hunting has been inferred based on other lines of evidence, especially for North American sites (e.g., Rawn-Schatzinger, 1987, 1992; Meachen-Samuels and Van Valkenburgh, 2010; Graham et al., 2013; Van Valkenburgh et al., 2016). Since this low predation on proboscideans by Late Pleistocene predators is also observed in areas devoid of prehistoric humans, such as eastern Siberia and Alaska/Yukon before 30,000 years ago (Bocherens, 2015), it shows that this proboscidean predation was low during the Late Pleistocene in the absence of humans. Therefore, none of the large predators (cave lion, cave hyena, wolf, brown bear) occurring in Eurasia during the Late Pleistocene seems to have been a regular predator of woolly mammoth or other proboscideans. This leaves only prehistoric humans exerting a predatory pressure on mammoth that was not occurring through predation by animal predators. It is therefore likely that human hunting led to increased mortality of mammoths, an animal that probably had a rather low reproductive turnover, although African elephant populations can recover successfully from mass mortality events (Haynes, 1991). Interestingly, palaeogenetic research has shown that a mitochondrial clade of mammoths coming from Siberia expanded into Europe between ~35,000 and 15,000 years ago (Palkopoulou et al., 2013;

Fellows Yates et al., 2017), and prehistoric human hunting probably contributed to the decline of mammoth populations in Europe, facilitating the immigration of Siberian populations into Europe (Fig. 13.4). In ecological terms, this decline of mammoth populations either could have opened possibilities for other herbivores consuming plant resources unused by the missing mammoths or could have led to a collapse of the ecosystem due to the loss of a key ecological function, such as maintaining a patchwork environment and accelerating nutrient recycling (e.g., Zimov et al., 1995).

The isotopic tracking of Late Pleistocene mammal bone collagen not only allows the reconstruction of the proportion of prey consumed by predators and human hunters, but also provides indication on the niche partitioning among herbivores and possible changes linked to different levels of competition among species. For instance, if one species becomes less abundant, another species might take advantage of this new situation and start exploiting the food resources previously consumed by the declining species. Since woolly mammoth is almost systematically the only herbivorous species taking advantage of the forage with high $\delta^{15}\text{N}$ values, it is interesting to consider the few cases where another species also occurs in the same range of isotopic values. Among the other herbivorous mammals that regularly co-occur with woolly mammoth, horse has been found in several instances to shift its isotopic distribution towards the one usually exhibited by the mammoth (Fig. 13.4). So far, such a phenomenon has been noticed during the early Upper Palaeolithic in Belgium and in the Swabian Jura, in southwestern Germany (Drucker et al., 2015; Wißing et al., 2019). In both areas, mammoths were intensively exploited, as demonstrated by isotopic tracking of human bone collagen in Belgium (Wißing et al., 2019) or by the abundance of tools and jewelry made of mammoth ivory and bone in the Swabian Jura (Münzel et al., 2017; Wolf and Vercoutère, 2018). Interestingly, this pattern seems to occur in the Upper Palae-

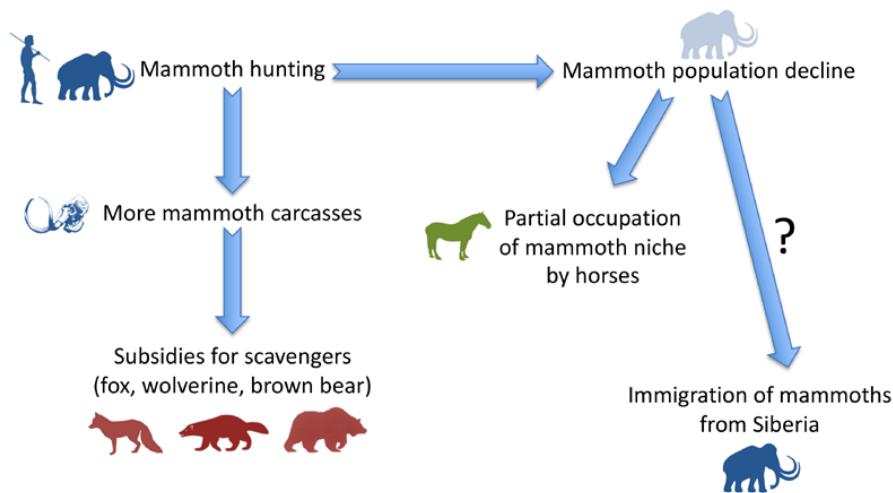


Figure 13.4: Possible ecological consequences of mammoth hunting by early modern humans in Europe.

olithic, but not in the Middle Palaeolithic, although both late Neanderthals and early modern humans hunted and consumed mammoth. One difference could be the intensity of this predatory pressure, linked to the higher population density of modern humans compared to Neanderthals (Conard et al., 2006).

Finally, an additional ecological effect of mammoth hunting by hominins could be to provide scavengers with additional food resources that would otherwise not be available (Fig. 13.4). Such impacts of human subsidies on predators have been documented in recent contexts (e.g., Newsome et al., 2015, Hulme-Beaman, et al., 2016), but few studies have considered this aspect in prehistoric ones (e.g., Bocherens et al., 2015; Baumann et al., 2020a, b). In sites where mammoths were heavily exploited by hominins, isotopic tracking of collagen from predatory species with scavenging habits suggests that some species that could not hunt such a large prey by themselves, e.g., foxes, wolverine and brown bears, had more access to this resource than in other contexts (Bocherens et al., 2015). More studies are necessary to confirm such a trend, but it seems that the carcasses of mammoths hunted by hominins could have provided food resources to some scavenging species and possibly allowed them to thrive.

13.6 CONCLUSIONS

Carbon and nitrogen isotopic tracking with bone collagen has already yielded very important evidence for the high amount of mammoth meat consumption by late Neanderthals in western Europe, and early modern humans in western, central and eastern Europe from around 45,000 to 30,000 years ago. This approach complements efficiently other disciplines, such as zooarchaeology, archaeology and palaeogenetic, and contributes to provide a more accurate picture of the exploitation of mammoths by hominins. In addition, this approach allows evaluation of the ecological impacts of mammoth hunting, on the mammoths themselves, on their potential competitors and on the scavengers taking advantage of a new food resource. As modern humans entered Europe, they already started affecting their ecosystem through the predatory pressure they exercised on a keystone megaherbivore, the woolly mammoth, well before the final extinction of this proboscidean in Europe ~12,000 years ago.

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