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Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe

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ABSTRACT

The Late Pleistocene site "Troisième caverne" of Goyet (Belgium) has yielded the broadest set of Neandertal remains in North-Western Europe and is associated with a rich and diverse large mammal assemblage. We reconstructed the dietary ecology at the site using stable isotope tracking (δ^{13} C and δ^{15} N) of bone collagen. The δ^{13} C and δ^{15} N values of all species are consistent with those observed in other "mammoth steppe" sites. The relative contribution of potential prey species to the diet of carnivores (including Neandertals) was evaluated using a Bayesian model. The distribution of individuals from herbivorous species and carnivorous ones was determined through cluster analysis in order to identify ecological niches, regardless of the individual species attribution. The Neandertals within the predator guild and the mammoth and reindeer as representatives of the herbivores occupied the most specific and most narrow ecological niches. The "Troisième caverne" of Goyet can be regarded as a key site for the investigation of Late Pleistocene Neandertal ecology north of the Alps.

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1. Introduction

Neandertals went extinct approximately 40,000 years ago (Higham et al., 2014), around the time anatomically modern humans (AMH) began to replace the previous Neandertal populations (Hublin, 2015; Nigst et al., 2014). The dietary strategies and the related cognitive abilities can provide insights into potential arguments for the Neandertal extinction (e.g. d'Errico and Sánchez Goñi, 2004; Finlayson et al., 2004; Bocherens and Drucker, 2006; Bocherens et al., 2014b). Several approaches were conducted to reconstruct Neandertal diet, e.g. zooarchaeology (Gaudzinski-Windheuser and Kindler, 2012a,b; Germonpré et al., 2014), dental microwear patterns (Pérez-Pérez et al., 2003; Harvati et al., 2013),

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tooth calculus analysis (Henry et al., 2011; Hardy et al., 2012), lithic use-wear and residue analysis (Hardy and Moncel, 2011) and the investigation of stable carbon and nitrogen isotopes of bone and teeth collagen (e.g. Bocherens et al., 1991, 2001, 2005b; Bocherens, 2009b; Bocherens et al., 2013; Richards et al., 2000; Richards and Schmitz, 2008; Richards and Trinkaus, 2009). All the different projections present different, in some cases even on the first view apparently contradictory, results equivalent to their specific possibilities. Nevertheless, there is common agreement of the regular consumption of large ungulate meat. In the current state of research, it has been accepted that Neandertals were able to hunt actively (e.g. Richards et al., 2000; Bocherens and Drucker, 2006; Serangeli and Bolus, 2008; Rendu et al., 2012; Gaudzinski-Windheuser and Kindler, 2012a,b; Germonpré et al., 2014), in contrast to around two decades ago (e.g. Binford, 1985; Stiner, 1991; Marean, 1998).

What remains in dispute is the potential role of smaller mammals or birds in Neandertal diet, as well as the significance of fresh and/or marine resource exploration (e.g. Richards et al., 2001; Hardy and Moncel, 2011; Blasco and Fernández Peris, 2012a,b;

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Bocherens et al., 2014d). Another striking point is the significance of plant food consumption. Several interpretations have been proposed about plant food consumption: Did it occur just by chance, very regularly, only in certain ecosystems, or even for medicinal reasons (e.g. El Zaatari et al., 2011; Henry et al., 2011, 2014; Hardy et al., 2012; Salazar-García et al., 2013)?

The archaeological and anthropological record in Belgium provides a unique situation: the several previously presented remains from Spy, Scladina, Walou, Trou de l'Abîme at Couvin and Engis (e.g. Bocherens et al., 2001, 2013; Draily, 2004; Toussaint et al., 2006; Semal et al., 2009, 2013; Toussaint et al., 2010; Germonpré et al., 2014) emphasized the richness of Neandertal fossils with associated artifacts and faunal remains in this area. The "Troisième caverne" of Goyet (Belgium) contributed significantly to the archaeological record. The site yielded the most extensive assemblage of Neandertal remains in terms of numbers of specimens and individuals in Northern Europe (Rougier et al., 2012, in prep.) providing the rare opportunity for a valid reconstruction of the ecology of Neandertals at this site, and more generally in the region. Not only a considerable spectrum of Neandertal remains have been identified in the last years, but also a broad spectrum of herbivorous and carnivorous species from the same ecosystem. The ecological context allows to reconstruct the trophic structures through the investigation of stable isotopic composition. Furthermore, the chemical preservation of the organic parts of the bone material is excellent in contrast to most of the sites in, for example, Southern Europe.

Altogether, this site provides one of the best opportunities to reconstruct the ecology of Neandertals within their ecosystem through stable isotopic investigation.

The stable isotopic composition of collagen is directly correlated to the isotopic signature of consumed dietary protein. We applied statistical analysis of the Neandertal results and their potential prey to establish a quantitative and qualitative estimation of the composition of their diet. Since the isotope composition of bone collagen reflects the average protein input of the most recent years of an individual, we can estimate ecological behavior on a long term scale, in contrast to methods providing insights as snapshots or short term time ranges (e.g. tooth wear analysis, residue analysis on stone tools, investigation of the species composition of the faunal assemblage in the site).

Here we also provide information about the general structure of this ecosystem in the broader frame of the mammoth steppe ecosystem; we highlight aspects such as niche partitioning among herbivores and among carnivores with a special focus on the contribution of different prey species in the protein part of the Neandertal diet. While doing this we evaluated potential competition with other predators and highlight the relations among the carnivores guild. These results will be compared directly with the Neandertal results from Spy (Bocherens et al., 2013).

Paleodietary reconstruction using stable carbon and nitrogen isotopic signatures of collagen of European Pleistocene humans is an established technique that was first implemented on Neandertal remains from Marillac (Charente, France; today designated as "Les Pradelles") (Bocherens et al., 1991; Fizet et al., 1995). Since this early research, several Neandertal remains have been the subject of investigation using stable isotopes: early Late Pleistocene remains from Scladina cave in Belgium (Bocherens et al., 1999); the Late Pleistocene remains from Vindija in Croatia (Richards et al., 2000); Spy and Engis in Belgium (Bocherens et al., 2001, 2013); Saint-Césaire, Les Pradelles and Les Rochers-de-Villeneuve in France (Bocherens and Drucker, 2003a; Bocherens et al., 2005); Beauval et al., 2006). Neandertal in Germany (Richards and Schmitz, 2008) and Okladnikov Cave from South Siberia (Krause et al., 2007) have all been used to investigate Neandertal diet through the stable carbon and nitrogen isotopes of their remains. We will discuss our results in the context of previously published results to emphasize the pertinence of the Goyet site.

This paper focused on two essential aspects: the first is to describe the ecological background within the mammoth steppe ecosystem, and the second is to detail the ecology of the Goyet Neandertals and the potential implications.

2. Material and methods

2.1. The "Troisième caverne" of Goyet

The Goyet caves are located in the Mozet Commune in the Walloon Region in Belgium around 20 km away from the Spy site (Fig. 1) and consist of several archaeological sites. The "Troisième caverne" of Goyet is located within a karstic system on the bank of the Samson Valley, a tributary of the Meuse River. Most of the sediment was excavated by Edouard Dupont in 1868 (Dupont, 1872), without the methods used by modern excavators although the fieldwork was somehow advanced if we consider the standards for Paleolithic sites investigations at the time. Most of his work was recorded in writing (e.g. Dupont, 1872) and most of the artifacts were labeled. Dupont described five "fauna-bearing levels" at the site, which were originally considered to correspond to chronological units. However, the "fauna-bearing levels" consist of a mix of remains from different periods (e.g. Germonpré, 1997, 2001; Stevens et al., 2009a). Efforts were therefore made to directly date the human remains (Rougier et al., in prep.). Altogether the "Troisième caverne" vielded rich Late Pleistocene occupations from the Middle and Upper Paleolithic (Mousterian, Lincombian-Ranisian-Jerzmanowician, Aurignacian, Gravettian, and Magdalenian) including a considerable faunal assemblage (e.g. Germonpré, 1997; Germonpré and Sablin, 2001; Otte and Noiret, 2007; Flas, 2011; Pirson et al., 2012).

2.2. Comparison sites

To get a broader ecological dataset, we integrated the sites of Scladina and Spy to our study (Fig. 1). Both yielded material with a very similar ecological and temporal background to Goyet. Spy was excavated more than a century ago. The stratigraphic attribution of the remains it yielded does not follow modern standards (e.g. Pirson et al., 2012; Germonpré et al., 2014), therefore all of the faunal material in the present study is directly dated. The situation at Scladina is different. The faunal remains from the site are not directly dated but come from a well-stratified context. The site was discovered in 1971 and is still under investigation. All of the material considered in this study comes from complex 1A and is associated with a Mousterian technocomplex (Bonjean et al., 2009).

2.3. Skeletal material

2.3.1. Goyet

The human material studied was collected during the excavations of E. Dupont in 1868 and identified as Neandertal during the reassessment of the "Troisième caverne" collections by Rougier et al. (in prep.). The Neandertal remains represent at least five individuals, with four adults represented by four right tibias, and one child represented by a single tooth (Rougier et al., in prep). The tooth was not sampled for stable isotope analysis since it would have been almost entirely destroyed in the process; the four tibias (tibia III represented by specimen Q305-7, tibia IV by Q55-4, tibia V by Q374a-1, and tibia VI by Q57-3) were analyzed (Table 1). In addition to these four identified individuals, stable carbon and nitrogen analyses were performed on eight diagnostic Neandertal

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