Dissertation presented for the MA in Archaeology, April 2017

*What was on their plate? A reconsideration of Neanderthal diets in Late Pleistocene Europe*

Exam number: B052884

Supervisor: Dr Catriona Pickard

Word count: 11,585
Contents

Abstract .................................................................................................................................................. 3
Acknowledgements ............................................................................................................................... 3
Illustrations ............................................................................................................................................. 4
Abbreviations ....................................................................................................................................... 4
Introduction ........................................................................................................................................... 5
Chapter 1 Neanderthals: a primer ........................................................................................................... 7
  Who, where, and when were the Neanderthals? .................................................................................. 7
  Why Neanderthals and why now? ....................................................................................................... 11
  How Neanderthals ate and why it matters from a medical perspective ............................................. 13
Chapter 2 Neanderthal diets: literature review ....................................................................................... 17
  Review of past research ...................................................................................................................... 17
    Dental wear patterns ......................................................................................................................... 17
    Lithic material .................................................................................................................................. 19
  Review of current practice ................................................................................................................ 20
    Stable isotopes: what they are ......................................................................................................... 20
    How we know what stable isotopes indicate .................................................................................. 23
    How to use stable isotopes for reconstructing Neanderthal diets ................................................. 23
    Dental calculus: what it is .................................................................................................................. 26
    How we know what dental calculus indicates ................................................................................ 28
    How to use dental calculus for reconstructing Neanderthal diets ................................................ 29
    Faecal biomarkers: what they are and their potential uses ............................................................. 31
Chapter 3 Materials and methods ......................................................................................................... 32
Chapter 4 Results .................................................................................................................................. 35
Chapter 5 Neanderthal diets: discussion ............................................................................................... 46
  Review of the isotopic evidence for Late Pleistocene Europe ............................................................ 46
  Neanderthal diets and stable isotopes: the assumptions .................................................................... 54
  Neanderthal diets and stable isotopes: the challenges .................................................................... 60
  Reconstructing Neanderthal diets using alternative methods ............................................................. 63
    Heavier stable isotopes ..................................................................................................................... 63
    Dental calculus .................................................................................................................................. 64
    Faecal biomarkers ............................................................................................................................ 67
    Reconsidering the ‘meat-eater’ narrative for Neanderthals .............................................................. 69
Conclusions ............................................................................................................................................. 71
Bibliography ......................................................................................................................................... 73

Note: items on this page include hyperlinks. Left click to navigate to a section of your choice.
Abstract

Archaeological research on Neanderthal diets has the potential to contribute to our understanding of present-day human health and nutrition. Neanderthal diets can be reconstructed on the basis of stable isotope ratios, as well as dental calculus samples and faecal biomarkers, providing analogous data for non-archaeologists to engage with. Interdisciplinary research on Neanderthals from Late Pleistocene Europe in particular deepens our understanding of current human population health, aligning the interests of archaeology with that of medicine and food policymakers.

Acknowledgements

I want to thank Dr Catriona Pickard and Dr Karen Hardy for their incisive comments and for their continued support as mentors. This piece of work would not be possible without them.
Illustrations

Figures

Figure 1. Geographic distribution of Neanderthal fossils in Europe and western Asia 8
Figure 2. Palaeoenvironments of Late Pleistocene Europe 9
Figure 3. Chronology, temperatures, and sea levels for the Pleistocene epoch 10
Figure 4. Carbon and nitrogen isotope fractionation 21
Figure 5. Carbon and nitrogen isotope ratios for terrestrial and marine organisms 22
Figure 6. Dental calculus formation 27

Figure 7. Dental calculus deposit from a Neanderthal, El Sidrón, Spain 27
  Figure 8a. FRUITS results for Neanderthal S-EVA-2152.1 [control] D-BO 36
  Figure 8b. FRUITS results for Neanderthal S-EVA-2152.1 [radical] D-BO 37
  Figure 8c. FRUITS results for Neanderthal M300 [control] D-BO 38
  Figure 8d. FRUITS results for Neanderthal M300 [radical] D-BO 39
  Figure 8e. FRUITS results for Neanderthal M400 [control] D-BO 40
  Figure 8f. FRUITS results for Neanderthal M400 [radical] D-BO 41
  Figure 8g. FRUITS results for Neanderthal M100 [control] D-BO 42
  Figure 8h. FRUITS results for Neanderthal M100 [radical] D-BO 43
  Figure 8i. FRUITS results for Neanderthal RFB7000 [control] D-BO 44
  Figure 8j. FRUITS results for Neanderthal RFB7000 [radical] D-BO 45

Figure 9. Map of Late Pleistocene Neanderthal sites with isotope data 49
Figure 10. Isotopic variations in Late Pleistocene European mammals and plants 57
Figure 11. Possible causes of carbon isotopic variations in herbivores and plants 58
Figure 12. Possible causes of nitrogen isotopic variations in herbivores and plants 58

Tables

Table 1. Energetics and foraging data for selected hunting and gathering populations 15
Table 2. List of published isotopic results for Late Pleistocene Neanderthals 47
Table 3. Summary of published isotopic results for Late Pleistocene mammals 48

Note: items on this page include hyperlinks. Left click to navigate to a section of your choice.

Abbreviations

C Carbon $\delta^{13}C$ Ratio between $^{13}C$ and $^{12}C$
N Nitrogen $\delta^{15}N$ Ratio between $^{15}N$ and $^{14}N$
D-BO Diet-body offset \% Parts per thousand, permil
FRUITS Food Reconstruction Using Isotopic Transferred Signals
Introduction

Neanderthal studies began more than 150 years ago with the discovery of a skullcap and partial skeleton at Neander Valley, Germany. This discovery led to the classification of Neanderthals as part of the genus *Homo* (King 1864), laying the foundations for decades of research to build upon. The reasons for focusing on Neanderthals relate to the stories they have to tell us about our evolutionary history.

The key motivation for writing this dissertation is to explore how Neanderthal studies can benefit current human populations. In relation to Neanderthal diets, there is potential for interdisciplinary research to provide essential information about the evolution and health of our own species, as well as inform our understanding about past environments in Europe during periods of environmental change such as the Late Pleistocene (Bocherens 2011). Information about past environments is all the more important in light of present-day concerns about climate change and its effect on landscapes, sea levels, and patterns of precipitation around the world (RS and USNAS 2014; see also Carlsson-Kanyama and González 2009). With this in mind, the research questions for this dissertation are:

1. In Europe, what archaeological evidence is there for Neanderthal diets during the Late Pleistocene and how has that evidence been interpreted?
2. How can archaeological accounts about Neanderthal diets contribute to the health and well-being of current human populations?
3. What are the possible directions for Neanderthal research moving forward?

In order to answer the research questions outlined above, this dissertation presents a synthesis of recent findings about Neanderthal diets in Late Pleistocene Europe. The piece begins with an overview of who Neanderthals were, why they’re important, and how their species lies at an intersection between medical and archaeological science. What follows is
a review of past and current research methods for appraising Neanderthal-related material. The subsequent discussion features published stable isotope data for Late Pleistocene Neanderthals; however, statistical analysis of the data, as well as findings from dental calculus deposits and faecal biomarkers, support a reconsideration of the published material.
Chapter 1  Neanderthals: a primer

Who, where, and when were the Neanderthals?

*Homo neanderthalensis*, referred to hereafter as Neanderthals, played a significant role in our evolutionary history. Neanderthal-like traits began to emerge in hominins as early as 400,000 years ago and became fully developed in the Middle and Late Pleistocene (Bischoff et al. 2003). Their geographic distribution through time was substantial, concentrated predominantly in Europe and parts of western Asia (Krause et al. 2007; Figures 1, 2, and 3). The species inhabited mainland Europe up to approximately 40,000 years ago at which time their numbers dwindled (Higham et al. 2014); however, radiocarbon evidence from Gibraltar, Spain suggests that members of the species survived in refugial areas until 28,000 years ago (Finlayson et al. 2006). Of note were the interbreeding events that occurred between Neanderthals and *Homo sapiens*, introducing Neanderthal DNA into our genome (Green et al. 2010; Prüfer et al. 2014). Neanderthal DNA has been shown to influence a wide range of clinical traits in current human populations, including susceptibility to depression, actinic keratosis, hypercoagulation, and narcotic use (Simonti et al. 2016). Therefore, an understanding of Neanderthal physiologies and diets is important for both archaeological and medical research moving forward.
Figure 1: Neanderthal geographic distribution reconstructed on the basis of hominin fossil remains (from Fiorenza et al. 2015:44; see also Krause et al. 2007:903, fig. 1). Note the concentration of sites found in Europe in comparison to that of western Asia. The suggestion therein is that Europe was more densely populated by Neanderthals than any other region; however, this could be an artefact of differential preservation between regions, as well as a reflection of what areas have and have not been investigated. For the time being, Europe holds the most material for the archaeological study of Neanderthals.
Figure 2: (A–C) Maps of Europe illustrating the different palaeoenvironments during the Late Pleistocene (modified from Fiorenza et al. 2015:46–48).

Dates are approximate.  

(A) MIS 5e: 125,000 – 120,000 BP  
(B) MIS 4: 65,000 BP  
(C) MIS 3: 39,000 – 36,000 BP
Figure 3: Oxygen isotope data derived from the LR04 stack of Lisiecki and Raymo (2005). Higher temperatures and higher sea-levels are represented at the upper end of the scale; while lower temperatures and lower sea-levels are represented at the lower end (original graph is modified from Railsback 2015).

**LGM:** Last Glacial Maximum.  **PGM:** Penultimate Glacial Maximum.

Note: the numbers on the graph (e.g., 5e, 4, 3a) relate to alternating warm and cold periods referred to generally as **Marine Isotope Stages (MIS).**
**Why Neanderthals and why now?**

The genetic relatedness between Neanderthals and *Homo sapiens* make the former a crucial resource from which tentative inferences about current human population health can be drawn (Green et al. 2010; Harris and Nielsen 2016; McCoy et al. 2017; Sankararaman et al. 2014, 2016; Voight et al. 2006). Medical specialists normally conduct clinical trials and metabolic ward studies in order to generate data (e.g., Aune et al. 2016, 2017; Craig and Mangels 2009; Cross et al. 2016; Jackson et al. 2016; Wang et al. 2014); while archaeologists instead turn to the past for answers (e.g., Warinner et al. 2015b). Yet the interests of the two parties have intersected before.

Abrams (1979) served as a case in point for the intersection between medical and archaeological science. Publishing their findings in the Journal of Applied Nutrition, Abrams (1979) examined data related to Australopithecines and to *Homo* species in order to determine the basic physiological needs of current human populations. The approach was simple: investigate foods that our ancestors consumed. Though Abrams (1979:44) focused predominantly on hunter-gatherer lifestyles (e.g., Hooper et al. 2015), the chronological framework – a timespan of four million years – was too conservative. Abrams (1979) also overlooked the importance of carbohydrates (i.e., plants) in human evolution (*contra* Kay 1977; see also Hardy et al. 2015).

The nutritional requirements and digestive physiologies of current human populations, as well as Neanderthals, can be inferred not only from the archaeological record, but also from non-archaeological material. Primatological studies, for example, support the interpretation that the ancestral line (Hominoidae), from which Neanderthals and *Homo sapiens* descend, was strongly herbivorous (Milton 1981, 1999a, 1999b, 2000a, 2000b, 2002; Milton and Demment 1988). This interpretation does not refute our shared ability among the higher primates to subsist on both plant- and animal-based foods. Rather, cross-species
comparisons challenge archaeologists to critically assess an archaeological record in which plant remains are poorly represented (Day 2013).

To account for the poor representation of plant remains in the archaeological record, Tyldesley and Bahn (1983) proposed that skeletal remains were essential to palaeodietary reconstructions. The authors pieced together previously separate strands of evidence, such as wood and tools, fruit and nuts, and cereals, into a cohesive web of indirect clues for hominin subsistence behaviours in the past (Tyldesley and Bahn 1983:53–55, 57–58). Lithic material and faunal assemblages can also indicate what hominins ate (e.g., Binford 1981; Blumenschine et al. 1987; Brain 1981; Marean and Assefa 1999; Moncel 2011; Speth and Tchernov 2001). But, where ‘lack of preservation prevents a more accurate assessment of the relative contributions to diet of meat and plants’ (Tyldesley and Bahn 1983:58), the authors argued that skeletal evidence was more direct. This idea is central to discussions about Neanderthal diets in Europe during the Late Pleistocene.
**How Neanderthals ate and why it matters from a medical perspective**

Sorensen and Leonard’s (2001) paper, for me, exemplified the convergence between archaeological science and medicine. The authors began with acknowledging the following paradox: Neanderthals were assumed to be inefficient foragers (Binford 1989, 1992; Soffer 1994; Trinkaus 1986, 1989), but their skeletal robusticity suggested higher activity levels, and thus higher energy requirements, compared to current human populations (Abbott et al. 1996; Ruff et al. 1993, 1994; Trinkaus 1989:55). First, faunal evidence from Middle and Late Pleistocene sites in France, Germany, and Russia proved that Neanderthals had been proficient top-level hunters (Chase 1989; Gaudzinski 1996; Gaudzinski and Roebroeks 2000; Marean and Kim 1998; Speth and Tchernov 1998). Stable isotope analysis of Neanderthal remains from Spy Cave in Belgium and Vindija Cave in Croatia corroborated the faunal evidence, suggesting that the Neanderthals from those sites had obtained protein almost exclusively from animal-based foods (Bocherens et al. 1999; Richards et al. 2000).

After establishing that Neanderthals had been efficient hunters and foragers, the authors turned to the second part of the paradox: that Neanderthal skeletal robusticity suggested higher energy requirements than those for current human populations. Sorensen and Leonard (2001:484–487) determined the energy requirements for Neanderthals by starting with basal metabolic rates that were derived from body weight estimates for humans (from FAO/WHO/UNU 1985). Sorensen and Leonard (2001:487–490) then used the approximate energy requirements – ranging from 3000–5500 kcal/day – to predict the foraging efficiency needed to survive an active hunter-gatherer lifestyle. Their results were comparable to those observed among living hunter-gatherers (Table 1), suggesting that Neanderthals did not have higher energy requirements in comparison to current human populations. There are problems with the study though: the authors’ use of body weight estimates for living humans was inappropriate; estimating Neanderthal skin surface area would have generated more
accurate basal metabolic rates in Neanderthals (Churchill 2007). Yet Sorensen and Leonard (2001) succeeded in demonstrating that Neanderthal research can help answer questions about the diets, health, and activities of present-day humans (Table 1). Integrating archaeological science with medicine, however, requires an awareness of current debates in the medical literature.

Robson (2009:135) summarised an important focus of current medical research:

‘What the world needs is an integrated and sustainable food policy [...] to promote health and help prevent disease.’

But, a global food policy requires a consensus which is lacking. If we refer back to Abrams (1979), it becomes clear why. Indian populations were criticised for their low intake of animal protein (Abrams 1979:55); while the food choices and lifestyles of the Greenland Inuits were viewed as conducive to good health (Abrams 1979:55–56; contra more recent findings from Bjerregaard et al. 2004; Jørgensen et al. 2008). Yet univariate explanations for good health in a given population fail to account for all the influencing factors and variables. Vegetarian diets in India, for instance, have been shown to have beneficial effects due to a greater intake of carbohydrates (i.e., plants) and micronutrients (e.g., vitamin C and folate) and a lower consumption of fat and protein compared to non-vegetarian diets (Shridhar et al. 2014). On the other hand, morbidity in south Asians can be increased as a result of ‘thin-fat syndrome’ which is caused by the excessive consumption of plant oils rich in omega-6 fatty acids (Kurpad et al. 2011). Population studies, as is the case for archaeological studies, must account for multiple variables if they are to be effective in elucidating the relationship between diet and health.
<table>
<thead>
<tr>
<th>Population</th>
<th>Male wt (kg)</th>
<th>Female wt (kg)</th>
<th>TEE* (kcal/day)</th>
<th>Foraging time (h/day)</th>
<th>Energy return (kcal/person/day)</th>
<th>Foraging efficiency (kcal/h foraged)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ache</td>
<td>56.9</td>
<td>51.0</td>
<td>3000</td>
<td>6.90</td>
<td>8280</td>
<td>1200</td>
</tr>
<tr>
<td>BaMbuti</td>
<td>51.3</td>
<td>40.4</td>
<td>—</td>
<td>5.00</td>
<td>6000</td>
<td>1200</td>
</tr>
<tr>
<td>Efe</td>
<td>43.3</td>
<td>40.6</td>
<td>2650</td>
<td>4.60</td>
<td>3588</td>
<td>780</td>
</tr>
<tr>
<td>Etolo</td>
<td>—</td>
<td>—</td>
<td>2626</td>
<td>—</td>
<td>—</td>
<td>750</td>
</tr>
<tr>
<td>G/wi</td>
<td>51.3</td>
<td>40.4</td>
<td>2050</td>
<td>5.20</td>
<td>5304</td>
<td>1020</td>
</tr>
<tr>
<td>Hadza</td>
<td>53.6</td>
<td>47.7</td>
<td>—</td>
<td>4.50</td>
<td>11,002</td>
<td>2445</td>
</tr>
<tr>
<td>Hiwi</td>
<td>57.8</td>
<td>48.2</td>
<td>2000</td>
<td>1.50</td>
<td>5665</td>
<td>3800</td>
</tr>
<tr>
<td>Inuit</td>
<td>65.0</td>
<td>55.0</td>
<td>3670</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>!Kung</td>
<td>46.0</td>
<td>41.0</td>
<td>2800</td>
<td>3.10</td>
<td>7900</td>
<td>2550</td>
</tr>
<tr>
<td>Machiguenga</td>
<td>51.8</td>
<td>44.5</td>
<td>3200</td>
<td>3.00</td>
<td>4500</td>
<td>1500</td>
</tr>
<tr>
<td>Yanomamo</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1500</td>
</tr>
<tr>
<td>Mean ± S.D.</td>
<td>53.3 ± 6.7</td>
<td>45.4 ± 5.4</td>
<td>2720 ± 607</td>
<td>4.2 ± 1.7</td>
<td>6529 ± 2400</td>
<td>1653 ± 970</td>
</tr>
</tbody>
</table>

*TEE values represent mid-sex averages.
Robson (2009:135) offered a nuanced approach by promoting a greater awareness about human nutritional requirements and showing how these requirements can be met by eating 'nutrient-dense, low-energy-dense' foods. Take normal brain function and hormone production as examples. They are dependent on access to bioavailable brain nutrients, the three most important of which are the omega-3 fatty acids: docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA); and the omega-6 fatty acid: arachidonic acid (AA) (Robson 2009:136). There is also a third type of omega-3 fatty acid called α-linolenic acid (ALA) which is derived from plants as opposed to animals. But, Robson (2009:136) argued that plant-derived ALA was an inferior substitute for DHA. Contrast this opinion with that of Sanders (2009) who demonstrated that the conversion of dietary ALA to DHA in the human liver was sufficient to meet omega-3 fatty acid requirements. Aside from the apparent bias against plant foods, Robson (2009) was successful in arguing that specific foods can prevent diet-induced disease in humans. Archaeological evidence supports a similar idea: that plant carbohydrates and plant-derived fatty-acids were important for hominin evolution and for health in general (Hardy et al. 2015; Langdon 2006; Sponheimer et al. 2013). Here the interests of the two parties, medical and archaeological, intersect again. Archaeological accounts about Neanderthal diets, and the diets of other hominin species, can serve to open an interdisciplinary dialogue about current human population health, enabling archaeologists to comment on and contribute to global food policies.
Chapter 2  Neanderthal diets: literature review

Review of past research

The prevailing narrative for Late Pleistocene Neanderthals is that they were top-level carnivores who practised a meat-based diet, consuming the meat of large herbivores and a small amount plant food to survive (e.g., Bocherens 2011; Bocherens et al. 1999, 2005; Richards and Trinkaus 2009; Richards et al. 2000). The basis for this narrative includes the archaeological analysis of faunal remains and tool technologies from Neanderthal sites, as well as the stable isotope analysis of Neanderthal remains. Before turning to the stable isotope ratios of Neanderthals, and to the dental calculus and faecal biomarker studies, there are two types of evidence for the diet-related behaviours worth reviewing: dental wear patterns and lithic material. These two, taken together, demonstrate the potential for flexibility in Neanderthal diets; flexible subsistence strategies become important when discussing other types of evidence.

Dental wear patterns

Dental wear patterns on Neanderthal teeth can help to determine diet-related behaviours. Puech (1981), for example, appraised dental wear present in two Neanderthals from La Ferrassie, Dordogne, France (see also Wallace et al. 1975). Puech (1981:424) asked what types of dental wear indicated food consumption and what types of wear were a direct result of ‘paramasticatory activities’ such as holding, gripping, clamping, cutting, or grinding with one’s teeth? Puech (1981) concluded, on the basis of severe wear on La Ferrassie I’s teeth, that Neanderthals were using their teeth in fundamentally different ways to other Homo species (Brace 1975). Similar studies argued that the unique morphology of Neanderthal anterior dentition was an adaptation to the heavy use of incisors and canines for processing fibrous food, for paramasticatory activities, or for both (Antón 1994; Boule and Vallois 1957;
Brace 1962; Brace et al. 1981; Coon 1962; Demes 1987; O’Connor et al. 2005; Smith 1976; Smith 1983; Trinkaus 1983). If Neanderthals developed distinctive dental wear patterns, the mastication of plant fibres was likely a contributing factor (El Zaatari et al. 2011).

But, assessing the rate of dental wear between groups of fossils is problematic. What previous studies failed to account for were discrepancies between individuals of varying ages-at-death and the corresponding level of dental wear. Clement et al. (2012) addressed the difficulties in comparing patterns of dental wear between Late Pleistocene Neanderthals. To account for variation in age and dental wear, they expressed anterior tooth wear and posterior tooth wear as a ratio for individual specimens. Their findings did not support previous interpretations. Clement et al. (2012:367) instead reported that ‘all Late Pleistocene hominins habitually applied heavy forces between their anterior teeth’. On the basis of dental wear patterns, Clement et al. (2012) demonstrated that the diet-related behaviours of Neanderthals were not so different to other hominins.
Lithic material

Lithic material is another resource from which the diet-related behaviours of Neanderthals can be inferred. Hardy and Moncel (2011), for instance, performed lithic residue and use-wear analyses on Neanderthal tools from Payre, Ardeche, France. Neanderthals frequented this site between 250,000 and 125,000 years ago (Moncel et al. 2002; Valladas et al. 2008). In relation to dietary information, the results of a microscopic analysis of 182 stone tools from Payre showed the processing of fish, bird, and other animal tissues, as well as the processing of plant material. Hardy and Moncel (2011) demonstrated a broad-based subsistence for Neanderthals, one that was dependent on both animal and plant consumption; moreover, they documented this flexible behaviour in Middle Pleistocene Neanderthals. It stands to reason that Neanderthals in Late Pleistocene Europe would have retained a degree of flexibility in their diets.
**Review of current practice**

The following is a review of key principles related to three types of evidence which are central to discussions about Neanderthal diets: stable isotopes, dental calculus, and faecal biomarkers.

**Stable isotopes: what they are**

Stable isotope analysis is an established method for reconstructing Neanderthal diets. Fiorenza et al. (2015:51, fig. 6) summarised the steps involved: the sampling, extraction, and analysis of bone collagen, for example, follow a modified Longin method (Longin 1971), though an added step known as ultrafiltration is possible to perform (Brown et al. 1988); however, the reliability of bone collagen is subject to strict criteria (Bocherens 2009:242). The results from bone collagen, if reliable, can be discussed in light of the archaeological and environmental contexts from which they derive.

But, what are stable isotopes? Isotopes are alternative forms of the same element. They have the same number of protons, but a different number of neutrons in their nuclei resulting in different atomic mass numbers. The most common elements that comprise food macronutrients (e.g., carbohydrates) are hydrogen, carbon, nitrogen, and oxygen, all of which have isotopes (Schoeninger 2010:446). The ratios between carbon and nitrogen isotopes (i.e., $\delta^{13}\text{C}, \delta^{15}\text{N}$) are particularly useful for dietary reconstructions, because the isotope ratios within organisms change as a result of food intake (Tykot 2004:434-436). The transfer of carbon and nitrogen isotopes from one organism to another is known as fractionation (Figure 4). Understanding how this process works is essential for stable isotope analysis, as is an awareness of how different environmental factors, such as the canopy effect and aridity (Heaton et al. 1986; van Klinken et al. 1994), can influence the results (Figure 5).
Figure 4. Schematic representation of carbon and nitrogen isotope fractionation, showing how the consumption of C₃ and C₄ plants (central panel) can affect the isotope ratios in animal tissues (from Lee-Thorp and Sponheimer 2006:135; see also Tykot 2004:435, fig. 1). The schematic also illustrates the mean differences in nitrogen isotope ratios between steps in the nitrogen cycle (right panel). Results from bone collagen and apatite differ because they reflect different aspects of consumer diets; collagen indicates dietary protein intake, whereas apatite indicates the dietary intake as a whole, including carbohydrate, lipid, and protein sources (Kellner and Schoeninger 2007).

Note: for plants that follow the C₃ pathway (e.g., herbaceous plants and trees), the average δ¹³C values are −26 to −28 parts permil (‰); while for plants that follow the C₄ pathway (e.g., tropical and salt grasses), the average value is around −12‰ (O’Leary 1988; Schoeninger 2010:447). The accumulation of ¹³C will be more pronounced in animals consuming more C₄ plants than C₃ plants (Schoeninger 2010:447). In addition, the δ¹³C and δ¹⁵N values in plants will fluctuate due in part to changing environmental conditions, such as the amounts of CO₂ and sunlight available to them (refer to Figure 5). What is important to note here is that there were no edible C₄ plants in Late Pleistocene Europe (Richards and Trinkaus 2009). C₃ plants were predominant.
Figure 5: Basic demonstration of the different stable carbon and nitrogen isotope ratios of terrestrial and marine organisms (modified diagram is from Svyatko 2008, but original diagram is from Schulting 1998).

Note: $\delta^{13}C$ and $\delta^{15}N$ values are for flesh in this diagram. For bone collagen values, add 5‰ to $\delta^{13}C$. $\delta^{15}N$ values for flesh and bone collagen are about the same.
How we know what stable isotopes indicate

Stable isotope analysis started with animal studies. DeNiro and Epstein (1978), for example, performed analyses on the soft and hard tissues of animals. They demonstrated that δ^{13}C values in animal tissues correlate positively with the δ^{13}C values in their food; the same was demonstrated for δ^{15}N values in animal tissues (DeNiro and Epstein 1981; Hare et al. 1991). Krueger and Sullivan (1984) later proposed a model to describe the relationship between the δ^{13}C values found in the hard tissues of animals and the δ^{13}C of their diets. Their use of published data from wild fauna and from archaeological hominins was an effective method, serving as the proof-of-concept for future stable isotope research. What Krueger and Sullivan (1984) produced was the ‘routing model’: the δ^{13}C values in bone collagen (δ^{13}C_{collagen}) relate to dietary protein intake; while the δ^{13}C values in bone apatite (δ^{13}C_{apatite}) relate to the intake of carbohydrates, lipids, and proteins, or ‘total energy’ intake (δ^{13}C_{diet}). Kellner and Schoeninger (2007) performed a meta-analysis of experimental data from rats, mice, and pigs, in order to test the routing model. Their results confirmed the previous conclusions with one amendment: if used independently, the δ^{13}C values in collagen and in apatite do not produce accurate reconstructions of the diet as a whole. But, if compared, δ^{13}C_{collagen} and δ^{13}C_{apatite} are promising resources for reconstructing δ^{13}C_{diet}.

These are established principles that Neanderthal stable isotope studies are founded upon. What remains debatable is how accurate routing models for animals are if applied to archaeological hominin remains.

How to use stable isotopes for reconstructing Neanderthal diets

How have stable isotopes informed discussions about Neanderthal diets? The prevailing narrative has been mentioned before, but the basis for this interpretation can be sketched here. Bocherens (2011), for instance, summarised direct evidence for the preferred prey of
two Neanderthals which dated to MIS 3: one from Saint-Césaire, France and one from Spy Cave, Belgium. Their argument rested on stable isotope analyses of the two Neanderthals and the associated faunal remains, suggesting that larger mammal species, such as mammoth and woolly rhino, were principal sources of protein for the two Neanderthals in question. Gaudzinski and Roebroeks (2011:64) produced a similar argument, though they included an important addendum:

‘animal remains are indirect measures of past diets at best, as they may relate to single events or activities typical of specific parts of a landscape only.’

In other words, integrating stable isotope data with other pieces of evidence is problematic (Bocherens 2011:76–79; Lee-Thorp and Sponheimer 2006:135–143)

What are the advantages of stable isotope analysis? First, the results relate to individuals and not a larger group, which means the results for individuals of different ages, sexes, and origins can be compared (Tykot 2004:433–434). What follows are comparisons that can be inter-site, inter-regional, and diachronic. Similar applications of isotope analysis have been performed successfully on a number of Neanderthal and early modern human samples in Europe (Beauval et al. 2006; Bocherens et al. 2001, 2005; Fizet et al. 1995; Richards and Schmitz 2008; Richards et al. 2000, 2001a, 2008; Trinkaus et al. 2009). Second, the skeletal material from which isotopic data is derived tends to be robust. Reliable results have been obtained from very small samples that were millions of years old (Klein 2013; Lee-Thorp et al. 1989).

Yet the contention about isotope analysis and its contribution to palaeodietary reconstructions relates not to the method, but to the interpretation of isotope ratios such as δ\textsuperscript{13}C and δ\textsuperscript{15}N (Makarewicz and Sealy 2015). There are practical difficulties, for example, in determining the trophic level of Neanderthals based on their isotope ratios (Schoeninger 1985). Nitrogen can only be obtained from skeletal tissues that retain protein such as bone
collagen (Hedges and Reynard 2007:1241–1243). Yet even if reliable bone collagen is present, researchers do not agree on what effects diet has on nitrogen isotope ratios: Pearson et al. (2003) and Sponheimer et al. (2003a, 2003b) proposed that high protein diets result in higher $\delta^{15}N$ values; while Robbins et al. (2005) suggested the opposite. The uncertainties about what isotope ratios indicate are enough to question how accurate previous studies were in their representation of Neanderthal diets in Late Pleistocene Europe (e.g., Bocherens et al. 1999, 2005; Richards et al. 2000).
Dental calculus: what it is

Dental calculus is the product of several processes, but oral bacterial species, sugars, and saliva are essential to calculus formation (Figure 6). For example, salivary compounds and enzymes can breakdown starch into simple sugars which bacteria then metabolise (Marcotte and Lavoie 1998; Roberts 1979). The bacteria form a film that adheres to the surface of the teeth. Calcium phosphate mineral salts rapidly replace the bacteria resulting in plaque formation and then calcification, trapping microorganisms and micro-debris in situ (Hillson 2005; Weyrich et al. 2015:119; White 1997; see also Figure 7). Calculus can form above and below the gingiva, referred to as supra- (above) or sub- (below) gingival calculus respectively (White 1997). Calculus formation is exacerbated by poor oral hygiene, but also by genetic pre-dispositions, by the consumption of carbohydrates, and even by the simple act of chewing (Al-Zahrani et al. 2004; Arensburg 1996; Dawes 1970; Dawes et al. 2015; Gaar et al. 1989; Humphrey and Williamson 2001; Lieverse 1999; Lieverse et al. 2007).

In addition to trapping microorganisms, the calculus preserves remnant food debris (Henry and Piperno 2008; Henry et al. 2011; Warinner et al. 2014). Dental calculus has even been found on teeth from Miocene and Pliocene deposits (Blumenschine et al. 2003; Hershkovitz et al. 1997), preserving material that was 9.3 and 1.84 million years old respectively. Furthermore, calculus formation ceases at death, which means inclusions of debris after death are unlikely to happen (Middleton and Rovner 1994). Dental calculus thus preserves an antemortem record of the oral microbiome and of the microscopic debris (e.g., food, pollen, grit) that came into direct contact with the surface of faunal and hominin teeth (Buckley et al. 2014; Blondiaux and Charlier 2008; Dobney 1994; Dobney and Brothwell 1987; Hardy et al. 2012; Vandermeersch et al. 1994).
Figure 6: The particles and biomolecules that not only affect dental calculus formation, but can also become incorporated and preserved within the calculus matrix (from Metcalf et al. 2014:322).

Figure 7. Dental calculus that formed on an upper molar of a Neanderthal individual, El Sidrón, Spain (original image is credited to the Paleoanthropology Group MNCN-CSIC; see also Weyrich et al. 2017).
How we know what dental calculus indicates

The proof-of-concept studies for dental calculus were first performed on samples from cattle, sheep, and horse teeth (Armitage 1975). Oral phytoliths, the silica component of plant cells, were present in these animal samples, prompting further archaeological research. Dobney and Brothwell (1986, 1987, 1988), for instance, practised macroscopic quantification and description of dental calculus (see also Belcastro et al. 2007; Hillson 2000; Humphrey et al. 2014; Jankauskas and Palabeckaite 2006; Keenleyside 2008; Lillie 1996). Macroscopic analysis, however, is limited by the number of dental calculus deposits present, especially in cases where deposits detach from the tooth surface and become lost postdepositionally (Buikstra and Ubelaker 1994), creating a biased sample. On the other hand, microscopic analysis generates high resolution images, enabling the identification of food particles and in situ microorganisms found in dental calculus samples even under circumstances where calculus deposits are few in number (Charlier et al. 2010; Dobney 1994; Power et al. 2014).

Previous microscopic-based research on dental calculus worked under a crucial assumption: that much of the preserved material inside the samples represented food consumed, offering insight into what items were intentionally eaten in the past (Radini et al. 2016a, 2016b). Yet dietary information obtained from calculus samples is not as straightforward as originally assumed (Hillson 1979; Lillie and Richards 2000; Meiklejohn and Zvelebil 1991). There is now an increasing awareness of how debris from non-dietary-related sources can become embedded in the dental calculus matrix (Beck and Torrence 2006). Accidental inhalation or ingestion of non-dietary debris, oral hygiene practices, and paramasticatory processes are just some of the pathways through which particles enter and remain inside the mouth (Blatt et al. 2011; Blondiaux and Charlier 2008; Buckley et al. 2014; Charlier et al. 2010; Hardy 2016; Hardy et al. 2017).
It is worth mentioning here that dental calculus has also been used for stable isotope analysis in addition to bone collagen (Scott and Poulson 2012); however, Salazar-García et al. (2014) demonstrated that there is no correlation between isotope ratios found in bone collagen and in bulk dental calculus. Dental calculus samples are thus unsuitable for use in stable isotopes studies. Their use in stable isotope analysis will only result in the destruction of the sample and the loss of valuable microscopic remains without much benefit in return.

**How to use dental calculus for reconstructing Neanderthal diets**

Dental calculus preserves direct evidence of foods eaten as opposed to stable isotopes which only reflect sources of protein or which only provide an imprecise measure of ‘total energy’ intake (i.e., from $\delta^{13}$Capatite only). Entrapped food particles are useful for answering questions about diet, environment, and disease in the past. Recent discussions of dental calculus deposits have focused on ancient humans and Neanderthals in particular (Henry and Piperno 2008; Henry et al. 2011; Li et al. 2013; Piperno and Dillehay 2008; Wesolowski et al. 2010). Yet the weaknesses of dental calculus studies lie in the analytical and identification techniques involved, because they are difficult to perform accurately. To analyse plant microfossils trapped within dental calculus, for example, the sample must be submerged in water; however, there are risks of contamination and de-calcification of the sample as a consequence of submersion (Henry et al. 2014:46–48). The analysis part is not without flaws either: identifying starch grains and phytoliths to the species level, for instance, is nearly impossible on account of the structural similarities between vastly different species (Hardy et al. 2009).

Similar to studies based on stable isotopes, there are also concerns about how much of a person’s diet is represented in dental calculus deposits given the complex formation processes (Hillson 2005; Lieverse 1999; Marcotte and Lavoie 1998). The use of dental
calculus deposits for indicating Neanderthal diets must be accompanied by a robust understanding of the different pathways through which debris becomes incorporated into the dental calculus matrix. Accounting for the variation between samples will then lead to more accurate identifications, descriptions, and interpretations of the contents of dental calculus deposits (Radini et al. 2017; see also Buckley et al. 2014; Hardy et al. 2012; Horrocks et al. 2014; Wang et al. 2015; Warinner et al. 2014, 2015a, 2015b; Weyrich et al. 2015, 2017 for examples of good practice).
Faecal biomarkers: what they are and their potential uses

Faecal biomarkers are measurable indicators of biological processes; some are the result of microbial action, but most can be traced to hominin and animal waste (Bull et al. 2002; Sistiaga et al. 2014b). Sterols and stanols are lipids that remain relatively stable after consumption, making them ideal faecal biomarkers to trace (Floate 1970; Peters et al. 2005; Sistiaga et al. 2014a). 5β-stanols, for example, result from the metabolic reduction of cholesterol and phytosterols in mammals; these stanols have been shown to indicate dietary preferences (Bull et al. 2002; Macdonald et al. 1983). The process by which sterols and stanols are converted is still poorly understood, though several microorganisms have been identified as potential influencing factors (Eyssen et al. 1973; Freier et al. 1994; Gérard 2014; Gérard et al. 2007; Ren et al. 1996; Velga et al. 2005). Faecal biomarkers hold great promise then for elucidating the interaction between microorganisms and their hosts.

Identifying Neanderthal faecal matter remains a challenge, because preservation and excavation conditions differ between sites. But, once more samples are found, they will be a valuable tool for palaeodietary reconstructions (Bryant and Dean 2006:58–60). The application of faecal matter analysis to archaeological contexts has been successful already (Bull et al. 2002; D’Anjou et al. 2012; Evershed et al. 1997; Gülacara et al. 1990; Lin et al. 1978; Sistiaga et al. 2014a), leading to a deeper understanding of diets that were specific to past individuals; however, this research is still relatively new. The small number of Neanderthal faecal samples that are available provide tentative evidence for aspects of Neanderthal diets such as meat and plant consumption (Sistiaga et al. 2014b).
Chapter 3  Materials and methods

The published stable isotope data for Neanderthals and fauna from Late Pleistocene Europe created the opportunity for me to critically assess the prevailing narrative about Neanderthal diets. Bocherens (2003) and Fabre et al. (2011) provided the bulk of the raw data, though their datasets had to be compiled and formatted to suit the statistical analysis outlined below (refer to Table 2 and Table 3 for compiled data). Their datasets also had several problems which were not possible to fix. One, the authors derived their data from Neanderthal and faunal bone collagen only. Best practice would be to correlate results from bone collagen with that of bone apatite (Kellner and Schoeninger 2007). Two, the number and the types of fauna at Neanderthal sites differed, restricting which Late Pleistocene Neanderthals were suitable for dietary analysis (Bocherens 2011). Three, the format of published isotope ratios from Bocherens (2003) was drastically different to Fabre et al. (2011), especially in relation to their supplementary material. Neanderthal research seems to lack a standardised format for stable isotope ratios, though an open-access, communally curated database could solve this problem (refer to Kristiansen 2014:17–18). In spite of the complications, my statistical analysis of the published datasets provided tentative dietary reconstructions for five Late Pleistocene Neanderthals.

To assess the relative contributions of different food sources to the isotope ratios of Late Pleistocene Neanderthals, I applied FRUITS, a Bayesian mixing model, to a select few. Fernandes et al. (2014) designed this model specifically for dietary reconstructions (e.g., Sayle et al. 2016), though the application of mixing models to isotope data for Neanderthals is not unusual. Bocherens et al. (2005) performed a similar analysis of the Saint-Césaire I Neanderthal using a multi-source mixing model (from Phillips and Gregg 2003). My criteria for selecting appropriate consumers and foods sources were the following: the Neanderthals (consumers) and their associated fauna (food sources) had to be from the same site and
period; and the food sources used in the mixing model had to be shared in common across the chosen sites. Five Neanderthals from three sites in France fit the criteria. The sites: Jonzac, Les Pradelles, and Saint-Césaire had Neanderthals with associated fauna and they shared three types of associated fauna in common, including bovids, horses, and reindeer (Table 3). The stable isotope data for the five Neanderthals and their associated fauna then had to be entered into the mixing model.

In regards to the food sources, the mean of the $\delta^{13}C$ and $\delta^{15}N$ values from each faunal type became the source values and the standard deviations became the ‘uncertainty’ values (Table 3); the uncertainty values acted as the margins of error in this case. C$_3$ plants represented a fourth food source, but I lacked isotope ratios for plants from the Late Pleistocene period. After referring to the rates of isotope fractionation previously summarised in Figure 4, I reduced the bovid $\delta^{13}C$ values by 5‰ and the bovid $\delta^{15}N$ values by 4‰ in order to estimate the isotope ratios for C$_3$ plants (Table 3; see also Ambrose 1991:297-299; Hartman 2011:124; Jenkins et al. 2001:338).

There is precedent for inferring plant isotope ratios from bovid isotope ratios (Hoppe et al. 2006). But, bovid isotope ratios reflect the isotope ratios for C$_3$ grasses which are, for bovids, their primary food source. Assuming that Late Pleistocene Neanderthals (i.e., the consumers) practised broad-based subsistence strategies, similar to their Middle Pleistocene predecessors (Hardy and Moncel 2011), the plant isotope ratios should include high uncertainty values in order to account for the consumption of different plant foods (El Zaatari et al. 2011, 2016; Fiorenza et al. 2011; Sorensen and Leonard 2001). To determine the uncertainty values, I referred to Schoeninger (2010:447–453) and their review of the typical ranges of carbon and nitrogen isotope ratios for C$_3$ plants. I halved the typical ranges estimated by Schoeninger (2010:448, fig. 25.1) in order to be conservative. Hence, I estimated the uncertainty values for the plant $\delta^{13}C$ to be 4‰ and for the plant $\delta^{15}N$ to be 3‰.
In regards to the consumers (i.e., the five Neanderthals), I noted that the consumer diet-body offset for $\delta^{15}$N was important for understanding the trophic level of the consumer (Bocherens and Drucker 2003b; Hedges and Reynard 2007; Schoeninger 1985). First, I assumed the consumer diet-body offset for $\delta^{13}$C to be 0. The (r) model developed by Fernandes (2015) would be suitable for analysing sources of dietary carbon in consumers, but sources of dietary nitrogen were more relevant to these experiments. Second, I used two consumer diet-body offsets for $\delta^{15}$N in order to compare what difference the offsets made to the results. 4.6‰ served as the ‘control’ offset; while 6.3‰ became the ‘radical’ offset (refer to O’Connell et al. 2012). The mixing model generated ten box plots of the results: five using the 4.6‰ offset (Figures 8a, 8c, 8e, 8g, 8i) and five using the 6.3‰ offset (Figures 8b, 8d, 8f, 8h, 8j).

One thing to note, however: Fernandes et al. (2014) recommended that expert prior information (e.g., data from physiological or metabolic studies) be included in order to obtain more precise dietary reconstructions. I lacked this expert information due to my inexperience. Furthermore, my estimation of the $C_3$ plant isotope ratios, and the uncertainty values, was based on several assumptions that may prove to be incorrect. Though their precision is in question, the results of the model emphasise that the consumer diet-body offset has significant implications for the reconstruction of Neanderthal diets.

Findings from the stable isotope data and the mixing model then had to be compared to other types of evidence, starting with dental calculus studies. The most comprehensive dental calculus studies published to date include those led by Stephen Buckley, Mark Horrocks, Anita Radini, Tingting Wang, Christina Warinner, and Laura Weyrich (Hardy 2016, pers. comm.). The dental calculus studies of Neanderthal material, as well as faecal biomarkers from Neanderthal contexts, formed a counterpoint to the stable isotope analyses of Neanderthal and faunal bone collagen and to the results from the mixing model.
Chapter 4  Results

In brief, the title of the box plots provides the consumer ID and data (i.e., the Neanderthal and their isotope ratios with uncertainty values in parentheses). The boxes provide a 68% confidence interval (corresponding to the 16th and 84th percentiles); while the whiskers provide a 95% confidence interval (corresponding to the 2.5th and 97.5th percentiles). The horizontal continuous line indicates the average, whereas the horizontal discontinuous line indicates the median (50th percentile). The x-axis represents the food sources and the y-axis represents the estimated percentage that each food source contributed to the overall diet of the consumer.

Refer to the discussion below for a reconsideration of the isotope ratios for seventeen Neanderthals from Late Pleistocene Europe (Table 2) and their associated fauna. The basis for the reconsideration includes:

1. the Bayesian modelling of isotope ratios for five Late Pleistocene Neanderthals from the same period and geographic area (Figures 8a–8j):
   - S-EVA-2152.1 (Jonzac, France) – shortened to SEVA2152;
   - M300 (Les Pradelles, France);
   - M400 (Les Pradelles, France);
   - M100 (Les Pradelles, France);
   - RFB7000 (Saint-Césaire, France);

2. findings from the dental calculus deposits and faecal biomarkers of Middle and Late Pleistocene Neanderthals.
Figure 8a: Proportion of animal- and plant-based foods for S-EVA-2152.1. δ¹⁵N diet-body offset ['control']: 4.6‰ (refer to O'Connell et al. 2012).
Figure 8b: Proportion of animal- and plant-based foods for S-EVA-2152.1. δ¹⁵N diet-body offset ('radical'): 6.3‰ (refer to O’Connell et al. 2012).
Figure 8c: Proportion of animal- and plant-based foods for M300. $\delta^{15}N$ diet-body offset ['control']: 4.6‰ (refer to O'Connell et al. 2012).
Figure 8d: Proportion of animal- and plant-based foods for M300. δ¹⁵N diet-body offset ['radical']: 6.3‰ (refer to O’Connell et al. 2012).
Figure 8e: Proportion of animal- and plant-based foods for M400. $\delta^{15}$N diet-body offset ['control']: 4.6‰ (refer to O'Connell et al. 2012).
Figure 8f: Proportion of animal- and plant-based foods for M400. $\delta^{15}N$ diet-body offset (‘radical’): 6.3‰ (refer to O’Connell et al. 2012).
Figure 8g: Proportion of animal- and plant-based foods for M100. $\delta^{15}\text{N}$ diet-body offset ['control']: 4.6‰ (refer to O'Connell et al. 2012).
Figure 8h: Proportion of animal- and plant-based foods for M100. δ\(^{15}\)N diet-body offset ['radical']: 6.3‰ (refer to O’Connell et al. 2012).
Figure 8i: Proportion of animal- and plant-based foods for RFB7000. δ¹⁵N diet-body offset ['control']: 4.6‰ (refer to O'Connell et al. 2012).
Figure 8j: Proportion of animal- and plant-based foods for RFB7000. $\delta^{15}\text{N}$ diet-body offset ['radical']: 6.3‰ (refer to O'Connell et al. 2012).
Chapter 5  Neanderthal diets: discussion

Review of the isotopic evidence for Late Pleistocene Europe

Before discussing the results of the mixing model, it is important to take stock and consider the actual number of Neanderthals for which there is isotopic evidence. For Late Pleistocene Europe, there are measurements of δ^{13}C and δ^{15}N for seventeen Neanderthal individuals from nine archaeological sites (Table 2; see also Figures 3 and 9 for periodisation and map). These numbers are staggeringly low considering the extent of Neanderthal presence in Europe during the Late Pleistocene; their occupation of the region for that period lasted at least 100,000 years (Richards et al. 2001a).

Table 2 lists the data for each of the seventeen Neanderthals; while Table 3 summaries the data for fauna from three French sites. Figure 9 on the other hand illustrates the wide geographic range of Neanderthals in Europe during MIS 3, serving as a reminder of the many types of environments that Neanderthals were able to inhabit successfully (see also Figure 2). With this in mind, the seventeen Neanderthals are not enough to reconstruct diet-related behaviours or determine food preferences for Neanderthal populations as a whole, much less for the species; however, the seventeen can still be assessed individually in order to obtain biographical information. Moreover, their isotope ratios can be compared in order to explore the similarities and differences between individuals and between sites. The following comparisons though will require the exclusion of several sets of measurements.
Table 2. List of published isotopic results for Neanderthal collagen samples found in Late Pleistocene contexts (after Bocherens 2009; Fábret 2011; see also Kurzmin and Keates 2014 for radiocarbon dates).

The list is arranged alphabetically by location and then chronologically. Dates are approximate. References are arranged alphabetically.

Not all results shown below matched the criteria proposed by Ambrose (1996) in regards to the concentration of carbon and nitrogen in collagen samples. This calls into question how reliable some of these results are.

1. Bocherens et al. (2001) compared the isotope values of MT200 to cow data from Schaldina.
2. Higham et al. (2006) revised the radiocarbon dates and the isotope values of VI-207 and VI-208 that were originally measured by Richards et al. (2000). Both sets of results are included.
3. Richards et al. (2008) published three results; however, S-EVA-21521 was found to be the most reliable result.
4. Beausset et al. (2006) compared the isotope values of RDV02-H8-51 to cow data from Les Pradelles.

<table>
<thead>
<tr>
<th>No analysis</th>
<th>Site (layer)</th>
<th>Location</th>
<th>Period (years before present)</th>
<th>Sample</th>
<th>Associated fauna</th>
<th>$\delta^{13}C$ (%)</th>
<th>$\delta^{15}N$ (%)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC18500</td>
<td>Schaldina Cave (4A)</td>
<td>Belgium</td>
<td>MIS 5c (100,000 BP)</td>
<td>maxilla</td>
<td>yes</td>
<td>-19.9</td>
<td>10.9</td>
<td>Bocherens et al. 1999; Bocherens et al. 2005</td>
</tr>
<tr>
<td>MT500</td>
<td>Schaldina Cave (3)</td>
<td>Belgium</td>
<td>MIS 5b (90,000 BP)</td>
<td>phalanx</td>
<td>yes</td>
<td>-21.2</td>
<td>11.8</td>
<td>Bocherens et al. 2001; Bocherens et al. 2005; Elwood et al. 2004</td>
</tr>
<tr>
<td>MT200 1</td>
<td>Spy Cave (SPY OMO 1)</td>
<td>Belgium</td>
<td>MIS 3 (40,000 - 35,000 BP)</td>
<td>scapula</td>
<td>yes</td>
<td>-19.8</td>
<td>11.0</td>
<td>Cordy 1988; Bocherens et al. 2001</td>
</tr>
<tr>
<td>MT100</td>
<td>Awirs Cave (Engis 2)</td>
<td>Belgium</td>
<td>MIS 3 (39,400 ± 2,170 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-19.6</td>
<td>12.6</td>
<td>Cordy 1988; Bocherens et al. 2001; Toussaint and Pirson 2005</td>
</tr>
<tr>
<td>2089-07 2</td>
<td>Vindija Cave (G1) (VI-207)</td>
<td>Croatia</td>
<td>MIS 3 (32,400 ± 1,800 BP)</td>
<td>mandible</td>
<td>yes</td>
<td>-24.6</td>
<td>11.1</td>
<td>Higham et al. 2006</td>
</tr>
<tr>
<td>2089-06 2</td>
<td>Vindija Cave (G1) (VI-208)</td>
<td>Croatia</td>
<td>MIS 3 (32,400 ± 800 BP)</td>
<td>parietal</td>
<td>yes</td>
<td>-20.2</td>
<td>10.3</td>
<td>Higham et al. 2006</td>
</tr>
<tr>
<td>8296 2</td>
<td>Vindija Cave (G1) (VI-206)</td>
<td>Croatia</td>
<td>MIS 3 (29,000 ± 400 BP)</td>
<td>mandible</td>
<td>yes</td>
<td>-19.5</td>
<td>10.1</td>
<td>Richards et al. 2000; Richards et al. 2001a; Smith et al. 1999</td>
</tr>
<tr>
<td>8295 2</td>
<td>Vindija Cave (G1) (VI-206)</td>
<td>Croatia</td>
<td>MIS 3 (28,000 ± 400 BP)</td>
<td>parietal</td>
<td>yes</td>
<td>-20.5</td>
<td>10.8</td>
<td>Richards et al. 2000; Richards et al. 2001a; Smith et al. 1999</td>
</tr>
<tr>
<td>RDV02-H8-51 4</td>
<td>Les Rochers</td>
<td>France</td>
<td>MIS 3 (45,200 ± 1,100 BP)</td>
<td>femur</td>
<td>yes</td>
<td>-19.0</td>
<td>11.6</td>
<td>Beauval et al. 2006; Beauval et al. 2006</td>
</tr>
<tr>
<td>27801</td>
<td>Les Pradelles (9), formerly known as 'Marillac'</td>
<td>France</td>
<td>MIS 3 (45,000 - 40,000 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-20.2</td>
<td>9.3</td>
<td>Bocherens et al. 1991; Fizet et al. 1995</td>
</tr>
<tr>
<td>64801</td>
<td>Les Pradelles (10), formerly known as 'Marillac'</td>
<td>France</td>
<td>MIS 3 (45,000 - 40,000 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-19.1</td>
<td>11.6</td>
<td>Fizet et al. 1995</td>
</tr>
<tr>
<td>M300</td>
<td>Les Pradelles, formerly known as 'Marillac'</td>
<td>France</td>
<td>MIS 3 (45,000 - 40,000 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-19.1</td>
<td>11.5</td>
<td>Bocherens et al. 2005</td>
</tr>
<tr>
<td>M400</td>
<td>Les Pradelles, formerly known as 'Marillac'</td>
<td>France</td>
<td>MIS 3 (45,000 - 40,000 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-19.5</td>
<td>11.4</td>
<td>Bocherens et al. 2005</td>
</tr>
<tr>
<td>M100 2</td>
<td>Les Pradelles, formerly known as 'Marillac'</td>
<td>France</td>
<td>MIS 3 (45,000 - 40,000 BP)</td>
<td>skull</td>
<td>yes</td>
<td>-21.8</td>
<td>8.4</td>
<td>Bocherens et al. 2005</td>
</tr>
<tr>
<td>RPB7000</td>
<td>Saint-Césaire (Ejop)</td>
<td>France</td>
<td>MIS 3 (36,200 ± 750 BP)</td>
<td>fibula</td>
<td>yes</td>
<td>-19.8</td>
<td>11.4</td>
<td>Bocherens and Dacker 2003a; Bocherens et al. 2005; Hübner et al. 2012</td>
</tr>
<tr>
<td>NN4</td>
<td>Kleine Feldhofer Grotte</td>
<td>Germany</td>
<td>MIS 3 (40,360 ± 760 BP)</td>
<td>fibula</td>
<td>yes</td>
<td>-18.8</td>
<td>na</td>
<td>Schmitz et al. 2002</td>
</tr>
<tr>
<td>Nea1</td>
<td>Kleine Feldhofer Grotte</td>
<td>Germany</td>
<td>MIS 3 (39,900 ± 620 BP)</td>
<td>humerus</td>
<td>yes</td>
<td>-21.6</td>
<td>7.9</td>
<td>Bonani 2006; Richards and Schmitz 2008; Richards et al. 2000; Schmitz et al. 2002</td>
</tr>
<tr>
<td>NN1</td>
<td>Kleine Feldhofer Grotte</td>
<td>Germany</td>
<td>MIS 3 (39,240 ± 570 BP)</td>
<td>humerus</td>
<td>yes</td>
<td>-21.5</td>
<td>9.0</td>
<td>Bonani 2006; Richards and Schmitz 2008; Richards et al. 2000; Schmitz et al. 2002</td>
</tr>
<tr>
<td>Site</td>
<td>Location</td>
<td>Period</td>
<td>Fauna</td>
<td>Sample size</td>
<td>Max (%)</td>
<td>Min (%)</td>
<td>Mean (%)</td>
<td>SD (σ)</td>
</tr>
<tr>
<td>------------</td>
<td>----------</td>
<td>--------</td>
<td>-------</td>
<td>-------------</td>
<td>---------</td>
<td>---------</td>
<td>----------</td>
<td>--------</td>
</tr>
<tr>
<td>Jonzac</td>
<td>France</td>
<td>MIS 3</td>
<td></td>
<td>δ¹³C 20</td>
<td>-19.5</td>
<td>-20.7</td>
<td>-20.2</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 20</td>
<td>9.5</td>
<td>4.1</td>
<td>5.6</td>
<td>1.37</td>
</tr>
<tr>
<td>Les Pradelles</td>
<td>France</td>
<td>MIS 3</td>
<td>BOVID</td>
<td>δ¹³C 5</td>
<td>-19.7</td>
<td>-20.1</td>
<td>-19.8</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 5</td>
<td>8.1</td>
<td>5.9</td>
<td>6.8</td>
<td>0.93</td>
</tr>
<tr>
<td>Saint-Césaire</td>
<td>France</td>
<td>MIS 3</td>
<td></td>
<td>δ¹³C 2</td>
<td>-19.9</td>
<td>-20.5</td>
<td>-20.2</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 2</td>
<td>7.8</td>
<td>5.3</td>
<td>6.5</td>
<td>1.76</td>
</tr>
<tr>
<td>Jonzac</td>
<td>France</td>
<td>MIS 3</td>
<td>HORSE</td>
<td>δ¹³C 10</td>
<td>-20.1</td>
<td>-21.1</td>
<td>-20.4</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 10</td>
<td>7.1</td>
<td>3.7</td>
<td>5.2</td>
<td>0.99</td>
</tr>
<tr>
<td>Les Pradelles</td>
<td>France</td>
<td>MIS 3</td>
<td>HORSE</td>
<td>δ¹³C 22</td>
<td>-19.2</td>
<td>-22.2</td>
<td>-20.6</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 22</td>
<td>7.9</td>
<td>2.3</td>
<td>5.0</td>
<td>1.41</td>
</tr>
<tr>
<td>Saint-Césaire</td>
<td>France</td>
<td>MIS 3</td>
<td>HORSE</td>
<td>δ¹³C 5</td>
<td>-20.3</td>
<td>-21.7</td>
<td>-21.0</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 5</td>
<td>8.5</td>
<td>5.6</td>
<td>6.5</td>
<td>1.17</td>
</tr>
<tr>
<td>Jonzac</td>
<td>France</td>
<td>MIS 3</td>
<td>REINDEER</td>
<td>δ¹³C 12</td>
<td>-18.4</td>
<td>-20.2</td>
<td>-19.2</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 12</td>
<td>9.4</td>
<td>5.3</td>
<td>7.2</td>
<td>1.09</td>
</tr>
<tr>
<td>Les Pradelles</td>
<td>France</td>
<td>MIS 3</td>
<td>REINDEER</td>
<td>δ¹³C 12</td>
<td>-19.0</td>
<td>-20.4</td>
<td>-19.7</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 12</td>
<td>5.5</td>
<td>0.9</td>
<td>3.6</td>
<td>1.16</td>
</tr>
<tr>
<td>Saint-Césaire</td>
<td>France</td>
<td>MIS 3</td>
<td>REINDEER</td>
<td>δ¹³C 8</td>
<td>-18.8</td>
<td>-19.6</td>
<td>-19.1</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>δ¹⁵N 8</td>
<td>6.7</td>
<td>3.5</td>
<td>4.8</td>
<td>1.21</td>
</tr>
</tbody>
</table>
Figure 9: Nine archaeological sites dated to the Late Pleistocene for which isotopic data has been retrieved from Neanderthal individuals (modified from Fiorenza et al. 2015:48). These individuals inhabited: conifer woodland [COW], mixed conifer and deciduous forest [CDF], and shrub tundra [STU].

Note: the Scladina Cave Neanderthals (in blue) are dated to MIS 5; refer to Figure 2(A) for their palaeoenvironmental contexts.
The reasons for excluding certain measurements are case-specific. NN 4 from Kleine Feldhofer Grotte, for instance, lacked a measurement for δ¹⁵N (Schmitz et al. 2002); its carbon isotope ratio must be excluded for this reason. In addition, Neanderthals 27801 and 64801 from Les Pradelles exhibited ‘ambiguous chemical compositions’, casting doubt onto the reliability of their respective isotope ratios (Bocherens et al. 2005:76). The two Vindija Cave individuals are also troublesome: later authors (Higham et al. 2006) published isotope ratios that differed from the original investigators (Smith et al. 1999; Richards et al. 2000; Richards et al. 2001a). Bocherens (2009:245) explained these discrepancies, noting that the Neanderthal remains from Vindija contained poorly preserved collagen and that Richards et al. (2000) did not successfully purify the collagen during their palaeodietary analysis. Yet the isotope ratios for Neanderthal VI-207 from Higham et al. (2006) are peculiar; their measurement for δ¹³C is −24.6‰, a value that falls outside the expected range for both Neanderthals and herbivores from the above dataset (Table 3). Their published values for Neanderthal VI-208 seem more reliable, differing from the original investigators by only 0.3‰ and 0.5‰ for δ¹³C and δ¹⁵N respectively. With this in mind, the measurements for Neanderthal VI-207 will have to be taken from Richards et al. (2000) (−19.5‰, 10.1‰); while the revised measurements for Neanderthal VI-208 will be taken from Higham et al. (2006) (−20.2‰, 10.3‰).

The difference in biological age between the Neanderthal individuals warrants the exclusion of another individual. Neanderthal MT100 (Engis 2) from Awirs Cave is a juvenile of, perhaps, five or six years of age (Tillier 1983). Breast milk consumption at this young age is one explanation for why the juvenile has an unusually high δ¹⁵N value of 12.6‰ (Fogel et al. 1989; Jenkins et al. 2001; Katzenberg and Pfeiffer 1995), providing good cause to exclude its measurements. By contrast, Neanderthal SC18800 (SCLA 4A-2) is
approximately eleven years old (Otte et al. 1993), a post-weaning stage at which the effects of nursing would be insignificant (Bocherens et al. 2005:78).

Yet the dates of the Neanderthals from Scladina Cave are worth taking into account here. Though Neanderthals SC18800 and MT500 have reliable measurements for their δ¹³C and δ¹⁵N values and have fauna associated with them, the two have been dated to a much earlier period of the Late Pleistocene than the other fifteen individuals. The two Neanderthals from Scladina will be excluded in order to refrain from comparing individuals that lived at least 50,000 years apart from each other (refer to ‘Period’ column in Table 2 and to Figure 3).

After pruning the list of Neanderthals, what we are left with is a frustratingly small sample: we excluded six individuals, leaving a mere eleven left to consider. Of the eleven Neanderthals, one is from Belgium, two are from Croatia, six from France, and two from Germany (Figure 9). Note that these Neanderthals inhabited vastly different palaeoenvironments to each other. The expectation then would be that their isotope ratios are less likely to correlate.

The Croatian Neanderthal individuals comprise parts of the skull (e.g., mandible, parietal), which means different collagen turnover rates are not a problem in their case (Hedges et al. 2007). The δ¹⁵N values for the Croatian Neanderthals (–19.5‰, 10.1‰ and –20.2‰, 10.3‰) are lower than those from French sites; however, their δ¹³C and δ¹⁵N values are comparable to Neanderthal MT200 from Spy Cave, Belgium (–19.8‰, 11.0‰). Yet the Croatian and Belgian Neanderthals inhabited two different ecosystems: mixed conifer and deciduous forest and shrub tundra respectively (Figure 9). The three Neanderthals somehow maintained similar ratios of carbon and nitrogen isotopes in spite of the differences in location and environments; this quirk in the data was not addressed by the original investigators (e.g., Richard et al. 2001a). In addition, the isotope ratios for the French
Neanderthals are remarkably similar. With the exception of Neanderthal M100 (H2), the French Neanderthals have $\delta^{13}C$ values ranging from $-19.8\%$ to $-19.0\%$ and $\delta^{15}N$ values which range from $11.2\%$ to $11.6\%$. The suggestion then is that Neanderthals who inhabited parts of France were eating similar food sources in similar proportions, but the results of the Bayesian mixing model do not support this (Figures 8a–8j).

The sixth French Neanderthal, M100 (H2) from Les Pradelles, appears to be somewhat of an outlier with $-21.8\%$ for $\delta^{13}C$ and $8.4\%$ for $\delta^{15}N$. What is puzzling is that Neanderthal M100’s contemporaries from the same site, Neanderthals M300 and M400, do not present with similarly unusual isotope ratios. The difference is not related to the type of bone sampled; the three Les Pradelles individuals had their skull fragments used for collagen extraction. The three of them are adults, which means biological age is unlikely to be a marked influencing factor either. But, Neanderthal M100’s $\delta^{13}C$ and $\delta^{15}N$ values do match those of the two German Neanderthals: Nea 1 ($-21.6\%, 7.9\%$) and NN1 ($-21.5\%, 9.0\%$). The isotope ratios suggest the feeding habits of these three Neanderthals were different to the other eight individuals, because the $\delta^{15}N$ values for Neanderthals M100, Nea 1, and NN1 resemble those of a herbivore rather than a carnivore (refer to Table 3; see also Figures 5 and 10).

Here the results of the mixing model FRUITS offer new insights. Returning to Neanderthal M100, it is significant that the estimated contribution of plant-based foods for this individual’s diet ranges from at least 10% to 65%; moreover, the ‘control’ case and the ‘radical’ case correlate with each other in relation to plant consumption (Figures 8g and 8h). This finding supports the idea that Neanderthal M100 subsisted on more plant foods than its contemporaries. What remains uncertain is whether or not the matching isotope values of Neanderthals Nea 1 and NN1 also correspond to the consumption of more plant foods.
In sum, the published isotope data for Neanderthals and the results of the mixing model suggest that the contributions of animal- and plant-based foods to Neanderthal diets varied considerably from one individual to the next. Isotope ratios of consumers – if studied in isolation – appear to be a crude measurement of actual dietary intake, especially if we consider the 95% confidence intervals for each food source analysed by the mixing model (Figures 8a–8j). Of note is that the expected contributions of animal- and plant-based foods change drastically depending on the consumer diet-body offset used in the mixing model; the accepted range of 3‰–5‰ for consumer offsets (e.g., Bocherens and Drucker 2003b) may need to be reconsidered in light of this.
Neanderthal diets and stable isotopes: the assumptions

The merits of stable isotope analysis for Neanderthal studies are clear: isotope ratios reflect habits of eating that were practised over the course of several months or years (Hedges et al. 2007; Tykot 2004). Neanderthal isotope ratios derived from bone collagen, for example, shed light on potential sources of food for Neanderthals in Late Pleistocene Europe. Yet there are several problems to address; these problems not only apply to past research, but also to this dissertation.

The first problem lies in data collection. As useful as they are for indicating diets, Neanderthal and faunal isotopes ratios are too few in number for conclusions to be made about European-based populations or about the Homo neanderthalensis species in general. Attempting to do so is not best practice.

The second problem lies in how reliable isotope ratios are. Most dietary reconstructions based on the bone collagen of Neanderthals work under several assumptions:

1. the δ¹³C and δ¹⁵N values in consumers correspond to the types of plant- and animal-based foods they consumed during life (Ambrose 1993);
2. more specifically, the nitrogen isotope ratios in the bone collagen of the consumer relate to the types and amounts of protein consumed;
3. the length of time in life reflected in isotope ratios depends on where bone collagen is extracted from (Hedges et al. 2007);
4. the changes in nitrogen isotope ratios from one trophic level to the next, referred to as the ‘trophic level effect’ or ‘enrichment’, are accumulative (DeNiro and Epstein 1978; Minagawa and Wada 1984; see also Figure 4);
5. the ‘trophic level effect’ occurs at a predictable rate (e.g., Figure 10).

Assumptions in archaeology are necessary due in part to the fragmented nature of the archaeological record. Carbon and nitrogen isotope ratios then are crucial pieces of data for
dietary reconstructions; however, Bocherens et al. (2005) cautioned that plant foods tend to be lower in protein than meat, creating the potential for plant foods to be isotopically invisible if the consumer is practising an omnivorous diet.

Of note are the first and second assumptions: that isotope ratios relate to the foods which Neanderthals ate. In other words, the isotope ratios for Neanderthals reflect what was on their plates (Tykot 2004). Yet Late Pleistocene Europe underwent severe environmental change in relation to temperature, precipitation, and vegetation (Bradtmöller et al. 2012; see also Figure 2). Plant $\delta^{15}$N values have been shown to fluctuate due to temperature changes during the Late Pleistocene period (Drucker and Bocherens 2004; Drucker et al. 2003a, 2003b; Hardy 2010; Jouzel et al. 2006; Richards and Hedges 2003). Furthermore, plant $\delta^{15}$N values tend to vary widely by plant type (Bocherens 2003; see also Figures 11 and 12). In light of these facts, the estimated isotope ratios for C$_3$ plants used in the Bayesian mixing model FRUITS do not seem radical. Rather, the estimates were conservative (refer to Figure 10). More importantly, if Neanderthals were consuming a significant amount of plant foods directly, or indirectly through eating the meat of herbivores, their isotope ratios would also tend to fluctuate.

Diet-related behaviours can also affect consumer isotope ratios as was suggested in the cases of Neanderthals M100, Nea 1, and NN1. Buck et al. (2016), for example, raised concerns about the effects of ‘gastrophagy’, the practice of eating the stomach contents of prey, on the isotope ratios of the consumer. While gastrophagy is a well documented practice in ethnographic studies (Buck and Stringer 2014), its effect on isotope ratios in Neanderthals is less clear; the stomach contents of their prey differed substantially.

In support of the previous statement – that the prey of Neanderthals had different stomach contents – the isotope ratios in herbivore bone collagen from Late Pleistocene Europe show consistent patterns of variation (Bocherens 2003), reflecting different food
preferences, different metabolisms, and changes to the environment (see also Figures 2 and 9). The findings from Svihus and Holland (2006) on reindeer nutrition corroborate the isotope ratios of reindeer from Late Pleistocene Europe. Svihus and Holland (2006) assessed the effects of lichen consumption in reindeer, emphasising that lichens were high in carbohydrates and low in protein. This provides the most parsimonious explanation for why Late Pleistocene reindeer exhibit the most positive $\delta^{13}C$ values out of the three faunal species analysed (refer to Table 3 and Figure 10; see also Batts et al. 2004; Beazley et al. 2002). In addition, Svihus and Holand (2006:647) argued that the consumption of lichens also correlates positively with nitrogen losses (McEwan and Whitehead 1970). In that case, you would expect the consumption of reindeer stomach contents to change the nitrogen isotope ratios of the consumer (e.g., a Neanderthal). Yet Buck et al. (2016:677) suggested gastrophagy would cause $\delta^{15}N$ enrichment in the consumer, conflating incorrectly the possible effects of gastrophagy with the known effects of breast milk consumption in nursing infants (Fuller et al. 2006; Humphrey 2014).

The argument by Buck et al. (2016) is made weaker still by their reference to warm-adapted forager groups (e.g., aboriginal Australians, the Kuria, the Khoesan, and the G/wi) rather than cold-adapted ones (see Daanen and Van Marken Lichtenbelt 2016; Launay and Savourey 2009); analogous data from cold-adapted foragers would have been more applicable to Neanderthal research. Buck et al. (2016) were correct in one regard though: in order to interpret stable isotope ratios accurately, it is essential to understand how diet-related practices and preferences can affect consumer isotope ratios. Further research is needed in order to determine what those effects are and whether they are significant.
Figure 10: Isotopic variations in the terrestrial trophic webs of Late Pleistocene European mammals and plants that were contemporaneous with Neanderthals (from Bocherens 2009:243). Note the large ranges both within and between trophic levels (i.e., steps in the pyramid).
Figure 11: Possible causes of carbon isotopic variations in herbivores and plants based on $\delta^{13}$C values measured in modern arctic, temperate, and steppic areas (from Bocherens 2003:58; for values, see Bocherens et al. 1994, 1996, 2000; Nelson et al. 1986; Rodière et al. 1996).

Figure 12: Possible causes of nitrogen isotopic variations in herbivores and plants based on $\delta^{15}$N values measured in modern arctic, temperate, and steppic areas (from Bocherens 2003:60; for values, see Bocherens et al. 1994, 1996, 2000; Nelson et al. 1986; Rodière et al. 1996).
Also of note is the third assumption: that the isotope ratios from different bones will relate to a shorter or longer period of time of an individual’s life depending on the collagen turnover rate specific to the bone analysed (Hedges et al. 2007). This is becoming less of an assumption and more of a known fact. But, as can be seen in the current Neanderthal dataset (Table 2), archaeologists are limited by the number and types of bones available to analyse. Comparing and contrasting isotope ratios between individuals becomes complicated, because archaeologists are not comparing like with like. Rather, they compare collagen from skulls, from teeth, from long bones, and from pedal phalanxes (Table 2), without accounting for the collagen turnover rates of different bones (Hedges et al. 2007). Even if the differences are small, ignoring them is not best practice either.

To finish, there are the fourth and fifth assumptions: that changes in nitrogen isotope ratios from one trophic level to the next are accumulative and predictable. This trophic level effect is usually assumed to be +3‰–5‰ in the archaeological literature (Figure 10; see also Bocherens and Drucker 2003b; DeNiro and Epstein 1981; Schoeninger and DeNiro 1984). But, isotopic variations occur between species and even between individuals depending on eating patterns, food preferences, and biological adaptations to their respective ecosystems (Fraser et al. 2006). Even in the small samples of Neanderthals and associated fauna, it is clear that isotopic variations between individuals living in the same ecosystem are common (Table 2 and Figure 9). Isotopic variations between individuals complicate archaeological interpretations, because they raise questions about whether isotope ratios are an artefact of food consumption or of biological differences, such as differing metabolisms and microbiomes.
Neanderthal diets and stable isotopes: the challenges

How accurate is the trophic level effect for Neanderthals if the estimates were originally based on animals? This is where medical science is beginning to provide tantalising answers. O’Connell et al. (2012) tested the trophic level effect in living humans by placing five males and six females on controlled, isotopically known diets. To reduce the effects of short-term changes to eating patterns on consumer isotope ratios, O’Connell et al. (2012) ensured that the diets of the test subjects matched closely with their habitual diets. Body tissue samples were taken after a 30-day period.

The results of O’Connell et al.’s (2012) longitudinal study were surprising: the $\delta^{15}N$ enrichment appeared to be $3.5\%$ based on the subjects’ red blood cells. The researchers then used measured offsets to determine an approximate rate in keratin and in bone collagen (see O’Connell et al. 2001 for living human data; see also O’Connell and Hedges 1999; Richards 2006 for archaeological human data). The estimated rate in bone collagen ranged from $5.9\%$ to $6.3\%$; however, the most conservative estimate came to $4.6\%$. The conservative estimate for bone collagen was calculated by assuming a minimum $\delta^{15}N$ enrichment in red blood cells and then applying the minimum offsets to keratin and to collagen. Notably, the conservative estimate is still at the upper end of the currently accepted range for $\delta^{15}N$ enrichment in previous palaeodietary reconstructions (e.g., Bocherens and Drucker 2003b). The conclusion of this longitudinal study was that the contributions of animal protein to prehistoric hominin diets have, perhaps, been overestimated (O’Connell et al. 2012:430–432). If $\delta^{15}N$ enrichment is indeed higher than the accepted range, then higher $\delta^{15}N$ isotope ratios in Neanderthals are not necessarily indicative of a disproportionately meat-based diet (as argued by Bocherens et al. 1999, 2005; Richards and Trinkaus 2009; Richards et al. 2000).
There are instances where the nitrogen balance within an organism is disrupted, for example, during pregnancy (Fuller et al. 2004) or during times of physiological stress (Fuller et al. 2005). Moreover, there are types of plants which distort $\delta^{15}N$ isotope ratios within the consumer; legumes are one example of this (Szpak et al. 2014), though plant-soil systems also play a role in determining the transfer of nitrogen through the food web (Szpak 2014). Stable isotope studies from Pan troglodytes verus – a species related to living humans and Neanderthals – shed light on hominin feeding patterns and behaviours through time (Fahy et al. 2013, 2014; however, see Schoeninger et al. 2016 for cautionary notes). But, even with cross-species comparisons, methodologies based solely on isotope studies fall short of providing direct evidence of plant- and animal-based food consumption by Neanderthals. This is especially true for parts of western Asia where bone collagen preserves poorly (Ambrose 1998), preventing isotope analysis from being performed on Neanderthal individuals from that region. Isotope studies then must be paired with other methods in order to more accurately reconstruct Neanderthal diets and to understand what their isotope ratios indicate.

But, how did other authors interpret the isotope ratios of Neanderthals? Richards and Trinkaus (2009) suggested – on the basis of the isotopic evidence – that Neanderthals in Late Pleistocene Europe were top-level carnivores who subsisted predominantly on meat from large herbivores. They contrast this behaviour with that of early modern humans who exhibited a wider range of isotopic ratios (Richards and Trinkaus 2009, tables S1 and S2), implying that the dietary breadth of early modern humans was greater than their Neanderthal counterparts. Yet their view fails to hold up to scrutiny if their interpretations are compared to those made for Neanderthals from Spanish and French contexts. Finlayson et al. (2006), as well as Hardy and Moncel (2011), demonstrated that Neanderthals practised varied diets which included the consumption of small game and aquatic resources. In light of these
findings, Neanderthals and early modern humans do not seem so different. The stable isotopes alone provided a skewed picture for Late Pleistocene Neanderthals unless they were compared with those of recent human populations (e.g., Schoeninger 2014).
**Reconstructing Neanderthal diets using alternative methods**

The analysis of light stable isotopes such as carbon and nitrogen has been shown to be problematic for palaeodietary reconstructions. Therefore, other types of evidence are worth including here as a counterpoint to carbon and nitrogen isotope-based interpretations of Neanderthal diets during the Late Pleistocene. This section is not intended to be exhaustive. Rather, it is demonstrative, highlighting three promising types of evidence for Neanderthal diets: heavier stable isotopes, dental calculus, and faecal biomarkers.

**Heavier stable isotopes**

Given the geographic distribution of Neanderthals in Late Pleistocene Europe (Figures 1 and 9), assessments of mobility from their place of birth to their place of death will be significant for palaeodietary reconstructions moving forward. Schoeninger (1982), for example, utilised strontium isotope analysis in order to investigate changes in skeletal morphology between archaic modern humans and fully modern humans (see also Sillen and Kavanagh 1982). In brief, the ratio between two strontium isotopes ($^{87}$Sr and $^{86}$Sr) – which accumulate in tooth enamel as a result of ingested food and water – can be used to determine the mobility of an individual and to reconstruct past ecosystems (Bentley 2006; Ericsen 1985). The hypothesis for the above study linked changes in diet and activity to a decrease in skeletal robustness through time. Schoeninger (1982) combined trace element analysis with x-ray diffraction patterns for both human and faunal bone in order to correct the margin of error introduced by diagenesis, i.e., by the chemical changes that occur to bone postmortem (Nelson et al. 1986). Postdepositional processes interfere with results, but Schoeninger (1982) handled them with a holistic approach to dietary reconstruction and with an awareness of the difficulties of inter-site comparisons. The ratio between sulphur isotopes in bone collagen have similar applications to Neanderthal research (Nehlich and
Richards 2009; Richards and Hedges 2003; Richards et al. 2001b). Heavier stable isotopes then are a viable option to explore in order to answer questions about Neanderthal diets and mobility.

**Dental calculus**

Dental calculus samples contain direct evidence for individual meals or once-off events during which teeth were used to cut, grind, and soften fibrous material (Radini et al. 2016a). A collection of calculus samples shed light on patterns of tooth use and dietary intake between individuals. In relation to reconstructing Neanderthal diets, the evidence and analysis of dental calculus from Neanderthal individuals is a nascent, but growing field (Henry et al. 2014).

In terms of dietary analysis, dental calculus samples from Neanderthals have contained evidence of plant food consumption, both raw and cooked (Buckley et al. 2014; Hardy et al. 2012). Evidence from Neanderthal dental calculus found at El Sidrón, Spain, for example, pointed to paramasticatory processes in Neanderthals who used their teeth as a third hand (Radini et al. 2016b); furthermore, Weyrich et al. (2017) identified several dietary components from the El Sidrón Neanderthals, including mushrooms, pine nuts, forest moss, and poplar (see also Power et al. 2015a). On the other hand, evidence from Sima del Elefante, Spain, indicated consumption of animal fat, as well as starchy carbohydrates from two plants – all of which were eaten raw by Neanderthals in this case (Hardy et al. 2017). These findings match those from molar macrowear and microwear studies on Neanderthal teeth from Pleistocene Europe (El Zaatari et al. 2011, 2016; Fiorenza et al. 2011), supporting the hypothesis that the dietary breadth of Neanderthals has been underestimated in previous studies (e.g., Bocherens et al. 1999, 2005; Richards and Trinkaus 2009; Richards et al. 2000).
Hardy et al. (2017) also inferred environmental data from their dental calculus samples: the inclusions of spores, insect fragments, and conifer pollen grains are consistent with a forested environment, confirming an environmental context for the Neanderthals from Sima del Elefante, Spain (Figure 9; see also Warinner et al. 2015a). The findings from Sima del Elefante also suggest that Neanderthals were capable of selecting and using plant resources suitable for consumption or for use as raw materials. Analogous data from modern chimpanzees (Huffman 2003; Janmaat et al. 2013; McGrew 2010a, 2010b), and even insects (Singer et al. 2009), support this suggestion.

In addition to understanding what plants are safe for consumption, Neanderthals seemed to have possessed knowledge of the medicinal properties of plants. Hardy et al. (2012), for instance, found evidence of self-medication in Neanderthal dental calculus samples. They identified compounds of two non-nutritional plants, yarrow and camomile, that are bitter-tasting to living humans and indeed to Neanderthals (Lalueza-Fox et al. 2009). But, the two plants are also known for their medicinal qualities (e.g., antimicrobial, anti-inflammatory). The suggestion therein was that the bitter-tasting plants were deliberately consumed by the Neanderthals in order to self-medicate (Hardy et al. 2013; but see Buck and Stringer 2014; Krief et al. 2015 for alternative hypotheses). Shotgun-sequencing of ancient DNA from Neanderthal dental calculus has provided more information: the sample for so-called El Sidrón 1 Neanderthal contained sequences of poplar and *Penicillium*; these have pain-relieving and antibiotic properties respectively (Weyrich et al. 2017). Reasons for this Neanderthal to self-medicate include a dental abscess and a gastrointestinal pathogen referred to as *Enterocytozoon bieneusi*, both of which were probably uncomfortable to live with (Hardy et al. 2012; Weyrich et al. 2017). The evidence of self-medication suggests a high degree of complexity in terms of plant lore and cognitive ability. For the Neanderthals in question, the act of selecting and consuming plants during times of physiological discomfort
(e.g., Hardy et al. 2016a) required cognitive decision-making that resembles what humans are capable of today (see also Hardy et al. 2016b).

The relationship between dental calculus and caries is another piece of the puzzle. Quantifying the prevalence of dental calculus and caries, for example, provides a general picture of dietary intake (Radini et al. 2017:73). High calculus deposition and low incidence of caries suggest a high protein intake (Keenleyside 2008; Lillie and Richards 2000). On the other hand, high incidence of both dental calculus and caries suggest a diet that is high in carbohydrates (Humphrey et al. 2014; White 1994). These inferences are problematic though – as are studies based on stable isotopes – because they lack specific details about macronutrient ratios, for example, or about actual foods that were consumed.

Analogous data from primatological studies is worth mentioning here. Power et al. (2015b), for example, performed a high resolution analysis of dental calculus samples from from the wild chimpanzees (*Pan troglodytes verus*) of Taï National Park. Their results demonstrated that some microremains trapped in dental calculus can be long-term dietary markers; while the amount of plant microfossils in calculus can reflect the proportion of plant foods in the diet. Leonard et al. (2015) came to similar conclusions after testing the dental calculus samples from a living human population (the Twe), though they cautioned that dental calculus is potentially a better indicator of plant consumption across a population rather than at an individual level. Dental calculus samples from archaeological contexts can be similarly informative if the appropriate methods are applied.

But, there is potential for archaeologists to overinterpret the results from dental calculus deposits. Henry et al. (2011), for instance, studied dental calculus samples from seven Neanderthal teeth. Their assertion was that Neanderthals Shanidar III, Spy I, and Spy II consumed cooked plant food and ingested a diverse range of plants, including ‘low-ranked’ underground storage organs (see also Power et al. 2015a). Henry et al. (2011) then
extended this point to include all hominins that existed as early as the Late Middle Palaeolithic (see also Bocherens 2011; Boscato et al. 2011; Ecker et al. 2013; Gaudzinski and Roebroeks 2011 for Middle Pleistocene perspective). This is, perhaps, an overinterpretation rather than a conclusive fact given the small sample of seven teeth from three Neanderthals, of which two are from Belgium (Spy I and II) and the other from Iraq (Shanidar III). But, it is remarkable that dental calculus deposits seem to preserve tentative evidence of cooking. The complexity of diet-related behaviours in Neanderthals becomes more and more apparent moving forward (e.g., Clement et al. 2012; Finlayson et al. 2006; Hardy and Moncel 2011).

Syntheses of evidence from multiple individuals and sites are more appropriate to draw substantial inferences from (Henry et al. 2014; Wang et al. 2015). Dental calculus studies have an advantage over the stable isotope analysis of bone collagen, because dental calculus preserves well in both Europe and western Asia. By contrast, Neanderthal bone collagen seems to only preserve well in Europe (Ambrose 1998). Dental calculus deposits thus create an opportunity to perform cross-regional studies on Neanderthal feeding patterns, resulting in a deeper understanding of Neanderthal behaviours and diets.

**Faecal biomarkers**

Faecal matter from archaeological contexts continues to contribute to our understanding of the meals and diets of past individuals (Bull et al. 2002; D’Anjou et al. 2012; Evershed et al. 1997; Gülacara et al. 1990; Lin et al. 1978; Sistiaga et al. 2014a). In relation to faecal biomarkers, Sistiaga et al. (2014b) successfully found evidence for plant consumption in sediment samples from Et Salt, Spain. The high proportion of coprostanol indicated meat consumption by Neanderthals; however, the presence of 5β-stigmastanol suggested that plant foods were another significant part of Neanderthal diets at this Middle Palaeolithic site.
(Sistiaga et al. 2014b:2–5). Faecal biomarkers are unique, because they preserve what were likely individual meals eaten by Neanderthals in this case. More samples must be recovered from Late Pleistocene Neanderthal sites in Europe in order to extrapolate further. But, even at this early stage, faecal biomarkers reveal plant-based food consumption by Neanderthals to a larger extent than would otherwise have been possible.
Reconsidering the ‘meat-eater’ narrative for Neanderthals

Much of the discussion up to this point has been devoted to evidence of plant-based food consumption by Neanderthals. But, there is no denying that meat was also a significant part of Neanderthal diets in Late Pleistocene Europe. The term ‘meat’, however, is problematic. What do archaeologists mean when they refer to ‘meat’ (e.g., Fiorenza et al. 2015)? The term remains nondescript in the literature without distinguishing, say, between muscle tissue and the visceral organs. The distinction is important though, because muscle tissue would be nutrient-poor in comparison to visceral organs, especially in terms of B vitamins and of minerals such as iron and zinc (Williams 2007:5). Consumption of one over the other likely affects the consumer isotope ratios; moreover, there is evidence that Neanderthals from Spain and France consumed aquatic resources such as fish (Finlayson et al. 2006; Hardy and Moncel 2011), which also affect consumer nitrogen isotope ratios (Richards et al. 2001a; Pettitt et al. 2003). Medical data from living populations has the potential to sharpen our understanding of how different diets, or even specific foods, can change consumer isotope ratios (DeNiro and Schoeninger 1983; O’Connell et al. 2012). With the above concerns in mind, archaeologists should think critically about what they mean when referring to ‘meat’ or other animal-based foods.

The effects of meat consumption in general is also worth commenting on. It seems that Neanderthals and other hominins were able to develop, evolve, and thrive despite the disadvantages associated with meat consumption in current human populations. Neanderthals were able to overcome, for example, increased exposure to pathogens and causative agents of cancer, as well as negative impacts to cardiovascular and bone health (Cao and Nielsen 2010; Cao et al. 2011; Chitnis et al. 2008; Davies et al. 2006; Finch 2010; Finch and Stanford 2004; Mensah 2014; Pan et al. 2011; Roberts 2008; Sandhu et al. 2002; Werner and Bruchim 2009). On the one hand, Fleming and Boyd (2000), Frank et al. (2009),
Halbesma et al. (2009), and Lagiou et al. (2012) demonstrate the dangers of high-protein consumption. Noto et al. (2013) and Schwingshackl and Hoffmann (2013) also identify the ill effects associated with low carbohydrate intake (i.e., low plant food intake). Further analysis of the Neanderthal genome may reveal how they overcame these ill effects (Cordain et al. 2002; Green et al. 2010). On the other hand, plant foods have been shown to be more nutritious and beneficial for long-term health in humans (Craig 2009; Perry et al. 2007; Slavin 2003; Wobber et al. 2008; Ye et al. 2012; see also Jacobs et al. 2009). This fact is also pertinent to understanding long-term health in Neanderthals. Targeted archaeological research into prehistoric plant-based food consumption may further elucidate the hominin relationship with plants through time (Day 2013; Lee-Thorp and Sponheimer 2006), and perhaps also corroborate the medical research on that topic.
Conclusions

Returning to the original research questions of this dissertation, we now have some answers. For one, the archaeological evidence for Late Pleistocene Neanderthal diets is extensive for European contexts. Yet there are concerns about the poorly informed use of a relatively small amount of stable isotope data (Makarewicz and Sealy 2015). Fluctuations in isotope fractionation and distribution through the food web, for example, weaken the validity of stable isotope studies, especially for Late Pleistocene European contexts. Two assessments formed a counterpoint to the stable isotope ratios of Neanderthals from Late Pleistocene Europe: (1) the Bayesian modelling of isotope ratios for five Late Pleistocene Neanderthals from France; and (2) a review of complementary evidence from the faecal biomarkers and dental calculus deposits of other Middle and Late Pleistocene Neanderthals. The results from the Bayesian mixing model and the complementary evidence both demonstrated that plant-based food consumption by Neanderthals was higher than previous isotope-based studies had suggested (Bocherens et al. 1999, 2005; Richards and Trinkaus 2009; Richards et al. 2000). Furthermore, the evidence from dental calculus suggested that Neanderthals possessed sophisticated knowledge of plant lore and of the medicinal properties of plant foods. An interdisciplinary approach to reconstructing Neanderthal diets, similar to the one applied in this dissertation, will produce a clearer picture of what foods were on Neanderthals’ plates in Late Pleistocene Europe.

In relation to how archaeological accounts about Neanderthal diets can contribute to modern medicine, the potential for interdisciplinarity has been demonstrated throughout this piece. Archaeological research, for example, suggests that plants formed an essential part of hominin diets and contributed to the development of our physiologies through time (Hardy et al. 2015; Kay 1977; Langdon 2006; Milton 2000b; Sponheimer et al. 2013); while meta-analyses of the medical literature indicate that a diet rich in plant-based foods and
materials improves health, prevents or even reverses disease, and proves to be more environmentally sustainable than a diet based on animal-derived fats and proteins (Aune et al. 2016, 2017; Craig and Mangels 2009; Wang et al. 2014). The two disciplines seem to agree on the importance of plant foods in the past and present. Interpretations of Neanderthal diets that do not engage with the above points are missing an opportunity to comment and reflect on how archaeological research may not be able to interpret or reconstruct the past without assistance from other disciplines.

In relation to the future directions for Neanderthal research and the intersection between archaeology and medicine, one thing is clear: archaeologists would be naive to think that what we disseminate into the public domain has no effect on public opinion and policy. Rather, our contributions can be positive by demonstrating the unique relationships that hominins have developed with both plants and animals through time. These stories are worth sharing and celebrating in order to instil in the public a sense of how the human condition is not a fixed state. The environment shapes us, just as we shape the environment, prompting us to make more informed decisions about what foods to eat or how to adapt to a changing world (Carlsson-Kanyama and González 2009; Robson 2009).
Note: for ease of access, Digital Object Identifiers (DOI) have been used to identify references; however, some references are only available via Uniform Resource Locator (URL) or in print.


DOI: https://doi.org/10.1002/(SICI)1096-8644(199604)99:4<585::AID-AJPA5>3.0.CO;2-T


DOI: https://doi.org/10.3290/j.ohpd.a9761


DOI: https://doi.org/10.1016/0305-4403(90)90007-R


DOI: https://doi.org/10.1016/0305-4403(91)90067-Y


DOI: https://doi.org/10.1007/BF02437397


DOI: https://doi.org/10.1016/0305-4403(75)90056-4


DOI: https://doi.org/10.1136/bmj.i2716

DOI: [https://doi.org/10.1093/ije/dyw319](https://doi.org/10.1093/ije/dyw319)


DOI: [https://doi.org/10.1016/j.chemgeo.2003.11.007](https://doi.org/10.1016/j.chemgeo.2003.11.007)


DOI: [https://doi.org/10.1073/pnas.0502656102](https://doi.org/10.1073/pnas.0502656102)


URL [accessed 30 March 2017]: [https://goo.gl/NflRhv](https://goo.gl/NflRhv)

DOI: [https://doi.org/10.1017/S0033822200032124](https://doi.org/10.1017/S0033822200032124)


DOI: [https://doi.org/10.1002/ajpa.20530](https://doi.org/10.1002/ajpa.20530)


DOI: [https://doi.org/10.1007/s10816-006-9009-x](https://doi.org/10.1007/s10816-006-9009-x)


DOI: [https://doi.org/10.1006/jasc.2002.0834](https://doi.org/10.1006/jasc.2002.0834)


DOI: [https://doi.org/10.1080/14034940410028398](https://doi.org/10.1080/14034940410028398)


DOI: [https://doi.org/10.1002/oa.1173](https://doi.org/10.1002/oa.1173)


DOI: [https://doi.org/10.1002/oa.931](https://doi.org/10.1002/oa.931)


DOI: [https://doi.org/10.1086/203544](https://doi.org/10.1086/203544)

DOI: [https://doi.org/10.1126/science.1075374](https://doi.org/10.1126/science.1075374)


DOI: [https://doi.org/10.1002/oa.662](https://doi.org/10.1002/oa.662)


DOI: [https://doi.org/10.1016/0047-2484(91)90021-M](https://doi.org/10.1016/0047-2484(91)90021-M)


DOI: [https://doi.org/10.1016/0031-0182(94)90095-7](https://doi.org/10.1016/0031-0182(94)90095-7)


DOI: [https://doi.org/10.1016/S0031-0182(96)00068-5](https://doi.org/10.1016/S0031-0182(96)00068-5)


DOI: https://doi.org/10.1086/201570


DOI: https://doi.org/10.1086/202699

DOI: [https://doi.org/10.1016/j.quaint.2010.10.015](https://doi.org/10.1016/j.quaint.2010.10.015)


DOI: [https://doi.org/10.1017/S0033822200044118](https://doi.org/10.1017/S0033822200044118)


DOI: [https://doi.org/10.1016/j.palaeo.2005.11.032](https://doi.org/10.1016/j.palaeo.2005.11.032)


DOI: [https://doi.org/10.1016/j.quascirev.2013.09.003](https://doi.org/10.1016/j.quascirev.2013.09.003)


DOI: [https://doi.org/10.1016/j.jasrep.2015.09.025](https://doi.org/10.1016/j.jasrep.2015.09.025)

DOI: [https://doi.org/10.1371/journal.pone.0100808](https://doi.org/10.1371/journal.pone.0100808)


DOI: [https://doi.org/10.1016/S0160-4120(01)00124-6](https://doi.org/10.1016/S0160-4120(01)00124-6)


DOI: [https://doi.org/10.1097/MCO.0b013e32833df691](https://doi.org/10.1097/MCO.0b013e32833df691)


DOI: [https://doi.org/10.3945/jn.110.129361](https://doi.org/10.3945/jn.110.129361)

DOI: [https://doi.org/10.3945/ajcn.2009.26736AA](https://doi.org/10.3945/ajcn.2009.26736AA)


DOI: [https://doi.org/10.1016/j.legalmed.2010.03.003](https://doi.org/10.1016/j.legalmed.2010.03.003)


DOI: [https://doi.org/10.1158/1078-0432.CCR-07-4879](https://doi.org/10.1158/1078-0432.CCR-07-4879)


DOI: [https://doi.org/10.1007/978-1-4020-5121-0_7](https://doi.org/10.1007/978-1-4020-5121-0_7)

DOI: [https://doi.org/10.1016/j.jhevol.2011.11.014](https://doi.org/10.1016/j.jhevol.2011.11.014)


DOI: [https://doi.org/10.1038/sj.ejcn.1601353](https://doi.org/10.1038/sj.ejcn.1601353)


DOI: [https://doi.org/10.3945/ajcn.2009.26736N](https://doi.org/10.3945/ajcn.2009.26736N)


DOI: [https://doi.org/10.1016/j.jada.2009.05.027](https://doi.org/10.1016/j.jada.2009.05.027)

DOI: [https://doi.org/10.1007/s40496-016-0080-4](https://doi.org/10.1007/s40496-016-0080-4)


DOI: [https://doi.org/10.1080/23328940.2015.1135688](https://doi.org/10.1080/23328940.2015.1135688)


DOI: [https://doi.org/10.1073/pnas.1212730109](https://doi.org/10.1073/pnas.1212730109)


DOI: [https://doi.org/10.1007/s00384-005-0776-8](https://doi.org/10.1007/s00384-005-0776-8)


DOI: [https://doi.org/10.1177/00220345700490061501](https://doi.org/10.1177/00220345700490061501)

DOI: https://doi.org/10.1016/j.archoralbio.2015.03.004


DOI: https://doi.org/10.1093/jxb/ert068


DOI: https://doi.org/10.1016/0047-2484(87)90005-4


DOI: https://doi.org/10.1016/0016-7037(78)90199-0


DOI: https://doi.org/10.1016/0016-7037(81)90244-1

DOI: [https://doi.org/10.1016/0305-4403(83)90002-X](https://doi.org/10.1016/0305-4403(83)90002-X)


DOI: [https://doi.org/10.1016/0305-4403(87)90024-0](https://doi.org/10.1016/0305-4403(87)90024-0)


DOI: [https://doi.org/10.1002/oaj.753](https://doi.org/10.1002/oaj.753)

URL [accessed 30 March 2017]: [https://goo.gl/1DT07h](https://goo.gl/1DT07h)


DOI: [https://doi.org/10.1016/S0031-0182(03)00366-3](https://doi.org/10.1016/S0031-0182(03)00366-3)


DOI: [https://doi.org/10.1016/S0012-821X(03)00514-4](https://doi.org/10.1016/S0012-821X(03)00514-4)


DOI: [https://doi.org/10.1016/j.jhevol.2013.06.013](https://doi.org/10.1016/j.jhevol.2013.06.013)

DOI: [https://doi.org/10.1016/j.jhevol.2011.05.004](https://doi.org/10.1016/j.jhevol.2011.05.004)


DOI: [https://doi.org/10.1371/journal.pone.0153277](https://doi.org/10.1371/journal.pone.0153277)


DOI: [https://doi.org/10.1016/j.jas.2003.08.009](https://doi.org/10.1016/j.jas.2003.08.009)


DOI: [https://doi.org/10.1016/S0047-2484(85)80029-4](https://doi.org/10.1016/S0047-2484(85)80029-4)


DOI: [https://doi.org/10.1006/jasc.1996.0132](https://doi.org/10.1006/jasc.1996.0132)


DOI: [https://doi.org/10.4061/2011/689315](https://doi.org/10.4061/2011/689315)


DOI: [https://doi.org/10.1073/pnas.1221991110](https://doi.org/10.1073/pnas.1221991110)


DOI: [https://doi.org/10.1002/ajpa.22464](https://doi.org/10.1002/ajpa.22464)


URL [accessed 30 March 2017]: [https://goo.gl/RSTzD7](https://goo.gl/RSTzD7)

DOI: https://doi.org/10.1111/arcm.12193


DOI: https://doi.org/10.1371/journal.pone.0087436


DOI: https://doi.org/10.1073/pnas.0909606106


DOI: https://doi.org/10.1086/381662


DOI: https://doi.org/10.1038/nature05195
DOI: [https://doi.org/10.1371/journal.pone.0014769](https://doi.org/10.1371/journal.pone.0014769)

DOI: [https://doi.org/10.1002/ajpa.22659](https://doi.org/10.1002/ajpa.22659)

DOI: [https://doi.org/10.1016/S0305-4403(95)80163-4](https://doi.org/10.1016/S0305-4403(95)80163-4)

DOI: [https://doi.org/10.1177/000331970005101003](https://doi.org/10.1177/000331970005101003)

DOI: [https://doi.org/10.1016/0038-0717(70)90005-2](https://doi.org/10.1016/0038-0717(70)90005-2)


DOI: [https://doi.org/10.3945/ajcn.2009.27601](https://doi.org/10.3945/ajcn.2009.27601)


DOI: [https://doi.org/10.1002/rcm.2424](https://doi.org/10.1002/rcm.2424)


DOI: [https://doi.org/10.1099/00207713-44-1-137](https://doi.org/10.1099/00207713-44-1-137)


DOI: [https://doi.org/10.1002/rcm.1708](https://doi.org/10.1002/rcm.1708)

DOI: [https://doi.org/10.1002/rcm.2090](https://doi.org/10.1002/rcm.2090)


DOI: [https://doi.org/10.1002/ajpa.20249](https://doi.org/10.1002/ajpa.20249)


DOI: [https://doi.org/10.1017/S0079497X00002723](https://doi.org/10.1017/S0079497X00002723)


DOI: [https://doi.org/10.1006/jhev.1999.0359](https://doi.org/10.1006/jhev.1999.0359)


DOI: [https://doi.org/10.3390/pathogens3010014](https://doi.org/10.3390/pathogens3010014)


DOI: [https://doi.org/10.1128/AEM.02806-06](https://doi.org/10.1128/AEM.02806-06)


DOI: [https://doi.org/10.1126/science.1188021](https://doi.org/10.1126/science.1188021)

DOI: [https://doi.org/10.1016/0305-4403(90)90050-F](https://doi.org/10.1016/0305-4403(90)90050-F)


DOI: [https://doi.org/10.1681/ASN.2008060649](https://doi.org/10.1681/ASN.2008060649)


DOI: [https://doi.org/10.1016/j.quascirev.2009.11.016](https://doi.org/10.1016/j.quascirev.2009.11.016)


DOI: [https://doi.org/10.1371/journal.pone.0023768](https://doi.org/10.1371/journal.pone.0023768)


DOI: [https://doi.org/10.1016/j.jas.2008.09.015](https://doi.org/10.1016/j.jas.2008.09.015)


DOI: [https://doi.org/10.1007/s00114-012-0942-0](https://doi.org/10.1007/s00114-012-0942-0)


DOI: [https://doi.org/10.1017/S0003598X00049528](https://doi.org/10.1017/S0003598X00049528)


DOI: [https://doi.org/10.1086/682587](https://doi.org/10.1086/682587)


DOI: [https://doi.org/10.1016/j.quaint.2015.04.033](https://doi.org/10.1016/j.quaint.2015.04.033)

DOI: [https://doi.org/10.15184/acy.2016.134](https://doi.org/10.15184/acy.2016.134)


DOI: [https://doi.org/10.1007/s00114-016-1420-x](https://doi.org/10.1007/s00114-016-1420-x)


DOI: [https://doi.org/10.1016/0305-4403(91)90066-X](https://doi.org/10.1016/0305-4403(91)90066-X)


DOI: [https://doi.org/10.1534/genetics.116.186890](https://doi.org/10.1534/genetics.116.186890)


DOI: [https://doi.org/10.1111/j.1365-2435.2010.01782.x](https://doi.org/10.1111/j.1365-2435.2010.01782.x)

DOI: [https://doi.org/10.1038/322822a0](https://doi.org/10.1038/322822a0)


DOI: [https://doi.org/10.1016/j.jas.2006.10.015](https://doi.org/10.1016/j.jas.2006.10.015)


DOI: [https://doi.org/10.1002/ajpa.20598](https://doi.org/10.1002/ajpa.20598)


DOI: [https://doi.org/10.1016/j.jas.2007.12.005](https://doi.org/10.1016/j.jas.2007.12.005)


DOI: [https://doi.org/10.1073/pnas.1016868108](https://doi.org/10.1073/pnas.1016868108)


DOI: [https://doi.org/10.1006/jhev.1997.0149](https://doi.org/10.1006/jhev.1997.0149)


DOI: [https://doi.org/10.1073/pnas.0510005103](https://doi.org/10.1073/pnas.0510005103)


DOI: [https://doi.org/10.1038/nature13621](https://doi.org/10.1038/nature13621)

DOI: [https://doi.org/10.1080/00438243.1979.9979758](https://doi.org/10.1080/00438243.1979.9979758)


DOI: [https://doi.org/10.1098/rstb.2015.0008](https://doi.org/10.1098/rstb.2015.0008)


DOI: [https://doi.org/10.1130/G22745.1](https://doi.org/10.1130/G22745.1)


DOI: [https://doi.org/10.1080/03036758.2013.842177](https://doi.org/10.1080/03036758.2013.842177)

DOI: [https://doi.org/10.1073/pnas.1212924109](https://doi.org/10.1073/pnas.1212924109)


DOI: [https://doi.org/10.1079/PNS2003257](https://doi.org/10.1079/PNS2003257)


DOI: [https://doi.org/10.3109/03014460.2014.923939](https://doi.org/10.3109/03014460.2014.923939)


DOI: [https://doi.org/10.1067/mpr.2001.113778](https://doi.org/10.1067/mpr.2001.113778)


DOI: [https://doi.org/10.1073/pnas.1318176111](https://doi.org/10.1073/pnas.1318176111)

DOI: [https://doi.org/10.1002/ajhb.22821](https://doi.org/10.1002/ajhb.22821)


DOI: [https://doi.org/10.3945/ajcn.2009.26736B](https://doi.org/10.3945/ajcn.2009.26736B)


DOI: [https://doi.org/10.1007/s10071-013-0617-z](https://doi.org/10.1007/s10071-013-0617-z)


DOI: [https://doi.org/10.1007/s004420100755](https://doi.org/10.1007/s004420100755)

DOI: [https://doi.org/10.1016/j.atherosclerosis.2007.01.008](https://doi.org/10.1016/j.atherosclerosis.2007.01.008)


DOI: [https://doi.org/10.1038/268628a0](https://doi.org/10.1038/268628a0)


DOI: [https://doi.org/10.1002/oa.934](https://doi.org/10.1002/oa.934)


DOI: [https://doi.org/10.1002/ajpa.20618](https://doi.org/10.1002/ajpa.20618)


DOI: https://doi.org/10.1073/pnas.1307308110


DOI: https://doi.org/10.1038/nature06193


DOI: https://doi.org/10.15184/aqy.2014.7


DOI: https://doi.org/10.1021/bk-1984-0258.ch014

DOI: [https://doi.org/10.1097/MCO.0b013e32834b6e5e](https://doi.org/10.1097/MCO.0b013e32834b6e5e)


DOI: [https://doi.org/10.2458/56.16936](https://doi.org/10.2458/56.16936)


DOI: [https://doi.org/10.1136/bmj.e4026](https://doi.org/10.1136/bmj.e4026)


DOI: [https://doi.org/10.1098/rsbl.2009.0532](https://doi.org/10.1098/rsbl.2009.0532)


DOI: [https://doi.org/10.1079/BJN20061805](https://doi.org/10.1079/BJN20061805)


DOI: [https://doi.org/10.2486/indhealth.47.221](https://doi.org/10.2486/indhealth.47.221)

DOI: [https://doi.org/10.1002/ajpa.20519](https://doi.org/10.1002/ajpa.20519)


DOI: [https://doi.org/10.1016/0047-2484(89)90048-1](https://doi.org/10.1016/0047-2484(89)90048-1)


DOI: [https://doi.org/10.1016/j.jasrep.2015.03.009](https://doi.org/10.1016/j.jasrep.2015.03.009)


DOI: [https://doi.org/10.1016/j.jas.2012.11.018](https://doi.org/10.1016/j.jas.2012.11.018)


DOI: [https://doi.org/10.1002/(SICI)1099-1212(199907/08)9:4<219::AID-OA475>3.0.CO;2-V](https://doi.org/10.1002/(SICI)1099-1212(199907/08)9:4<219::AID-OA475>3.0.CO;2-V)

DOI: [https://doi.org/10.1002/ajpa.20672](https://doi.org/10.1002/ajpa.20672)


DOI: [https://doi.org/10.1086/204479](https://doi.org/10.1086/204479)


DOI: [https://doi.org/10.1006/jasc.1999.0544](https://doi.org/10.1006/jasc.1999.0544)


DOI: [https://doi.org/10.1029/2004PA001071](https://doi.org/10.1029/2004PA001071)


DOI: [https://doi.org/10.1038/230241a0](https://doi.org/10.1038/230241a0)


DOI: [https://doi.org/10.1016%2Fj.jas.2015.02.035](https://doi.org/10.1016%2Fj.jas.2015.02.035)


DOI: [https://doi.org/10.1002/(SICI)1520-6505(1999)8:1<22::AID-EVAN7>3.0.CO;2-F](https://doi.org/10.1002/(SICI)1520-6505(1999)8:1<22::AID-EVAN7>3.0.CO;2-F)


DOI: [https://doi.org/10.1086/204691](https://doi.org/10.1086/204691)


DOI: [https://doi.org/10.1038/ng.2930](https://doi.org/10.1038/ng.2930)


DOI: [https://doi.org/10.1006/jasc.1994.1046](https://doi.org/10.1006/jasc.1994.1046)


DOI: [https://doi.org/10.1525/aa.1981.83.3.02a00020](https://doi.org/10.1525/aa.1981.83.3.02a00020)


DOI: [https://doi.org/10.1016/S0899-9007(99)00078-7](https://doi.org/10.1016/S0899-9007(99)00078-7)


DOI: [https://doi.org/10.1016/S0899-9007(00)00293-8](https://doi.org/10.1016/S0899-9007(00)00293-8)


DOI: [https://doi.org/10.1016/0016-7037(84)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7)

Moncel MH 2011. Technological behaviour and mobility of human groups deduced from lithic assemblages in the Late Middle and Early Late Pleistocene of the Middle Rhône Valley (France). In: Conard NJ and Richter J (eds). *Neanderthal lifeways, subsistence and technology: one hundred fifty years of Neanderthal study*. New York: Springer, 261–287.


DOI: [https://doi.org/10.1007/s12520-009-0003-6](https://doi.org/10.1007/s12520-009-0003-6)


DOI: [https://doi.org/10.1016/0016-7037(86)90250-4](https://doi.org/10.1016/0016-7037(86)90250-4)


DOI: [https://doi.org/10.1371/journal.pone.0055030](https://doi.org/10.1371/journal.pone.0055030)


DOI: [https://doi.org/10.1006/jasc.1998.0383](https://doi.org/10.1006/jasc.1998.0383)

DOI: [https://doi.org/10.1006/jasc.2001.0698](https://doi.org/10.1006/jasc.2001.0698)


DOI: [https://doi.org/10.1002/ajpa.22140](https://doi.org/10.1002/ajpa.22140)


DOI: [https://doi.org/10.1002/ajpa.20025](https://doi.org/10.1002/ajpa.20025)


DOI: [https://doi.org/10.2307/1310735](https://doi.org/10.2307/1310735)


URL [accessed 30 March 2017]: [https://goo.gl/9dBhTu](https://goo.gl/9dBhTu)

DOI: [https://doi.org/10.3945/ajcn.111.018978](https://doi.org/10.3945/ajcn.111.018978)


DOI: [https://doi.org/10.1007/s00442-003-1221-8](https://doi.org/10.1007/s00442-003-1221-8)


DOI: [https://doi.org/10.1038/ng2123](https://doi.org/10.1038/ng2123)


DOI: [https://doi.org/10.1017/S0003598X00061305](https://doi.org/10.1017/S0003598X00061305)

DOI: https://doi.org/10.1007/s00442-003-1218-3


DOI: https://doi.org/10.1073/pnas.0808752105


DOI: https://doi.org/10.1016/j.jas.2014.04.016


DOI: https://doi.org/10.1016/j.jas.2015.04.003


DOI: https://doi.org/10.1038/srep15161

DOI: https://doi.org/10.1038/nature12886


DOI: https://doi.org/10.1086/202699


DOI: https://doi.org/10.15184/agy.2016.21

DOI: [https://doi.org/10.1002/ajpa.23147](https://doi.org/10.1002/ajpa.23147)

Railsback B 2015. Some fundamentals of mineralogy and geochemistry: marine isotope stages and substages. *Department of Geology at University of Georgia*.

URL [accessed 24 Feb 2017]: [https://goo.gl/UYfx7S](https://goo.gl/UYfx7S)


DOI: [https://doi.org/10.1016/0039-128X(95)00173-N](https://doi.org/10.1016/0039-128X(95)00173-N)


DOI: [https://doi.org/10.1016/S0031-0182(03)00229-3](https://doi.org/10.1016/S0031-0182(03)00229-3)

DOI: [https://doi.org/10.1017/S0003598X00097210](https://doi.org/10.1017/S0003598X00097210)


DOI: [https://doi.org/10.1073/pnas.0903821106](https://doi.org/10.1073/pnas.0903821106)


DOI: [https://doi.org/10.1073/pnas.120178997](https://doi.org/10.1073/pnas.120178997)


DOI: [https://doi.org/10.1073/pnas.111155298](https://doi.org/10.1073/pnas.111155298)


DOI: [https://doi.org/10.1016/S0012-821X(01)00427-7](https://doi.org/10.1016/S0012-821X(01)00427-7)

DOI: [https://doi.org/10.1016/j.jhevol.2008.02.007](https://doi.org/10.1016/j.jhevol.2008.02.007)


DOI: [https://doi.org/10.1007/s00442-005-0021-8](https://doi.org/10.1007/s00442-005-0021-8)


PubMed Central ID: [https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1704330/](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1704330/)


DOI: [https://doi.org/10.1177/0884533608324586](https://doi.org/10.1177/0884533608324586)


DOI: [https://doi.org/10.1177/026010600902000205](https://doi.org/10.1177/026010600902000205)


URL [accessed 1 March 2017]: https://goo.gl/ILTGri


DOI: https://doi.org/10.1002/ajpa.1330910103


DOI: https://doi.org/10.1002/ajpa.1330930103


DOI: https://doi.org/10.1016/j.jas.2014.03.026

DOI: [https://doi.org/10.1016/j.plefa.2009.05.013](https://doi.org/10.1016/j.plefa.2009.05.013)


DOI: [https://doi.org/10.1093/jnci/94.13.972](https://doi.org/10.1093/jnci/94.13.972)


DOI: [https://doi.org/10.1038/nature12961](https://doi.org/10.1038/nature12961)


DOI: [https://doi.org/10.1016/j.cub.2016.03.037](https://doi.org/10.1016/j.cub.2016.03.037)


DOI: [https://doi.org/10.1016/j.quageo.2016.07.001](https://doi.org/10.1016/j.quageo.2016.07.001)

DOI: https://doi.org/10.1073/pnas.192464099


DOI: https://doi.org/10.1002/ajpa.1330580105


DOI: https://doi.org/10.1016/S0047-2484(85)80030-0


DOI: https://doi.org/10.1002/9781444320039.ch25


DOI: https://doi.org/10.1146/annurev-anthro-102313-025935

DOI: [https://doi.org/10.1016/0016-7037(84)90091-7](https://doi.org/10.1016/0016-7037(84)90091-7)


DOI: [https://doi.org/10.1002/ajp.22496](https://doi.org/10.1002/ajp.22496)


URL [accessed 30 March 2017]: [https://goo.gl/n5j4PY](https://goo.gl/n5j4PY)


DOI: [https://doi.org/10.1017/S000711451300216X](https://doi.org/10.1017/S000711451300216X)


DOI: [https://doi.org/10.1016/j.jas.2011.09.029](https://doi.org/10.1016/j.jas.2011.09.029)
DOI: https://doi.org/10.1186/1475-2891-13-55

DOI: https://doi.org/10.1002/ajpa.1330250505

DOI: https://doi.org/10.1126/science.aad2149

DOI: https://doi.org/10.1371/journal.pone.0004796

DOI: https://doi.org/10.1016/j.jas.2013.10.016

DOI: [https://doi.org/10.1371/journal.pone.0101045](https://doi.org/10.1371/journal.pone.0101045)


DOI: [https://doi.org/10.1079/PNS2002221](https://doi.org/10.1079/PNS2002221)


DOI: [https://doi.org/10.1073/pnas.96.22.12281](https://doi.org/10.1073/pnas.96.22.12281)


DOI: [https://doi.org/10.1086/201687](https://doi.org/10.1086/201687)


DOI: [https://doi.org/10.1006/jhev.2001.0472](https://doi.org/10.1006/jhev.2001.0472)


DOI: [https://doi.org/10.1002/oa.655](https://doi.org/10.1002/oa.655)


DOI: [https://doi.org/10.1016/S0305-4403(03)00066-9](https://doi.org/10.1016/S0305-4403(03)00066-9)

DOI: [https://doi.org/10.1073/pnas.1222579110](https://doi.org/10.1073/pnas.1222579110)


DOI: [https://doi.org/10.2307/4003160](https://doi.org/10.2307/4003160)

Svyatko S 2008. Information about stable carbon and nitrogen isotope analysis. *Centre for Climate, the Environment, and Chronology (CHRONO)*.


DOI: [https://doi.org/10.3389/fpls.2014.00288](https://doi.org/10.3389/fpls.2014.00288)


DOI: [https://doi.org/10.1016/j.jas.2014.02.007](https://doi.org/10.1016/j.jas.2014.02.007)

URL [accessed 30 March 2017]: https://goo.gl/TiBAAv


DOI: https://doi.org/10.1146/annurev.an.15.100186.001205


URL [accessed 30 March 2017]: https://goo.gl/ANj0wH


DOI: https://doi.org/10.1016/0277-3791(83)90004-5


DOI: https://doi.org/10.1016/j.quageo.2008.01.001


DOI: https://doi.org/10.1029/94GL00177


DOI: [https://doi.org/10.1016/j.femsle.2004.10.042](https://doi.org/10.1016/j.femsle.2004.10.042)


DOI: [https://doi.org/10.1371/journal.pbio.0040072](https://doi.org/10.1371/journal.pbio.0040072)


DOI: [https://doi.org/10.1086/201570](https://doi.org/10.1086/201570)


DOI: [https://doi.org/10.1002/oa.2467](https://doi.org/10.1002/oa.2467)

DOI: [https://doi.org/10.1136/bmj.g4490](https://doi.org/10.1136/bmj.g4490)


DOI: [https://doi.org/10.1038/ng.2906](https://doi.org/10.1038/ng.2906)


DOI: [https://doi.org/10.1098/rstb.2013.0376](https://doi.org/10.1098/rstb.2013.0376)


DOI: [https://doi.org/10.1016/j.jhevol.2014.10.016](https://doi.org/10.1016/j.jhevol.2014.10.016)

DOI: [https://doi.org/10.1080/13813450902783106](https://doi.org/10.1080/13813450902783106)


DOI: [https://doi.org/10.1016/j.jas.2009.12.037](https://doi.org/10.1016/j.jas.2009.12.037)


DOI: [https://doi.org/10.1016/j.jhevol.2014.06.018](https://doi.org/10.1016/j.jhevol.2014.06.018)


DOI: [https://doi.org/10.1038/nature21674](https://doi.org/10.1038/nature21674)


DOI: [https://doi.org/10.1111/j.1747-0080.2007.00197.x](https://doi.org/10.1111/j.1747-0080.2007.00197.x)


DOI: [https://doi.org/10.1016/j.jhevol.2008.03.003](https://doi.org/10.1016/j.jhevol.2008.03.003)


DOI: [https://doi.org/10.3945/jn.111.155325](https://doi.org/10.3945/jn.111.155325)