Palaeoecology and Subsistence Strategies in Belgium and Northwestern Europe during the MIS 3 through the Reassessment of Forgotten Collections: A Methodological Approach

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Palaeoecological reconstructions are fundamental for the understanding of interactions between all the mammalian communities in a given environment and their choices in terms of habitat, diet and migrations. During the Late Pleistocene in north western Europe, hyenas and human groups shared essentially the same ecological niche. A comparison of their crossed relationships could therefore yield important data on the palaeoecological context. Unfortunately, numerous Palaeolithic sites in north western Europe were excavated well before modern archaeological techniques were devised. Thus the faunal assemblages collected during those early excavations do not have any stratigraphic context and the results extracted from these collections by classical approaches are therefore limited. However, in the karstic region of the Meuse Valley (southern Belgium), many sites have yielded massive amounts of archaeological and palaeontological material dated to the MIS 3. One of the challenges of this on-going doctoral research is to attempt to study this area by attempting an ecological reconstruction based on these old faunal collections in order to highlight settlements and dispersions of the MIS 3 key-species like ungulates, carnivores and humans.

Introduction

The on-going study of the recently excavated site of Tiène des Maulins (Rochefort, southern Belgium) (Groenen 2005), which was occupied by both humans and hyenas during the Marine Isotopic Stage 3 (i.e. 60,000–28,000 BP) (Maree 1983), has prompted a comparative analysis of subsistence strategies of these two top-predators on a regional scale. The karstic landscape of the Meuse Valley in Belgium constitutes one of north western Europe’s “hotspots” in terms of archaeological finds. With its variety of topographies and biomes, the region hosted a great diversity of mammalian communities as well as Middle and Upper Palaeolithic human groups that intensively occupied the valley during the climatically instable MIS 3 (Otte 1979; Toussaint et al. 2011). As such, this geographical area constitutes the ideal basis for a reconstruction
of the competitive relationships between the main predators of this period within their ecosystem.

Due to an early interest for the “antediluvian” civilisations in this region, most of the archaeological collections result from old excavations. The eminent director of the Royal Belgian Institute of Natural Sciences, Edouard Dupont alone excavated more than sixty major Palaeolithic sites during the second half of the 19th-century (Dupont 1872; Toussaint et al. 2011). These early excavations are poorly documented in terms of archaeological and stratigraphic data. Although this might constitute an obstacle for a “classical” zooarchaeological approach, the sheer quantity of faunal remains accumulated during early excavations allows an overview of the complete spectrum of cold, temperate and montane taxa (Stewart et al. 2003). The aim of this paper is to propose a methodological approach for palaeoecological reconstruction through the case studies of Trou Magrite and Caverne Marie-Jeanne, two old faunal collections from Belgium.

A top-predators approach

In Belgium, numerous Palaeolithic sites have yielded proof of the high presence of hyenas in their faunal assemblages, which undoubtedly confirms a large availability of prey in the region at this time: Scladina, Trou de l’Abime, Trou du Diable, Goyet, Bois-Laiterie, Trou Walou, Caverne Marie-Jeanne, Spy etc. (Gautier de Heinzelin 1980; Turner 1981; Bourdillat 2008; Pettitt & White 2012; Discamps 2011; Diedrich 2014). These two species at the top of the trophic level are thus in perpetual inter-competition relationships. They have the particularity of accumulating prey carcasses in the same types of sites (mainly karstic shelters/caves), which are well documented in the region due to an early scientific interest. Hence, a multi-proxy comparison between the archaeological and palaeontological registers of these two species appears to be the ideal way to reconstruct their palaeoecological context.

In a sustainable ecosystem, populations are regulated by diverse bottom-up and top-down controls. All the elements are interdependent: climate changes impact vegetation distribution and biomass; vegetation availability impacts ungulates shifts and biomass; and ungulates availability impacts top-predators behaviours. For example, large mammal herds like reindeer make long-distance shifts over the year to compensate the lack of food during the “bad” season or to avoid too many insects during the warm/mild one (Loe et al. 2007). In addition to the climate changes, most mammals respond to physiological changes in the annual cycle (breeding season, birth season etc.), which affect their migration patterns and the sexual and/or numerical composition of their groups. Besides, a high predator density affects the sexual and/or numerical composition of the ungulate populations and makes them migrate to reduce the top-down forces.

In this theoretical framework, it seems that the only way to infer the intensity of these past bottom-up and top-down forces is to take an interest in the territorial and dietary aspect of the predators and their prey: What is the chronology of the occupations of humans and hyenas groups on a given site? Did humans and hyenas share the same diet or did they have specific habits to overcome the periodical lack of resources? Did the big ungulates live in the Meuse Valley all year long or did they migrate in the area for short periods of time according to seasons and vegetation availability?
Materials
In Belgium, very few Palaeolithic sites are recently excavated. In order to flesh our corpus out we decided to take advantage of the huge potential of old collections, which provide an exhaustive insight of the fauna on a given site.

Thanks to a scientific collaboration with the Royal Belgian Institute of Natural Sciences where the majority of Belgian Palaeolithic faunal material is curated, two sites were short-listed among the available collections (Figure 1): Trou Magrite (Belgium) and Caverne Marie-Jeanne (Belgium). These sites were chosen according to relevant criteria to assure the comparative approach (Table 1). They had to:

- Be located in the same geographically coherent region (Meuse Valley);
- Show different types of occupations (butchery site, camp site, hyena den);
- Be fully or mostly excavated.

| Site                  | Chronology | Site function         | Number of faunal remains |
|-----------------------|------------|-----------------------|--------------------------|
| Trou Magrite          | MIS 3      | Mainly Human occupations | >30,000                  |
| Caverne Marie-Jeanne  | MIS 3      | Mainly Hyaena den      | ±5000                    |

Table 1: Short presentation of the two old faunal collections included in this study.
1) Trou Magrite

Trou Magrite is a rock-shelter situated on the right bank of the Meuse River and was lengthily occupied by human groups during Middle and Upper Palaeolithic (Otte 1979; Otte & Straus 1995). E. Dupont mainly excavated the site during the 1860s. The faunal assemblage is dominated by (%NISP) Horse (34.1%), Reindeer (25.7%) and Rhinoceros (11.3%). The large carnivores are represented by Canids (3%) and Hyaenas (2.3%).

2) Caverne Marie-Jeanne

Caverne Marie-Jeanne is a small cave also situated on the right bank of the Meuse River. The layers 3 and 4 were largely occupied by hyenas (Gautier & de Heinzelin 1980), despite few artefacts suggesting a brief human visit (Ballmann et al. 1980). Only layer 4 is included in this study. The faunal assemblage is overwhelmingly dominated by (%NISP) Hyaenas (50.9%), then Fox (15.6%) and Horse (7.5%).

Methods

Dealing with old collections

As explained above, the specific challenge of our study is to overcome the lack of archaeological context by favouring ecological data in order to obtain new global insight on the palaeoecological context of the MIS 3. From this perspective, the main difficulty is to determine to what extent old collections can bring new, valuable data.

A lot of studies of old collections have already shown the potential of such endeavours. In Belgium for example, the reassessment of early-excavated sites has delivered some of the leading data on the regional Palaeolithic (Germonpré et al. 2009; 2015; Peigné et al. 2009; Bocherens et al. 1999; 2001; Stevens et al. 2008; Charles 1998; Semal et al. 2009). These studies mainly focus on one type of population (Canids, Ursids, Neanderthals, etc.) using different types of techniques (micro-wear analysis, stable isotopes, ancient DNA, etc.). Supported by new radiocarbon dates, these approaches demonstrated the huge potential of these old museum collections, offering new data on the palaeontological context and on the adaptation of the different populations, bringing relative and absolute chronological data and pointing out some specific cultural behaviour.

This on-going doctoral research tends to explore another aspect of these collections, by trying to highlight how humans and hyenas coexisted.

Zooarchaeological study

At first, the classical data generally used in zooarchaeology were collected and analysed in order to compare the two collections selected: taxonomical and anatomical identification, degree of bone fragmentation, gnawing marks and butchery marks and weathering stages were recorded among other criteria. Despite the lack of stratigraphic data, this complete taphonomical study aims to yield some key information, like the features of carcass exploitation (hunted or scavenged), the agent who had primary access to the carcass (Human or Hyena) and the selection of prey (species, age profile, sex). Even if this step cannot bring detailed data about the subsistence strategies for each occupation (e.g. differences between Mousterian and Aurignacian groups), it is a necessary step to obtain crucial information about quantitative and qualitative composition of the faunal assemblages and how they have been accumulated.

Territories and seasonality

The second step of this study is to obtain spatial organisation on the territory. Reconstructing settlement patterns of the past living groups is a major issue for our knowledge of the inter-specific relationships and subsistence strategies.

There are several ways to obtain information about the territorial reach of different groups during the Palaeolithic. Raw material studies are the first and most commonly exploited one. In north western
Europe, several sites were studied in this way (Di Modica 2010; Wragg Sykes 2009; 2012) but more geological studies need to be done to increase territorial data. The second way is to focus on seasonality. Seasonal data obtained through the study of dental eruption stages and tooth-wear analysis are vastly utilised. Moreover, in these last decades a new analytical method, cementochronology, has been developed (Monks 1981; Stutz 2002; Gourichon 2004; Rendu 2007). This technique relies on the depositional rate of the cementum around the tooth roots of mammals, which varies depending on seasonal cycle. Applied to archaeological studies, this technique offers very reliable data about the age and the season of death of the individuals, providing more precise information than those obtained through the observation of tooth eruption, replacement and wear.

As part of this on-going doctoral project, a collaboration with the international research project (ANR) “CemenTAA” was engaged. Financed by the National French Funding Agency for Research, this collaborative project coordinated by William Rendu (CNRS-New York University) and Lionel Gourichon (CNRS-Université de Nice) aims to develop and improve techniques and methodological approaches to study seasonality in prehistoric context.

The results furnish seasonal data on Equids, Bovids, Cervids and probably Hyenas, and give an overview of their annual presence in the environment. Similarities and differences between the sites are crucial to highlight seasonal migrations.

**Preliminary results**

The preliminary results already show interesting information. Although the faunal spectra (ungulates) are more or less the same in both sites with high proportions of Horse, Bos/Bison and Rhinoceros, the species exploited by humans or by hyenas, the fragmentation ratio, the treatment of animal carcasses and the body parts differ consequently.

Furthermore, preliminary seasonal data show that hyenas probably occupied these sites at a different season than humans, indicating that the two predators shared the territory seasonally, maybe looking for different prey. Indeed, it is interesting to notice that hyenas hunted Rhinoceros whereas no proof of Rhinoceros exploitation by prehistoric people has been found in these collections. These data are partially confirmed by the recent studies on stable isotopes in Goyet cave (δ¹³C and δ¹⁵N) (Wiśing et al. in press). Thus, is the difference in the diet of the two predators a result of a nutritional stress during changes in the herbivore biomass? Can we confirm that humans preferred to hunt during the “bad” season in this region, as suggested by A. Stutz after an isolated test in cementochronology at Trou Magrite (Stutz et al, 1995)? Does it reinforce the hypothesis that the Meuse Valley was periodically a cryptic zone during cold climate phases of the isotopic stage 3 (van Andel & Davies, 2003)?

To improve the resolution of this dataset, several recently excavated sites from Northern France will be added to this study in the future.

**Conclusion**

The study of a recently excavated site – Tiène des Maulins – led us to find new scientific approaches in order to contextualize our data despite the lack of well-excavated Palaeolithic sites in the region. In order to take advantage of the potential of the old museum collections, our palaeoecological approach based on the deciphering of interspecific relationships, the relation between the large carnivores and the large herbivores and their settlement patterns seems to be a good way to generate new data on the adaptation of the mammalian communities facing constant climatic and ecological changes during the MIS 3.

By studying old museum collections as well as recently excavated sites from the same region (collections from northern France will also be included in the doctoral thesis) and by comparing the seasonal and dietary data of the top-predators (Hyena and Human) and their prey, our on-going study will provide a
global overview of the settlement patterns of the key-species of this period and will highlight the specific responses to ecological pressures in north western Europe.

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Competing Interests
The author declares that they have no competing interests.

References
Ballmann, P, De Coninck, J, de Heinzelin, J, Gautier, A, Geets, S and Rage, J C 1980 Les dépôts quaternaires: inventaire paléontologique et archéologique. In: Gautier, A and de Heinzelin, J (Eds.) La Caverne Marie-Jeanne (Hastiére-Lavaux, Belgique). Bruxelles: Mémoire Institut Royal des Sciences Naturelles, 177, pp. 3–24.

Bocherens, H, Billiou, D, Patou-Mathis, M, Otte, M, Bonjean, D, Toussaint, M and Mariotti, A 1999 Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of late interglacial Neandertal and mammal bones in Scladina Cave (Belgium). Journal of Archaeological Science, 26: 599–607. DOI: http://dx.doi.org/10.1006/jasc.1998.0377

Bocherens, H, Toussaint, M, Billiou, D, Patou-Mathis, P, Bonjean, D, Otte, M and Mariotti, A 2001 New isotopic evidence for dietary habits of Neandertals from Belgium. Journal of Human Evolution, 40: 497–505. DOI: http://dx.doi.org/10.1006/jhev.2000.0452

Bourdillat, V 2008 Hommes – Carnivores? Caractériser l’action de l’hyène des cavernes: de l’utilisation des données fossiles pour l’interprétation des sites mixtes. Unpublished thesis (PhD), Museum national d’Histoire naturelle de Paris.

Charles, R 1998 Late magalenian chronology and faunal exploitation in the North-Western Ardennes. Oxford: British Archaeological Reports International Series, 737.

Diedrich, C G 2014 Palaeopopulations of Late Pleistocene Top Predators in Europe: Ice Age Spotted Hyenas and Steppe Lions in Battle and Competition about Prey. Paleontology Journal: 1–34.

Di Modica, K 2010 Les productions lithiques du Paléolithique moyen de Belgique: variabilité des systèmes d’acquisition et des technologies en réponse à une mosaïque d’environnements contrastés. Unpublished thesis (PhD), Université de Liège.

Discamps, E, Jaubert, J and Bacherellie, F 2011 Human choices and environmental constraints: deciphering the variability of large game procurement from Mousterian to Aurignacian times (MIS 5–3) in South-western France. Quaternary Science Reviews, 30: 2755–2775. DOI: http://dx.doi.org/10.1016/j.quascirev.2011.06.009

Dupont, E 1872 Les tems préhistoriques en Belgique. L’homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse, Bruxelles, Ed. C. Muquardt, 250 p.

Gautier, A and de Heinzelin, J D 1980 La caverne Marie-Jeanne (Hastiére-Lavaux, Belgique). Bruxelles: Mémoires de l’institut Royal des Sciences Naturelles.

Germonpré, M, Sablin, M V, Laznickova-Galetova, M, Despres, V, Stevens, R E, Stiller, M and Hofreiter, M 2015 Palaeolithic dogs and Pleistocene wolves revisited: a reply to Morey (2014). Journal of Archaeological Science, 54: 210–216. DOI: http://dx.doi.org/10.1016/j.jas.2014.11.035

Germonpré, M, Sablin, M V, Stevens, R E, Hedges, R E M, Hofreiter, M, Stiller, M and Després, V R 2009 Fossil dogs and wolves from Paleolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. Journal of Archaeological Science, 36(2): 473–490. DOI: http://dx.doi.org/10.1016/j.jas.2008.09.033

Germonpré, M, Udrescu, M and Fiers, E 2014 Possible evidence of mammoth
hunting at the Neanderthal site of Spy (Belgium). *Quaternary International*, 337: 28–42. DOI: http://dx.doi.org/10.1016/j.quaint.2012.10.035

**Gourichon, L** 2004 Faune et saisonnalité. L’organisation temporelle des activités de subsistance dans l’Epipaléolithique et le Néolithique précéramique du Levant nord (Syrte). Unpublished thesis (PhD), Université Lumière-Lyon 2.

**Groenen, M** 2005 Interprétation des datations absolues aurignaciennes et moustériennes pour la grotte-abri du Tiène des Maulins. *NotaePrehistoricae*, 25: 71–79.

**Kruuk, H** 1972 *The spotted hyena, a study of predation and social behavior*. Chicago: Chicago University Press.

**Loe, L E, Bonenfant, C, Mysterud, A, Severinsen, T, Oritsland, N A, Langvatn, R, Stien, A, Irvine, R J and Stenseth, N C** 2007 Activity pattern of arctic reindeer in a predator-free environment: no need to keep a daily rhythm. *Oecologica*, 152(4): 617–624. DOI: http://dx.doi.org/10.1007/s00442-007-0681-7

**Maree, B** 1983 La grotte du Tienne des Maulins à Éprave (Rochefort). *Notae Praehistoricae*, 3: 25–26.

**Monks, G G** 1981 Seasonality studies. In: Schiffer, M B (Ed.) *Advances in Archaeological Method and Theory (4)*. New York: Academic Press, pp. 177–240. DOI: http://dx.doi.org/10.1016/b978-0-12-003104-7.50009-0

**Otte, M** 1979 Le paléolithique supérieur ancien en Belgique. Monographies d’Archéologie Nationale (5). Bruxelles: Musées Royaux d’art et d’histoire.

**Otte, M and Straus, L G** 1995 Le Trou Magritte. Fouilles 1991–1992. ERAUL, 69, Liège

**Peigné, S, Goillot, C, Germonpré, M, Blondel, C, Bignon, O and Merceron, G** 2009 Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of Ursus spelaeus from Goyet, Belgium. *PNAS*, 106(36): 15390–15393. DOI: http://dx.doi.org/10.1073/pnas.0907373106

**Pettitt, P and White, M** 2012 *The British Late Middle Palaeolithic: an interpretative synthesis of Neanderthal occupation at the northwestern edge of the Pleistocene world*. London: Routledge.

**Rendu, W** 2007 Planification des activités de subsistance au sein du territoire des derniers Moustériens. Cémentochronologie et approche archéozoologique de gisements du Paléolithique moyen (Pech de l’Azé I, La Quina, Mauvern) et Paléolithique supérieur ancien (Isturitz). Unpublished thesis (PhD), Université de Bordeaux I.

**Semal, P, Rougier, H, Crevecoeur, I, Jungels, C, Flas, D, Hauzeur, A, Maureille, B, Germonpré, M, Bocherens, H, Pirson, S, Cammaert, L, De Clerck, N, Hambucken, A, Higham, T, Toussaint, M and Van Der Plicht, J** 2009 New data on the Late Neandertals: direct dating of the Belgian Spy fossils. *American Journal of Physical Anthropology*, 138: 421–428. DOI: http://dx.doi.org/10.1002/ajpa.20954

**Stevens, R E, Jacobi, R, Street, M, Germonpré, M, Conard, N, Münzel, S C and Hedges, R E M** 2008 Nitrogen isotope analyses of reindeer (Rangifer tarandus), 45,000 BP to 9,000 BP: Palaeoenvironmental reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 262: 32–45. DOI: http://dx.doi.org/10.1016/j.palaeo.2008.01.019

**Stewart, J R, van Kolfschoten, T, Markova, A and Musil, R** 2003 The Mammalian Faunas of Europe during Oxygen Isotope Stage Three. In: van Andel, T H and Davies, W (Eds.) Neanderthals and Modern Humans in the European Landscape during the Last Glaciation, 60,000 to 20,000 years ago: Archaeological Results of the Stage Three Project. McDonald Institute Monograph Series, Chapter 7, pp. 103–130.

**Stutz, A J** 2002 Polarizing Microscopy Identification of Chemical Diagenesis in Archaeological Cementum. *Journal of Archaeological Science*, 29: 1327–1347.
Stutz, A J, Lieberman, D and Spiess, A E 1995 Toward a reconstruction of subsistence economy in the upper Pleistocene Mosan Basin: Cementum increment evidence. In: Otte, M and Strauss, L G (Eds.) Le Trou Magrite, fouille 1991–1992. ERAUL, Liège, pp. 167–187.

Toussaint, M, Di Modica, K and Pirson, S (dir.) 2011 Le Paléolithique moyen en Belgique. Mélanges Marguerite Ulrix-Closset. Bulletin des chercheurs de la Wallonie, hors série n°4, ERAUL, 128, 420 p.

Turner, A 1981 Aspects of the Palaeoecology of Large Predators, including Man, during the British Upper Pleistocene, with particular emphasis on Predator-Prey Relationship. Unpublished thesis (PhD), University of Sheffield.

Van Andel, T H and Davies, W D (eds.) 2003 Neanderthals and Modern Humans in the European Landscape of the Last Glaciation – Archaeological Results of the Stage 3 Project. Cambridge: The McDonald Institute for Archaeological Research.

Wragg Sykes, R 2009 Neanderthals in Britain: Late Mousterian Archaeology in Landscape Context. Unpublished thesis (PhD), University of Sheffield.

Wragg Sykes, R 2012 Neanderthals 2.0? Evidence for expanded social networks, ethnic diversity and encultured landscapes in the Late Middle Palaeolithic. In: Ruebens, K, Romanowska, I and Bynoe, R (Eds.) Unravelling the Palaeolithic: Ten years of research at the Centre for the Archaeology of Human Origins (CAHO, University of Southampton), Archaeology Monograph Series 8. Southampton: University of Southampton.