A view to a kill : investigating Middle Palaeolithic subsistence using a optimal foraging perspective

Dusseldorp, G.L.

Citation

Dusseldorp, G. L. (2009, April 2). *A view to a kill : investigating Middle Palaeolithic subsistence using a optimal foraging perspective*. Retrieved from https://hdl.handle.net/1887/13713

2 Neanderthal Biology

2.1 Introduction

This chapter deals with the distinctive biological features of Neanderthals. Knowledge of these features will be used as a basis for the adaptation of Optimal Foraging Theory (OFT) to study Neanderthal subsistence strategies. Unfortunately, establishing such a basis is not straightforward, since specific way in which Neanderthal adaptations took shape is not always clear. First, I will introduce the evolutionary history of Neanderthals as it is perceived at present. This will be followed by an examination of their distribution patterns and how these relate to the conditions to which they were adapted. This will be combined with an overview of the skeletal clues regarding Neanderthal adaptations. Much has been written about the consequences of having a large brain for a variety of phenomena, from the organisation of the adaptive tract, to the evolution of language, to its influence on an organism's life-history. The Neanderthal brain and its effects will therefore be considered in a separate section. The combined effects of Neanderthal brain size, build, and distribution are thought to have had drastic consequences for their dietary niche, which will be discussed next. This will be followed by a discussion of the implications of the dietary niche and data on life-histories for the social organisation of Neanderthals. This will result in an overview of the specific adaptations of the "Neanderthal animal" which will be used as input for OFT models in chapter 4.

2.2 Neanderthal evolution

Neanderthals are usually seen as a distinct species of hominin, *Homo neanderthalensis*, although some scientists prefer to classify them as a subspecies of *Homo sapiens*: *Homo sapiens neanderthalensis* (see for example discussion in Ahern, Hawks, and Lee 2005, Harvati, Frost, and McNulty 2004). Because of genetic, anatomical and behavioural differences between anatomically modern humans (AMH) and Neanderthals I prefer to group Neanderthals as a separate species: *H. neanderthalensis*. Fossils of Neanderthals have been found over a wide area, from Northwest Europe to the Levant and further eastward to southern Siberia (Krause *et al.* 2007). First I will sketch the current views of the evolution of the hominin lineage in Europe.

The exact evolutionary origins of Neanderthals are uncertain. Europe has been occupied by hominins from at least 1 million years ago, but "Classic" Neanderthals are usually placed between 120 thousand years ago (ka) and the time of their extinction about 30 ka (*e.g.* Klein 2003). Several species have been proposed as being ancestral to the "classic Neanderthals". The oldest species of hominin present in Europe is *Homo antecessor*, found at Atapuerca TD 6 and Sima del Elefante.[1] This name was chosen because the discoverers thought that this species was the ancestor of both Neanderthals and AMH. The species shows a combination of primitive and derived features. The midface topography is considered to be derived and this midface form is a feature that is shared by Neanderthals and AMH (Bermúdez de Castro *et al.* 1997). At present, the species is only known from Spain, where it is present from 1.2-1.1 mya. (Carbonell *et al.* 2008).

The re-dating of the *Homo heidelbergensis* sample from Sima de los Huesos led the team to retract the hypothesis that H. antecessor could be ancestral to *H. heidelbergensis*. The Sima de los Huesos fossils show a combination of primitive traits and apomorphies (derived traits) only present in other European fossils, most notably in Neanderthals but not in AMH. This population can therefore be considered ancestral to Neanderthals, but not to ourselves (Arsuaga *et al.* 1997). The fossils were originally dated to about 300 ka, but redating has shown them to be considerably older, probably about 600 ka (Bischoff *et al.* 2007). Since there are significant dental differences between Homo antecessor, most fossils of which are dated to about 800 ka and the *Homo heidelbergensis* fossils, the research team considers it unlikely that *Homo antecessor* was the ancestor of *Homo heidelbergensis* (Bermúdez de Castro *et al.* 2004b).

---

[1] It has been suggested that these fossils belong to the same species as fossils found in North Africa that were described as *Atlanthropus mauretanicus* and should therefore be called *Homo mauretanicus* (Stringer 2003).

It is now thought that in the early Middle Pleistocene, a new species arrived in Europe, *Homo heidelbergensis* (Bermúdez de Castro *et al.* 2004b). This hypothesized new migration into Europe is supported by important changes in the character of the European Archaeological record, most notably the sudden appearance of the Acheulean at around 500 ka (Bermúdez de Castro *et al.* 2004b, Langbroek 2003, Roebroeks and Van Kolfschoten 1995). Furthermore, genetic evidence suggests a migration out of Africa between 700 and 500 ka (Templeton 2002). Most researchers think that it was this population of newly arrived *H. heidelbergensis* that would give rise to the "classic Neanderthals".

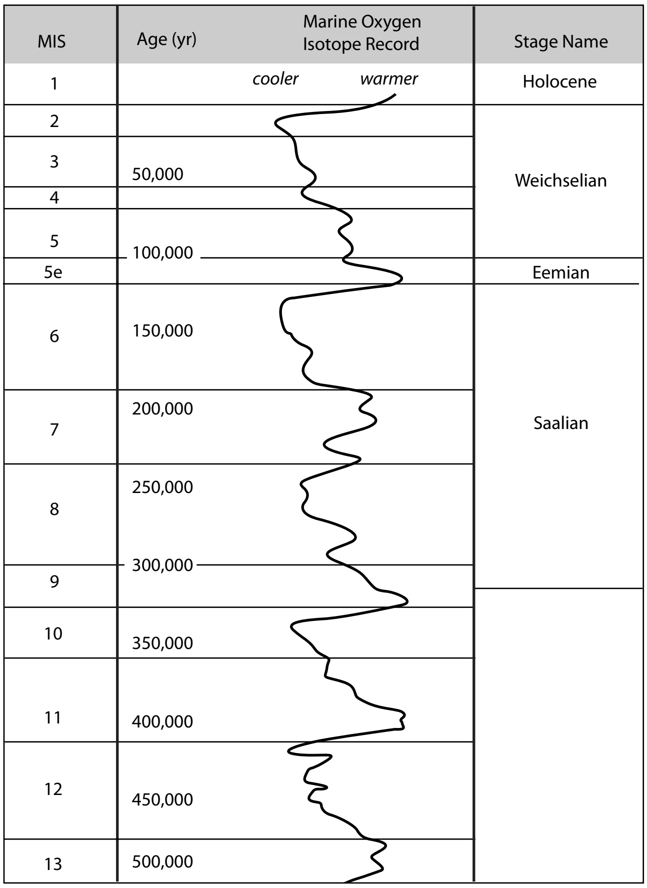

Figure 2.1: Scheme showing a climatic curve illustrating warm and cold periods during the last 500 ka. And the corresponding Marine Isotope Stages and dates. Adapted from the time chart of the AHOB project (http://www.nhm.ac.uk/hosted_sites/ahob/Chart.pdf).

The Sima de los Huesos fossils show many Neanderthal characteristics. Moreover, the dentition of the type specimen of *H. heidelbergensis* is also very Neanderthal-like (Bermúdez de Castro *et al.* 2004b, 1423). Similarly, Neanderthal characteristics have been observed in some other fossil specimens that are assigned to *H. heidelbergensis*, such as the Swanscombe skull (Stringer 2002, Stringer and Hublin 1999). This shows that the Neanderthalisation process started at least around 500 ka. Therefore, the lineage evolving in Europe could be called *H. neanderthalensis*, evolving anagenetically in Europe from an ancestral population that could be characterised as the chronospecies *H. heidelbergensis* (Bermúdez de Castro *et al.* 2004a, 39). Hence, all archaic hominin specimens from northwestern Europe dating between 400 and about 30 ka will be considered as belonging to the species *Homo neanderthalensis*.

There is one competing hypothesis, which states that the archaeological record changes drastically at the beginning of the Middle Palaeolithic, around 300-250 ka. Technological change is evident in the adoption of the Levallois technique for stone reduction. Furthermore, the earliest unequivocal indications for the use of fire appear in Europe. This has led some authors to presume the migration of a new species of hominin into Europe, namely *Homo helmei* from Africa (*e.g.* Lahr and Foley 1998). However, the fossils of *H. helmei* are younger than the oldest characteristic Neanderthal fossils, so they cannot be the ancestors of Neanderthals (Stringer 2002). Moreover, developments foreshadowing the Levallois technique are already seen in the European Lower Palaeolithic (White and Ashton 2003). The "*H. helmei*" scenario is therefore most likely incorrect, although contact between the African and European populations may have occurred from time to time, for example in the Levant.

In addition to their emergence, the process of extinction of the Neanderthals is also the subject of debate. An important question is whether Neanderthals were ancestral to AMH. It is now thought that the distinct Neanderthal and AMH forms arose independently in different areas. The oldest anatomically modern fossils that are known date to about 200 ka, in Ethiopia (McDougall, Brown, and Fleagle 2005). According to most authors, classic Neanderthals postdate 200 ka, showing that they are not ancestral to AMH. Moreover, typical Neanderthals persist in Europe until about 30 ka and these show no developments toward anatomical modernity (*e.g.* Klein 2003, 1526). Therefore, even though AMH and Neanderthals co-existed in some areas, there is no obvious evidence of crossbreeding.

The earliest contact between the species took place in the Levant. The earliest Middle Palaeolithic fossil known from this area is a partial skull from Zuttiyeh cave, dated between 250 and 300 ka.

However, it is unclear to what species this skull belongs. Some argue that it represents a population ancestral to *Homo sapiens sapiens*; others claim that it belongs to the Neanderthal lineage (Smith 1995). The oldest taxonomically distinct fossils in this region have been found at Tabun. The skeleton of a female Neanderthal has been excavated in layer C of this cave, as well as a maxilla, which after much debate has also been determined to be Neanderthal (Schwartz and Tattersall 2000). The layer probably dates to MIS 6, or maybe even late MIS 7 (Mercier *et al.* 1995).

AMH appear to arrive in the Levant in MIS 5, with fossils found in Skhul and Qafzeh, dated to 120 and 92 ka respectively (Mercier *et al.* 1993). All hominin fossils dated later than 90 ka from the area are Neanderthals. After about 50 ka they are finally replaced by AMH, or at least by assemblages we associate with AMH, since early upper Palaeolithic human remains are very rare in this area (Smith 1995). The interpretation of this fossil record is far from straightforward. AMH are only known from two sites and it is unclear whether they are replaced by Neanderthals after MIS 5e, although all more recent fossils are Neanderthals. It could be suggested that Neanderthals were present in MIS 6, as shown by the Tabun C fossils. The warmer climate of MIS 5 would have led to their replacement by anatomically (but not behaviourally) modern humans, who were in turn replaced by Neanderthals as the climate cooled again.

Later during the Weichselian, AMH migrated out of Africa again, finally replacing the European and Asian hominin populations. During the expansion of behaviourally modern populations across Europe there were opportunities for contact. In certain areas Neanderthals and modern humans co-existed at least for a short period of time, although its duration is unclear. Some authors think it may only have been for about 1000 to 2000 years. Dating the time of co-existence is problematic, given the difficulties inherent in calibrating ^{14}C dates at the lower limit of their range (*e.g.* Jöris and Street 2008, Mellars 2006, Pettitt and Pike 2001). Some initial Upper Palaeolithic cultures appear across Europe and at least the Châtelperronian now appears to be solidly associated with Neanderthal fossils, as shown by the find of a skeleton at Saint-Césaire and a temporal bone at Arcy-sur-Cure (Hublin *et al.* 1996). It has been proposed that the Châtelperronian was the result of Neanderthals copying the behaviour of AMH. A thorough analysis of the novelties associated with such transitional cultures suggests that the roots of these phenomena do not lie in cultures associated with AMH (*e.g.* d'Errico *et al.* 1998). In some caves interstratifications of Aurignacian and Châtelperronian layers have been proposed (*e.g.* Gravina, Mellars, and Ramsey 2005, Mellars, Gravina, and Ramsey 2007). Other analyses suggest that the interstratifications are the result of taphonomic processes (*e.g.* d'Errico and Goñi 2003, 770, Zilhão *et al.* 2006).

The timing of the extinction of Neanderthals is also uncertain. There is a paucity of well-dated AMH fossils in the time range spanning the transition from the Middle Palaeolithic to the Upper Palaeolithic. The AMH remains of Vogelherd were thought to be associated with an early Aurignacian industry, but redating has shown that the fossils are Neolithic (Conard, Grootes, and Smith 2004). Mladeč, in the Czech Republic, has yielded early Aurignacian stone tools and AMH fossils, but the fossils have been dated to the middle to late Aurignacian, at about 31 ka. Furthermore, there is ongoing discussion about whether they exhibit Neanderthal feautures (Wild *et al.* 2005). Theoretically, the early Aurignacian, which is usually ascribed to AMH, could thus have been produced by Neanderthals.

In addition to the dearth of well-dated early Upper Palaeolithic modern humans, there is uncertainty about the dates associated with the youngest Neanderthals. Very young dates, of up to 28 ka, for the Neanderthal occupation of Gibraltar have been proposed (Finlayson *et al.* 2006), and severely criticised (Zilhão and Pettitt 2006). After a thorough review of the available ^{14}C dates, Jöris and Street (2008) conclude that there are no reliably dated Neanderthal remains after 38 ka ^{14}C years before present, although industries associated with Neanderthals persist until slightly later. They assume that Neanderthals had disappeared after 35 ka ^{14}C years before present (Jöris and Street 2008).

An important site in the context of this debate is Peştera cu Oase in Romania. A mandible and a skull belonging to two individuals have been found there, dated to 35 ka. Unfortunately they are not associated with archaeological materials. Moreover, both specimens show some archaic features, not seen in AMH (Crevecoeur and Trinkaus 2004, Rougier *et al.* 2007, Trinkaus *et al.* 2003). This is apparent from the lingual bridging of the molars, which is unknown in late and middle Pleistocene hominins except for Neanderthals. The mandible has archaic molars, reminiscent of Neanderthals and other Pleistocene hominins (Crevecoeur and Trinkaus 2004, Trinkaus *et al.* 2003). This is striking, because Neanderthal dental morphological trait frequencies are unique within the hominin family. It is thought that Neanderthal dental morphology has evolved separately from the dental morphology of African populations of archaic *H. sapiens*. The phylogenetic position of this material is therefore unclear. The combination of derived modern features and archaic features may point to crossbreeding between early modern humans and Neanderthals. Alternatively, the remains may belong to descendants from primitive Middle Pleistocene Modern Humans and represent another group of humans than the earliest AMH that migrated out of Africa (Rougier *et al.* 2007). Cross-breeding of Neanderthals and AMH has also been proposed for the case of a juvenile skeleton from Portugal (Duarte *et al.* 1999).

Recently, DNA analyses have been used to suggest that admixture of genes from Neanderthals into the AMH genome did not happen. Several research groups have isolated strands of Neanderthal mitochondrial DNA. These seem to fall outside the range of modern human DNA (*e.g.* Beauval *et al.* 2005, Krings *et al.* 1999, Ovchinikov *et al.* 2000). The DNA shows that there is no closer relationship between modern Europeans and Neanderthals than between other humans and Neanderthals (Höss 2000). Initially, most of the recovered strands were short, containing only between 100 and 300 base-pairs. Nevertheless, the fact that strands from multiple individuals show that they are related, yet not identical suggests that they do not represent some form of contamination (Höss 2000, 454). Still, these results have been critisised. Some researchers suggest that the methods used were not ideal and that the effect of degradation has not been sufficiently accounted for. According to them, Neanderthals may be more closely related to modern humans than generally assumed (Guitierrez, Sánchez, and Marín 2002).

More recently, the complete mitochondrial genome of Neanderthals has been reconstructed (Green *et al.* 2008). The fact that the Neanderthal DNA differs on multiple points from that of modern humans but is internally consistent, points to the fact that Neanderthals formed a distinct evolutionary lineage. The age of the last common ancestor is difficult to reconstruct exactly from DNA analysis, but is estimated at 660 ± 140 ka (Green *et al.* 2008).

Since Neanderthal fossils have a number of apomorphies not shared with other hominins and their DNA is different from that of AMH, I see them as a separate species of hominin. I treat all European *Homo heidelbergensis* fossils as belonging to the Neanderthal lineage.

2.3 Neanderthal distribution patterns

Neanderthal fossils have been found across a large part of Eurasia, from eastern Russia to the Levant in the South and Britain in the Northwest (See figure 2.2). In the southern and eastern part of their range we cannot use Middle Palaeolithic stone tools as a proxy for the presence of Neanderthals, since Neanderthals and AMH apparently produced very similar assemblages (*e.g.* Shea 2003, Zilhão 2001). Middle Palaeolithic tools have been reported from the North European plain, for instance from Denmark (Johansen and Stapert 1995/1996). These can be confidently ascribed to Neanderthals. The northeastern limit of their range is still unclear. Some publications mention tools that may be Middle Palaeolithic from northern latitudes in Russia, but their provenance and dating are usually unclear (*e.g.* Pavlov, Roebroeks, and Svendsen 2004). Recently, Neanderthal-like mitochondrial DNA isolated from taxonomically indeterminate fossils in Siberia has extended the Neanderthal range eastwards by 2000 kilometres (Krause *et al.* 2007). The fossils and artefacts represent a period of time of hundreds of thousands of years, during which many range expansions and contractions probably took place. They do not reflect the distribution of Neanderthals at any one time, but show that Neanderthals survived in a wide range of environments during their existence.

Neanderthal fossils and tools have been found throughout a large area encompassing many different types of environment. Moreover, the climate during the period of their existence was very variable. The later part of the Pleistocene was characterised by a cyclical alternation of glacials and interglacials (See fig. 2.1). Marine and ice core isotope records have enabled accurate reconstructions of global climatic patterns, especially for the most recent glacial. (*e.g.* Andersen *et al.* 2004, Petit *et al.* 1999). For the palaeomagnetic Bruhnes chron, during which most of the substantial occupation of Europe took place we know of eight major glacial-interglacial phases. During these 800 ka at most 25 percent of the time sea-levels were high, indicative of present-day and warmer climates, but for over 75 percent of the time, they were lower, indicating colder climates (Gamble 1999, 104). Within these grand climatic cycles many shorter oscillations took place. During the Weichselian for example, we know of more than twenty abrupt changes in isotopic values of the ice cores, suggesting a very unstable climate (Andersen *et al.* 2004). The impact of these rapid oscillations on the continen-

Figure 2.2: Map showing the known distribution of Neanderthal fossil specimens in grey with the location of important fossil finds mentioned in the text: 1 Atapuerca (Sima del Elefante, TD 6 and Sima de los Huesos; 2 Mauer; 3 Neanderthal, Feldhofer grotte (type specimen); 4 Sclayn; 5 Swanscombe; 6 Mezmaiskaya; 7 Saint-Césaire; 8 Arcy-sur-Cure; 9 Skhul, Tabun, Kebara; 10 Peştera cu Oase; 11 Mladeč. Neanderthal distribution adapted from (Krause et al. *2007*).

tal climate and hence on human behaviour is not yet well-understood though. The resolution of pollen cores is too poor to precisely correlate all climatic events known from marine and ice cores with changes in pollen diagrams (Van Andel 2003, 13-15). In cold climatic phases climatic ameliorations did not have much impact in the northern pollen cores, but whether this is because of the resolution of the pollen cores or because climatic ameliorations had less effect at northern latitudes is unclear. What is clear though is that some ameliorations were of sufficient duration and warmth to cause the formation of palaeosols in the loess in Northern France and the Rhineland (Van Andel 2003, 15).

Reconstructing the preferred Neanderthal habitat is problematic. It is uncertain how well Neanderthals were able to deal with the cold and it is unknown what determined the limits of their distribution. Furthermore there is debate about whether Neanderthals were able to cope with the densely forested environments in interglacials in Europe. Even very early occupants of Europe were able to colonize northwestern Europe as shown by the site of Pakefield in East Anglia, dated to about 700 ka (Parfitt *et al.* 2005). The finds were accompanied by fossils that suggest the climate was warmer than it is presently. It has been suggested that these findings imply that the early hominin occupants of Europe preferred warm climates and as their habitat expanded to the North, they followed suit (Parfitt *et al.* 2005, Roebroeks 2005).

When the climatic tolerance of European hominins developed further, allowing them to survive in cold climates is not known yet. Evidence for the early occupation of northern Europe is quite scarce and many of the earliest sites like Pakefield and Boxgrove were situated in temperate environments. In the case of Boxgrove bifaces and refitting debitage have been found in mass movement gravel deposits overlying the warm sediments at the site. This implies that hominins were able to survive the cold phases of glacials at quite northern latitudes as early as MIS 12 (Roberts, Gamble, and Bridgland 1995, 171). The sites of Cagny La Garenne were also deposited in a periglacial environment in MIS 12 (Tuffreau, Lamotte, and Marcy 1997, 229-230). From MIS 8 we know a number of sites situated in a cold steppic environment, like Mesvin IV in Belgium, and Ariendorf 1 in Germany (Van Neer 1986, Roebroeks, Conard, and Van Kolfschoten 1992, 560). From this period onwards, Neanderthals are frequently associated with remains of arctic animals, which shows that they were perfectly able to cope with cold environmental conditions.

Remarkably, Neanderthal remains are better known from relatively cold climatic periods than from interglacials. Based on the paucity of sites in the last glacial, the Eemian, Gamble has postulated that Neanderthals were unable to deal with full interglacial forests. He argues that since there are dated faunas, but no archaeological sites in Western Europe interglacial forested environments were "human deserts". This situation is illustrated best by the Eemian, since this period is represented by the strongest peak in the isotope records (Gamble 1986, 367-370). Other authors have pointed out that we do know sites from full interglacial conditions in the Eemian and that the paucity of sites is probably due more to post-depositional processes than to hominin absence in northwestern Europe. In areas where the sedimentary conditions allowed preservation of interglacial sites, archaeological sites have been found (*e.g.* Roebroeks, Conard, and Van Kolfschoten 1992, Roebroeks and Speleers 2002). Until recently, these were located almost exclusively in central and eastern Germany, which led Gamble (1986; 1992) to suggest that the climate in these areas was more continental than in Western Europe and that there were no full interglacial forests in these areas. Recently, however interglacial archaeological levels were found at Caours in the Somme valley, showing that Neanderthals were present in oceanic interglacial environments (Antoine *et al.* 2006). Some authors have even proposed that Neanderthals were actually a mediterranean species that was able to occupy the higher latitudes of Europe only in milder climatic intervals. They propose that Neanderthals were severely affected by cold climates, surviving only in Mediterranean refugia (*e.g.* Finlayson 2005, 461).

It is certainly true that Neanderthals were not able to cope with the coldest periods of glacials in northern areas. However, during the early part of the Weichselian, Neanderthals occupied the North European plain most of the time. The dates of Micoquian sites in Germany and Poland only show a hiatus during the coldest phase of MIS 4, presumably reflecting a retreat areas further south (*e.g.* Jöris 2003). In Northern France, the beginning of MIS 4 shows an occupation hiatus, but the area is re-colonised at least from 55 ka (Locht 2005). This shows that the idea that Neanderthals did not fare very well in cold-temperate areas, as proposed by Finlayson (2005) can be discarded.

It is important to realise that the most severe glacial and interglacial periods had a relatively short duration. For the longest part of the period during which Neanderthals lived in Europe climatic conditions were intermediate between warm climates resembling the modern climate and very cold conditions. During the last glacial cycle for example, only 9 percent of the time was characterised by full interglacial conditions and 17 percent by full glacial conditions. The rest of the cycle was characterised by intermediate climates, with temperate, open environmental conditions (Gamble 1986, Gamble 1992). This, according to Gamble, is the type of environment that was encountered by Neanderthals most of the time and therefore the environment they were adapted to survive in.

Guthrie (1990; 2001) has characterized the environment of Eurasia and parts of Northern America during these intermediate time-periods as a "mammoth steppe". The mammoth steppe was a unique, "non-analogue environment", in which elements of both modern day arctic environments and arid steppe environments were present. It was characterized by a low amount of annual precipitation and a cold climate, although it covered areas at temperate latitudes. Despite the cold climate, the area received a lot of sunshine, and bioproductivity was therefore high. Estimates of bioproductivity, and herbivore biomass equal those of the modern day African savannahs (over 14 tonnes/km^2 against 0.5 tonnes/km^2 for present-day forested environments) have been advanced for this kind of landscape (*e.g.* Delpech 1999). Moreover, temperatures may have been higher on average than signalled by the faunal and floral indicators that were present in the area. Guthrie (2001, 572) suggests that most of the time, the climate would have been warm enough for species adapted to warmer environments to colonise the mammoth steppe. However, the very abrupt Dansgaard/Oescher events may have periodically "set the clock back to zero" for these colonisations. Neanderthals occupied this very rich environment in large parts of their range. Although they had to withdraw to the south during the coldest glacial phases, they were very well able to cope with the environments that prevailed for most of the duration of glacial periods. An important point made recently by Stewart is that Neanderthal sites are preferentially in areas of ecological diversity (Stewart 2005, 38). This is interesting, because a comparison of mammal faunas shows that Europe's ecology in Mammoth Steppe environments was already more diverse than it is at present (Stewart 2005). This may explain why Neanderthals seemed to thrive in both temperate glacial conditions and in warm Mediterranean conditions, since both environments were diverse and productive.

The paucity of Neanderthal sites during full interglacials, as discussed above, is due at least in part to taphonomic factors (*e.g.* Roebroeks, Conard, and Van Kolfschoten 1992, Roebroeks and Speleers 2002, Speleers 2000, Tuffreau 1988c). However, since in these periods much of the biomass is locked away in tree trunks and leaves, and herbivore biomass was low, Neanderthals may have been present in smaller numbers in forested environments than on the mammoth steppe.

2.4 Neanderthal anatomy and adaptation

In order to understand Neanderthal adaptations we need to know in what respects they were different from AMH and the consequences of these differences. The basic body plan of Neanderthals was quite similar to our own, but differences did exist. The functional implications of these differences are at first sight not great; many point to a heavier musculature in Neanderthals (Wood and Collard 1999, 69). I will briefly examine the most significant differences between Neanderthals and AMH's and the possible behavioural impacts of these differences on Neanderthal ways of life.

Neanderthals evolved during a succession of glacial-interglacial cycles, the glacial part of which was much longer than the interglacial part. Neanderthals must therefore have been able to survive the periods of extreme cold, but their adaptation was presumably shaped by the long periods of intermediate climates. The extent to which Neanderthals were effectively adapted to cold environments is debated. As discussed in the previous section it has been proposed that they were unable to deal with cold climatic circumstances (*e.g.* Finlayson 2005, 461). Others maintain that their anatomy betrays drastic adaptations to the cold (Holliday 1997, 256). Two traditional indices of cold adaptation are Bergmann's rule and Allen's rule. Bergmann's rule states that within a dispersed species the populations living in colder climates will have a greater body mass. Allen's rule predicts that populations living in cold climates will develop shorter extremities. This pattern is explained by the fact that the surface area to volume ratio is minimized by these developments minimising heat loss (Holliday 1997). Neanderthal anatomy conforms to these predictions about cold-adaptation. It is thought that their barrel-shaped ribcage, and a torso that was relatively large in comparison to the limbs resulted from cold-adaptation. Their limb proportions are also different than those of AMH; especially the lower limbs are shorter than would be expected in AMH of similar size (Steudel-Numbers and Tilkens 2004). The brachial index (the relative length of the ulna compared to the humerus) of Near Eastern Neanderthals is higher than that of European ones (Aiello and Wheeler 2003, 147). Furthermore, their body mass was greater than that of AMH. This suggests that they conformed to Allen's and Bergmann's rules (Aiello and Wheeler 2003, 147). Some authors have argued that many Neanderthal features more likely resulted from biomechanical adaptations than from thermoregulatory ones (*e.g.* Churchill 1998, Porter 1999). However, some of these biomechanical adaptations, such as limb robusticity, probably had the secondary effect of being beneficial in a thermoregulatory sense as well (Churchill 1998, 58-59). This combination of anatomical features has led many to conclude that Neanderthals were cold-adapted, or even a hyperarctic species (*e.g.* Holliday 1997).

Metabolic adaptations are also significant in populations that have to cope with cold climates. In modern human populations from cold areas the Basal Metabolic Rate (BMR, the energy production of an animal in rest) may rise by some 15% compared with "normal" controls (Steegman, Cerny, and Holliday 2002, 577). Furthermore, changes in the amount of specific tissues, such as Brown Adipose Tissue, a fat that plays a part in thermoregulation, may also have been important (Steegman, Cerny, and Holliday 2002). Finally, BMR increases with increasing body weight. Neanderthals are therefore expected to have a significantly higher BMR than AMH (Sorensen and Leonard 2001).

There are some problems in viewing Neanderthals as cold-adapted, or even hyperarctic. Two are of particular interest here. First, some authors have argued that applying Allen's and Bergmann's rules to Neanderthals compared to modern humans is incorrect. These rules were originally developed to explain patterns of adaptation among individuals within a species, not to explain differences between species. Differences in limb length and robusticity between species are, according to some authors, usually better explained as reflecting differences in locomotor behaviour (Stewart 2005, 42-43). However, as stated above, conformation to these rules has also been proposed within the Neanderthal sample.

Secondly, a recent study by Aiello and Wheeler (2003) suggests that the anatomical differences between Neanderthals and AMH had little influence on their climatic tolerance. Aiello and Wheeler (2003) focus on the critical temperature, *i.e.* the environmental temperature at which an animal must start producing heat in order to keep his body temperature optimal. This can be modelled using heat conductivity and BMR. Since the maximum metabolic rate of an organism is usually three times its BMR, these estimates can also be used to model the lowest temperature at which Neanderthals can survive without additional insulation (Aiello and Wheeler 2003, 148). If average human BMR, skin conductivity equal to that of modern humans, and a standardised relationship between surface area and body mass and stature are used, the Neanderthal's critical temperature is estimated at 27.3 °C, against 28.2 °C for early modern humans. The lowest temperature at which Neanderthals could survive without additional insulation would be 8.0 °C, against 10.5 °C for modern humans (Aiello and Wheeler 2003, 148). However, if a 15% increased BMR is assumed and the additional insulation provided by increased muscularity is taken into account, the critical temperature would drop to 25.3 °C and the lowest tolerable temperature tolerable would become 1.9 °C for Neanderthals (Aiello and Wheeler 2003, 150-151). The tolerance of extremely low ambient temperatures would necessitate high metabolism and could only be maintained if Neanderthals had a high dietary intake (Aiello and Wheeler 2003, 151).

The different limb proportions may have had an effect on Neanderthal cold adaptation, but they also point to differences between the locomotion of Neanderthals and AMH. Their limbs were relatively short compared to the torso, but the limbs themselves are also different compared to those of AMH. They are much more robust and show evidence of a much heavier musculature. Moreover, their lower limbs are very short; the crural index, the relative length of the tibia compared to the femur, of Neanderthals lies outside that of the modern range (Porter 1999, 65-66). Furthermore, the Neanderthal pelvis had a different shape than in AMH. The superior pubic ramus lies further forward, meaning that in females the birth canal would also lie further forward. It is possible that this is an adaptation to giving birth to large-brained babies. However, this pattern is most pronounced in males, therefore it is usually interpreted as indicating a difference in locomotion behaviour in Neanderthals (Tattersall 1999, 15).

The cost of locomotion is largely determined by the number of steps one has to take in order to travel a given distance, which is dependent on lower limb length and on the weight being transported. The impact of decreasing lower limb length and adding weight has been modelled on modern test subjects, assuming an average travel distance of 12.2 kilometres daily for hunter/gatherers. It appears that decreasing lower limb length by one centimetre would increase the cost of locomotion by 9.89 kcal daily. Adding one kilogram of weight would increase the cost by 13.7 kcal a day (Weaver and Steudel-Numbers 2005, 220). Because Neanderthals were heavier than AMH and had shorter lower limbs, they had to expend 30 percent more energy than AMH in order to travel a given distance (Steudel-Numbers and Tilkens 2004). Modelling based on differences in limb length alone has shown that Neanderthals spent 78 kcal per day more on mobility than early Upper Palaeolithic AMH. If differences in body mass are taken into account this figure would rise to Neanderthals 215 kcal (Weaver and Steudel-Numbers 2005, 220-221). These figures indicate that Neanderthal body proportions may have had severe consequences for their capacity for travelling and their foraging radii (Weaver and Steudel-Numbers 2005, 221).

Neanderthal limb structure was thus less efficient for locomotion than that of the AMH. It was probably better suited to conferring power for example when thrusting a spear (Steudel-Numbers and Tilkens 2004, 160). Therefore, their limb structure may signal an adaptation to a way of life in which short bursts of great power were of more use than being able to cover large distances efficiently (Steudel-Numbers and Tilkens 2004, Stewart 2005). Some authors have interpreted this as indicating an adaptation to ambush hunting in wooded environments, where sprinting is more important than covering large distances (*e.g.* Finlayson 2005, Stewart 2005). It has also been proposed that it may have been an adaptation to locomotion in conditions with a thick snowcover, helping them to close in on, and kill prey. Short lower limbs favour force over speed and would therefore be advantageous in such situations (Porter 1999, 58).

We can conclude that while Neanderthal body structure complies with the predictions of Allen's rule and Bergman's rule, their different limb structure also had important implications for Neanderthal locomotion. We can confidently assume that Neanderthals had an elevated BMR in order to cope with cold conditions, since this is a universal adaptation among populations living in cold climates.

2.5 Neanderthal brains

As stated in the introduction, many theories that attempt to explain the evolution of modern human features focus on the links between brain size, life histories and diet (*e.g.* Aiello and Wheeler 1995, Hawkes *et al.* 1998, Kaplan *et al.* 2000, Kaplan and Robson 2002). This makes sense because brain size poses significant constraints on human ways of life on a variety of levels. These theories are usually based on comparative studies of modern humans and living primates. Neanderthals present an excellent opportunity to evaluate the validity of these models, since they also had large brains, but are generally regarded as a separate species from AMH. As Neanderthal evolution presents a case of parallel evolution of large brains, it can therefore be used to test current hypotheses and can yield clues as to whether other scenarios explaining the evolution of modern human life histories, brain size and foraging strategies should be developed. In this section, I will review the current theories regarding the link between brain size, foraging and hominin evolution. This will be combined with a presentation of the available evidence on these features from the Neanderthal fossil record.

Neanderthals had an average brain size of 1512 cm^3, against 1355 cm^3 in AMH (Wood and Collard 1999, 69). Since their bodyweight was larger than that of modern humans too, the relative brain size of both species is roughly equal, 3.06 in Neanderthals versus 3.08 in AMH (*e.g.* Wood and Collard 1999, 69). Not only was the Neanderthal brain absolutely larger than that of modern humans, their braincase had a different form: it was low, long and had bulging sides. These differences are significant because the form of the braincase is determined by the growth of the brain during development (Tattersall 1999, 12). There is no clear relation between brain-form and organization, so the differences in form do not inform us if and how Neanderthal brains functioned differently from AMH ones. Since this unique brain form is developed within the womb and determines the form of the braincase and adjacent features such as the inner ear, it does help us to classify fossils that at first glance do not seem diagnostic (Hublin *et al.* 1996).

Possessing a large brain is alleged to have severe consequences for childbearing and child-rearing, diet and even life-histories in AMH (*e.g.* Aiello and Wheeler 1995, Gibbons 1998, Hawkes *et al.* 1998, Kaplan *et al.* 2000, Mussi 1999). Since Neanderthals had brains of roughly similar size as AMH, they faced similar consequences. In modern humans babies with fully developed brains are too large to pass through the birth canal. This problem has been "solved" in AMH by giving birth "too early". Since fully developed babies could not pass through the female birth canal, human babies have brains that are about 25 percent of the adult size when they are born, while monkey and ape brains are about 70 percent of their adult size (Coqueugniot *et al.* 2004, Rosenberg and Trevathan 1996). Despite the early birth of babies, the fit between cranium size and birth canal size is so close that the baby's head has to rotate at several points in the birthing process in order to make use of the maximum dimensions of the birth canal (Rosenberg and Trevathan 1996, 162).

The implications of the early timing of childbirth are far-reaching. Human babies require a much longer period of intensive maternal care compared to monkeys and apes. On the other hand, their brain develops in an enriched environment, stimulating cognitive development. This is probably a requirement for the uptake of spoken language (Coqueugniot *et al.* 2004, 299-300). In biology, species that give birth to their young in a relatively helpless state are dubbed altricial species. In the case of AMH this process is called secondarily altricial, since the altricial pattern of giving birth has evolved out of more precocial patterns in our primate ancestors (Rosenberg and Trevathan 2002, 1205). This secondary altriciality appears to have evolved late in the hominin lineage. The Mojokerto child, an Early Pleistocene *H. erectus* specimen, displays an ape-like speed of brain development, with a brain of 72% of the adult size at between of 0.5 and 1.5 years of age (Coqueugniot *et al.* 2004). Analysis of a Neanderthal neonate and two infants shows that Neanderthals followed the same pattern as modern humans. Brain size at birth was similar in Neanderthals as in recent AMH babies. Neanderthal adults had larger brains than AMH, and data from Neanderthal infants suggests that this size was attained by a higher rate of brain growth instead of a longer period of development (Ponce de León *et al.* 2008).

Furthermore, the brain consists of so-called "expensive tissue", which needs large amounts of energy even when at rest. A species cannot simply increase its brain size indefinitely, because this would severely impact its energy requirements. Consequently a creature will either need to furnish itself with a lot more calories and nutrients if it is to increase the amount of expensive tissue, or compensate for the increased size of the brain through a reduction of other expensive tissues (Aiello and Wheeler 1995). The latter strategy seems to be in evidence in human evolution. When we compare the expected amount of expensive tissues in a primate of human size to that actually present in humans, we see that the total size is the same. However, humans have a much larger brain than would be expected, whereas the gastro-intestinal tract is significantly smaller than expected for a primate of human size. Therefore, the increase in brain size during hominin evolution was compensated for by a reduction in gut-size (Aiello and Wheeler 1995, 203-204).

This seems an elegant solution, but it has far-reaching consequences. Because the smaller gut cannot digest specific types of food as thoroughly as a gut of the expected size for a primate of human size, the hominin diet must have diverged significantly from what our smaller-brained, ancestors with comparatively large guts ate. It is thought that the increase in hominin brain-size co-evolved with a greater reliance on high-quality foods, rich in energy, like tubers, fruit and meat (Aiello and Wheeler 1995, Kaplan *et al.* 2000, Milton 2003). In the temperate and cold environments in which Neanderthals lived, fruit and tubers were probably not available in large quantities. Therefore the share of meat is expected to have been very large in the Neanderthal diet.

The growth of the brain, which lasts until a child is about 4 years old, is also energetically expensive. This development is fuelled by the mother, first during gestation and afterwards during lactation (Gibbons 1998), which puts considerable strain on human mothers. After birth this strain continues as the mother lactates her child for an extended period of time. In Neanderthals, this problem is exacerbated by the higher rate of brain growth in children. A switch to high-quality foods may therefore enable children to draw more energy from their mother, without killing her (Gibbons 1998).

Another possible change in hominin dietary habits stemming from the reduction in gut size is an externalisation of part of the digestive process, for example by preparing the food using tools and more significantly by cooking it (Aiello and Wheeler 1995, Wrangham *et al.* 1999). Some authors think this change may have taken place early in the development of the human lineage. In support they cite possible evidence for the occurrence of fire at archaeological sites dated to about 1.6 mya (Bellomo 1994, Brain and Sillent 1988). Such evidence is very rare and unclear however. Only from the Middle Palaeolithic onwards do charcoal, burnt flints and hearths become common at sites, suggesting that the practice of cooking may have been the driving force behind the final phase of brain expansion in Neanderthals and archaic *H. sapiens* (Aiello and Wheeler 1995).

As has been argued, the development of large brains drastically changed the organisation of life of the species. Childbirth became more dangerous for mother and child than in our primate cousins. Especially mothers were put under severe energetic strain to fuel brain growth in their children, and the dietary needs of hominins were significantly altered. This leads us to expect that possessing large brains must have had significant adaptive advantages. Most importantly, we associate the possession of large brains with increased intelligence. The exact relationship between Encephalisation Quotient (EQ; relative brain size) and intelligence is unclear and EQ is not directly proportional to intelligence (*e.g.* Macphail 1982). It is assumed that there must have been a trade-off in which the disadvantages of having a large brain were offset by significant adaptive advantages, *i.e.* increased intelligence.

One of the inferred advantages of a larger brain, is the capacity for language. It has been proposed that in primates, brain size correlates with group size. If this correlation was also valid in fossil hominins, by about 500 ka group size had become so large that social relations could no longer be maintained only by grooming. Spoken language would enable more efficient maintaining of social bonds, since conversations can encompass a greater number of individuals (Dunbar 1992, Dunbar 2001). This hypothesis is hard to test archaeologically. Anatomically however, Neanderthals appear to have fulfilled all necessary conditions for the evolution of language. In order to use language, humans need to produce a much larger range of sounds than do chimpanzees. The human hyoid, which is descended compared to its position in the great apes, enables this (Nishimura *et al.* 2006). Hyoid bones have been preserved in *H. heidelbergensis* fossils from the Middle Pleistocene site of Sima de Los Huesos and in the Neanderthal skeleton of Kebara (Bar-Yosef *et al.* 1992, Martínez *et al.* 2008). Of course the hyoid may have been lowered in response to other evolutionary pressures and the ability to produce a larger range of sounds may have been a side-effect of this development (Martínez *et al.* 2008, Nishimura *et al.* 2006). It is striking however, that *H. heidelbergensis* at Sima de Los Huesos also had an ear with the structure needed to hear this increased range of sounds, something chimpanzees for example lack (Martínez *et al.* 2008, Martinez *et al.* 2004).

Another explanation of the value of a large brain focuses on foraging. It is thought that extractive foraging requires high intelligence, as does the mapping of complicated environments (Milton 1993, Reader and Laland 2002). According to this hypothesis, the large brain evolved simply to cope with ecological challenges. This hypothesis is supported by the fact that in primates there is a correlation between innovation frequency and brain size. Furthermore, most of these innovations take place in the foraging domain (Reader and Laland 2002). Further support for this hypothesis is the fact that in modern humans, foraging success seems to be related to experience, rather than physical strength (Gurven, Kaplan, and Guitierrez 2006, Kaplan *et al.* 2000, 160). These hypotheses need not be considered mutually exclusive; increased intelligence would certainly have been used in both domains. This is reinforced by the suggestion that similar decision-making mechanisms are used by modern humans in dealing with ecological and social problems (*e.g.* Todd 2000)

Neanderthals provide an interesting case with regard to evolutionary models for the increase in brain size. If, as I assume, Neanderthals were a separate species from AMH, their case can be used to test the validity of hypotheses about the causes of increasing brain size in human evolution.

2.6 Neanderthal dietary niche and its implications

While constraints on diet imposed on early hominins with brain sizes not too divergent from those of the common ancestor of chimpanzees and hominins may have been quite moderate, Neanderthals had roughly the same relative brain size as AMH. This means that the dietary requirements of their brain were comparable to those of AMH. A heavy reliance on high-quality food is therefore expected, especially since Neanderthals lived at temperate latitudes in climates that were at times much colder than at present. Plant growth was absent during a large part of the year, so high-quality plant foods would only have been available for a limited period each year. The only resource that was present in sufficient quantities year round was meat (*e.g.* Roebroeks, Conard, and Van Kolfschoten 1992, 551). Procuring meat is a dangerous job, however, certainly for mothers with helpless children. It is no coincidence that hunting is predominantly done by males, both in contemporary hunter/gatherer societies and among chimpanzees (*e.g.* Boesch 2003, Kaplan *et al.* 2000, Stanford 2001b). Scavenging, which has been proposed as an alternative to hunting, is also dangerous, since competition from other scavengers has to be faced (*e.g.* O'Connell *et al.* 2002, Tooby and DeVore 1987). We have seen that Neanderthals had high energetic demands because of their elevated BMR. Energetic needs of mothers with children were even more elevated, since children are not expected to take part in foraging activities and mothers therefore needed to provide them with sufficient high-quality food to fuel their growth, including the development of their expensive brains. The only type of food available to them in sufficient quantities across a large part of their range was meat. We do not know when a sexual division of labour was developed, but from the foregoing it follows that it must have been in place by the time hominins started to colonise temperate latitudes (*e.g.* Kaplan *et al.* 2000, Tooby and DeVore 1987).

The most direct method available for the reconstruction of Neanderthal diets is the analysis of stable isotopes extracted from their bones. Several types of isotope studies can be used to make inferences about diet. $^{13}C/^{12}C$ analyses can be used to discriminate between a diet based on C_4 and one based on C_3 plants. C_4 and C_3 employ different processes to fixate carbon from CO_2 in the atmosphere. Tropical grasses and most of our modern crops are C_4 plants. Most trees and forest plants, as well as temperate grasses are C_3 plants (Richards *et al.* 2001, Sponnheimer and Lee-Thorp 1999). In more northerly environments harbouring only C_3 plants, this type of analysis can be used to distinguish between the sort of environment food was obtained from, because forest plants contain slightly less ^{13}C than grassland and arctic plants (Bocherens and Drucker 2003). Furthermore, ^{13}C values can be used to distinguish between diets of terrestrial and marine origins, since marine animals show enriched ^{13}C values (Richards *et al.* 2001).

Other methods focus on the trophic level of foodstuffs. Animals prefer to use Calcium to build up their bones and discriminate against Strontium. Therefore, with each increase in trophic level, the ratio of Sr/Ca will show increased quantities of Ca. However, different plants contain different amounts of Sr, so some plant eaters may emit a carnivore-like signature. Furthermore, the amount of Sr in plants is also determined by the geological substrate, so migratory animals may blur the picture, because their signatures are averaged out (Wood and Strait 2004, 125-126). ^{15}N values can also be used to infer trophic level, since ^{15}N is preferentially selected by animals to construct proteins. Therefore, at each successive trophic level, a larger amount of ^{15}N is selected (Richards *et al.* 2001). However, this analysis can only be applied if sufficient collagen has been preserved in the bone (Bocherens and Drucker 2003, 6).

A number of Neanderthals from Belgium, France and Croatia, dating between 120 ka and 30 ka have been analysed. All isotope signatures point to a diet consisting almost entirely of animal matter (Bocherens and Drucker 2003, Richards *et al.* 2001, Richards *et al.* 2008b). ^{13}C values all suggest that prey animals came from open environments. For most individuals this was to be expected, since they lived during MIS 3 and 4. However, the oldest analysed individual lived in a warm period during MIS 5, either 5e or 5c, in Sclayn, Belgium. It was associated predominantly with remains of forest dwellers. However, its isotope signature suggests that it preyed on animals living in open environments. ^{15}N values showed that all analysed individuals were highly carnivorous, with values similar to those of hyenas, lions and wolves (Bocherens and Drucker 2003, 5-6). More recently Bocherens *et al.* (2005) have tried to apply a method that might allow the determination of the relative importance of different prey species in a predator's diet. This "multi-source mixing model" uses fractionation values of the ratio of ^{13}C and ^{15}N in the bones of different potential prey species and the predators in order to see which species probably contributed to the diet of the predators. The application of this technique to sites in southwestern France suggests that both hyenas and Neanderthals ate similar amounts of bovinae and large deer. Neanderthals seem to have focused heavily on woolly rhinoceros and mammoth, while hyenas on the other hand concentrated more heavily on reindeer than Neanderthals did (Bocherens *et al.* 2005, 80-81).

How consumed animal matter was procured cannot be determined from isotopic analyses. As pointed out in chapter 1, it was suggested in the 1980s that Neanderthals mainly scavenged for meat. More recent studies contradict this and it is now accepted the Neanderthals were successful hunters that were able to selectively hunt prime-aged prey. (*e.g.* Adler *et al.* 2006, Auguste 1995a, Costamagno *et al.* 2006, Gaudzinski and Roebroeks 2000, Steele 2004).

Remarkably, despite the fact that archaeozoology shows that Neanderthals were successful hunters, some researchers have proposed that they may have been less efficient foragers than AMH (*e.g.* Trinkaus and Hilton 1996). As pointed out, because of their heavy build and the cold climates in which Neanderthals lived, they probably had high energy demands (Sorensen and Leonard 2001). Estimations of their energy demands are about 4000-6000 kcal/day for men and between 3000 and 5000 kcal/day for women. Given the average foraging time in primates of about 5.7 hours/day (which is longer than human hunter/gatherers forage), they needed to produce between 770 and 1160 kcal per hour spent foraging. This is within the range of modern human hunter/gatherers. We can therefore assume that Neanderthals foraged at least as efficiently as contemporary hunter/gatherers (Sorensen and Leonard 2001, 491-492).

The wear on teeth that is caused by the processing of food can also tell us something about the properties of these foodstuffs. Comparisons with wear patterns in modern humans have been undertaken to deduce what kind of foodstuffs Neanderthals ate. It seems that Neanderthal teeth exhibit wear that in most cases falls neatly within the limits for carnivorous hunter/gatherers and in some cases falling within the limits for hunter/gatherers with a mixed diet. However, Neanderthal fossils show a large amount of variation that is attributed to the fact that the sample of Neanderthal fossils is derived from a large period of time and from very varied environmental conditions ranging from subtropical to arctic (Lalueza, Péréz-Perez, and D. Turbón 1996, 384). To complicate matters further, there is evidence for wear patterns caused by using teeth for non-masticatory purposes, for example tooth-picking (Lebel *et al.* 2001, Ungar *et al.* 1997).

2.7 Neanderthal lives

Large and expensive brains, high energetic needs and a diet of meat may have had important consequences on Neanderthal life-histories. Models of life-histories are based on AMH and living primates. They suggest some constraints to Neanderthal life-histories, but since they were a different species from AMH, they may have coped with the situation in different ways. Modern human life-histories differ significantly from those of other primates. The most important differences are our extended period of youth and our very long lifespans, also seen in ethnographically studied hunter/gatherers (e.g Hawkes *et al.* 1998, Kaplan *et al.* 2000, Sherman 1998). Many of the models explaining the evolution of changed patterns of life-histories in humans focus on the implications of brain size for the life-histories, which is why there may be parallels between modern human and Neanderthal life histories.

As discussed in the previous section, Neanderthal anatomy imposed heavy demands on females with children. It is believed that some kind of redistribution of food within the group must have come into place at some point during the evolution of the hominin lineage. There are two main competing hypotheses to explain how this was achieved.

First, there is the grandmothering hypothesis. This hypothesis explains the long human lifespan as an adaptation in which postmenopausal grandmothers help their daughters raise their offspring. Humans are the only known species of primate whose females have a long postmenopausal lifespan (Hawkes *et al.* 1998, 1336). This phenomenon may have evolved since, after a certain age, females would no longer be able to raise their own offspring effectively. Helping their daughters would then be a more profitable strategy, since the grandmother, mother and the mother's offspring share a large proportion of their genes (Hawkes *et al.* 1998). The role of grandmothers in foraging activities has been documented for example among the Hadza of Tanzania. Here, mothers, grandmothers and children forage as a team, with grandmothers working long hours in all seasons. Furthermore, their return rates are sometimes higher than those of their kin of reproductive age (O'Connell, Hawkes, and Blurton-Jones 1999). Moreover, male food-sharing does not play a large role within the family, since most of the best food that the males procure is shared outside the nuclear family (Hawkes 1993).

Prolonged survival after the reproductive age is rare in mammals. Therefore the grandmothering hypothesis is difficult to test. In some social mammals individuals live longer than their reproductive age but they do not appear to influence the fitness of their grandchildren. Among lions (*Panthera leo*) for example, the survival of grandchildren is only positively influenced if the grandmother is still reproductively active (Packer, Tatar, and Collins 1998). Among baboons (*Papio anubis*), presence of a grandmother does not affect the survival of grandchildren at all (Packer, Tatar, and Collins 1998). Another explanation is that natural selection on old individuals is not very strong. Therefore, the maladaptive menopause may not be selected against, since the females have already reproduced at a younger age. With the relationship of childhood, age of first reproduction, start of decline in reproduction, and age of death more or less constant across mammals, one could expect that humans with a childhood of ten years would start to show reproductive decline at forty and would live to 58 and 65 years of age. If one accepts that pre-modern mortality rates were high, this pattern might approximate hunter/gatherer life-histories (Packer, Tatar, and Collins 1998). However, in hunter/gatherers women frequently live considerably longer than this, so some selective benefits of longevity are still to be expected (Sherman 1998).

Although most species have been too poorly studied to determine the occurrence of a menopause and long post-reproductive lifespan, cetaceans represent a group of mammals that have a menopause and prolonged postmenopausal lifespan. Orca's (*Orcinus orca*) and the short finned pilot whale (*Globicephala macrorhynchus*) provide reasonably well-studied examples of this. The maximum lifespan of orcas is about 70 years, while reproduction ceases at about 45 years. In short-finned pilot whales, lifespan is about 63 years, while reproduction ceases at about 40 (Rendell and Whitehead 2001, 323). Both these species show long post-reproductive lifespans and may therefore be more relevant to testing the grandmothering hypothesis than lions and baboons with their far shorter post-reproductive lifespan (Packer, Tatar, and Collins 1998). A striking feature that orca's and pilot whales have in common is that they live in matrilineal groups, with complicated, group-specific behaviour that is probably cultural. Older females might therefore be a valuable source of knowledge that could influence the fitness of other group members, who are related to them, due to their living in matrilineal societies (Rendell and Whitehead 2001). Similar group-benefits have been proposed for long living matriarchs among African elephants (*Loxodonta africana*) (McComb *et al.* 2001).

An alternative for the grandmothering hypothesis, the "embodied capital model", has been proposed by Kaplan *et al.* (Gurven, Kaplan, and Guitierrez 2006, Kaplan *et al.* 2000, Kaplan and Robson 2002). This model focuses on the role of males and specifically of male hunting. Kaplan *et al.* have measured the caloric contribution of hunter-gatherer individuals throughout their lives. Their results show that during the long childhood children contribute far fewer calories than they consume. However, from about the age of 15 they start to produce a large surplus (Kaplan *et al.* 2000). This can be contrasted with the chimpanzee, where young individuals start producing the calories they need almost immediately after they are born. From these results, it seems likely that children need this long childhood in order to learn how to exploit their knowledge-intensive foraging niche. The surplus they produce reaches its maximum long after they have passed their physical prime. The surplus is especially high in hunting men, suggesting that this is an important factor in providing the non-producing children with their "missing" calories (Gurven, Kaplan, and Guitierrez 2006). This set-up can only work of course, if adults live long enough to provision the children, who by the age of 15 have consumed 25 percent of their lifetime energy consumption and produced only 5 percent (Kaplan *et al.* 2000, 161). High adult mortality in chimpanzees leaves too few older animals to provision the young, thus making it impossible for this species to extend the duration of childhood. Kaplan *et al.* (2000) conclude that intelligence, longevity and a high-quality diet must have co-evolved. This evolutionary process must also have had an impact on hominin social organization as well, since it is essential that the males, who produce the greatest surplus by hunting, share their food with the women raising children (Kaplan *et al.* 2000).

Both hypotheses have been based on modern humans, so it is interesting to see if either one applies to Neanderthal life-histories. I will therefore discuss the clues on life-histories that are provided by the Neanderthal fossil record. The rate of maturation of Neanderthals is an important point of discussion. On the basis of Neanderthal brain size it would seem logical that, like modern humans, Neanderthals would invest in a long lifespan, during which they can first acquire the complex behaviours needed to produce surpluses later in life, in order to finance the development of the brain in their children. It has been proposed that Neanderthals matured faster than modern humans however (Ramirez-Rozzi and Bermúdez de Castro 2004). These findings have been called into question by a different team of researchers whose results suggest that Neanderthal maturation fell within the range of variation seen in modern humans (Guatelli-Steinberg *et al.* 2005).

The maturation speed of individuals can be reconstructed using the periods of dental growth. Dental development correlates closely with life-histories. Teeth grow in layers and these layers show up as perikymata when teeth are microscopically examined. The average timespan of the formation of a layer in apes and humans is known to be about eight or nine days, but the variation in modern humans is large, although values lower than 6 days are unknown in both modern humans and apes. The maximum timespan may be up to 11 or 12 days. Within an individual, the number of days it takes to form a perikyma is constant, therefore, the more perikymata are visible in the enamel, the longer it took for the tooth to develop (Guatelli-Steinberg *et al.* 2005, Ramirez-Rozzi and Bermúdez de Castro 2004).

The two teams used different samples of modern humans for comparison. Ramirez-Rossi and Bermúdez de Castro used a sample of Upper Palaeolithic and Mesolithic modern humans and a sample of *H. heidelbergensis* and *H. antecessor* for comparison. They concluded that Neanderthals show significantly fewer perikymata than AMH, they also show lower numbers when compared to their predecessors. This leads them to conclude that Neanderthals must have matured about 15 percent faster than AMH's, reaching adulthood at about 15 years of age (Ramirez-Rozzi and Bermúdez de Castro 2004, 936-937). Guatelli-Steinberg *et al.* on the other hand compared the Neanderthals with three different samples: historical Inuit and two modern day samples, one from Newcastle and one from South Africa. It transpires that Neanderthals do show fewer perikymata than the Inuit, but there is no statistical difference with the Newcastle population. Moreover, they show significantly more perikymata than the South African population. They conclude that Neanderthal growth patterns fall within the modern human range (Guatelli-Steinberg *et al.* 2005).

Ramirez-Rossi and Bermúdez de Castro (2004, 938), propose that the high maturation rate may be an adaptation to elevated adult mortality. This is a plausible suggestion, since the many known Neanderthal fossils show signs of a highly dangerous lifestyle. For example, the pattern of bone fracture in Neanderthals is comparable only to rodeo-riders in modern humans (Berger and Trinkaus 1995). Moreover, Neanderthal palaeodemography is comparable to some populations of modern human hunter/gatherers, but a higher proportion of the population died as a young adult. This suggests that Neanderthal life expectancy was lower than in modern humans and that not many adults lived to a (relatively) old age. On the other hand taphonomic factors also influence the picture: most fossils were found in caves or rock shelters, at least in part because of preservation circumstances. If dying old adults were less frequently able to reach shelters, they may be underrepresented. Furthermore, choice for burial may have centred predominantly on young adults (Trinkaus 1995, 139). On the other hand, since life histories and brain size are strongly correlated in primates, faster maturation in a species with such large brains would be against ex[ectations (Guatelli-Steinberg *et al.* 2005).

Other studies have estimated maturation rate based on the emergence of teeth. The timing of the eruption of molars is correlated with important life-history traits (Dean 2006, 2801). The eruption of the first molar in the Scladina juvenile is thought to have taken place before the individual was six years of age, which is the time of eruption of the M1 in AMH, since the tooth was heavily worn by the time of death at 8 years of age. Moreover, the M2 had already emerged in this individual, while it emerges between 10 and 13 years of age in AMH (Smith *et al.* 2007). Therefore, the timing of tooth eruption in Neanderthals suggests that they developed faster than AMH juveniles.

Neanderthal teeth also provide insight in the levels of nutritional stress they experienced during teeth development. If there are nutritional shortages during teeth development, a defect called hypoplasia will develop. Some studies have suggested that Neanderthals exhibit more hypoplasias than modern humans, indicating more developmental stress (Guatelli-Steinberg, Larsen, and Huchinson 2004, 66). However, a comparison with historical Inuit teeth shows that Neanderthals have about the same frequency of hypoplasia. Furthermore, the number of perikymata within a hypoplasia is larger in the Inuit sample, suggesting that they are subject to more prolonged periods of stress (Guatelli-Steinberg, Larsen, and Huchinson 2004, 81). There is some evidence to suggest that Upper Palaeolithic modern humans show significantly more evidence of hypoplasia during infancy. This may point to an earlier cessation of lactation and thus earlier weaning of AMH, which might indicate a shorter inter-birth interval in Upper Palaeolithic modern humans (Skinner 1997, 690).

The combined evidence shows that Neanderthals may not have grown as old as modern humans. However, their childhood, even if it was shorter than in modern humans, is still quite long compared to that of other primates. The evidence regarding the duration of the childhood is ambiguous and contested though (compare for example Guatelli-Steinberg *et al.* 2005, Ponce de León *et al.* 2008, Ramirez-Rozzi and Bermúdez de Castro 2004, Smith *et al.* 2007). Moreover if we assume that Neanderthal children had the same rate of development as AMH children, the Neanderthal rate of growth would still be higher than in the case of AMH children because of larger body size and larger brains in Neanderthals. Therefore the need to provision Neanderthal children with large amounts of high-quality food in order to support their development is well established.

The grandmothering hypothesis does not explain how Neanderthal mothers could provision their children, since meat would in all probability be procured by men. Therefore, I prefer a model in which males provision the rest of the group. Still, an increase in longevity may have started developing in an earlier phase of human evolution, when plant foods were still an important part of the diet. This may have resulted in the modern human pattern of increased duration of childhood and increased adult lifespans of high productivity. Since old individuals were likely rarer than they are in modern human hunter/gatherer societies, we may envisage a role for them, not in the direct provisioning of children and grandchildren, but more as repositories of knowledge, like we see in elephants and whales. If groups consisted mainly of related individuals, this knowledge would still benefit an old individual's fitness, since it would be promoting her its kin's fitness. This role could be filled by both old males and females.

2.8 Concluding remarks

At the beginning of this chapter the choice to regard Neanderthals as a separate species from AMH was explained. The anatomical and genetic differences between Neanderthals are too large to merit the inclusion of the Neanderthals in *Homo sapiens*. As I will argue in the following chapter, the behavioural evidence supports this choice. Many of the characteristics of the biological niche of AMH appear to have come about because of the evolution of large brains. These characteristics include for example a high quality diet with an important role for meat and life-histories that are exceptional among mammals. These developments are also visible in Neanderthals.

Differences were present as well. Most obviously there are the increased energetic needs of Neanderthals, because of their larger bodies and, in cold climates, an increased BMR. Another difference is the higher cost of locomotion of Neanderthals as compared to modern humans. This may have had important consequences for Neanderthal foraging adaptations as we will see in later chapters. The increased rate of maturation of Neanderthal children is yet another difference that could have important consequences for foraging adaptations. Neanderthal children needed more calories than modern human children in order to be able to grow up faster and still have brains of equal size. However, there is less time available during childhood for learning, since they probably needed to contribute to the group's foraging effort from a younger age.

An important problem is the fact that Neanderthal dietary reliance on meat would lead us to assume a division of labour along sexual lines, based on primatological and ethnographical evidence. This has far-reaching consequences for the social organisation of Neanderthal society. Because of the heavy reliance on meat in the diet, it is unlikely that grandmothers played a very important role in the provisioning of their grandchildren. If this is correct, it would lead one to assume a fair amount of male parental investment (cf. Tooby and DeVore 1987). This is a problematic supposition, for ethnographical studies have shown that the meat that men procure while foraging is most often shared outside the nuclear family, contrary to what one would expect (Hawkes 1993). Furthermore, parental investment is only interesting for males if they have certainty of parenthood. Because of decreasing sexual dimorphism throughout human evolution and the need for cooperation between males while hunting, Neanderthals probably lived in multi-male groups in which a monogamous pair-bond might seem the obvious solution to this problem. In chimpanzees (*Pan troglodytes*), meat is used by males to attain access to females. Males invest a lot of time and energy in hunting, even when palm nuts are readily available and provide a higher caloric return rate and more saturated fat per weight unit than red colobus (*Piliocolobus badius*) meat (Stanford 2001b, 109). Stanford (*e.g.* 2001a; 2001b) sees meat as an important political tool for chimpanzee and it plays an important role in the formation and maintenance of coalitions in the fighting arena for the dominance hierarchy. This does not seem to be the case among most ethnographically known hunter/gatherers, where there is usually no visible dominance hierarchy. According to Stanford, when hunting success increased during hominin evolution, brain size increased and in the wake of this, group size increased as well. Therefore complex sharing conventions were needed in order to negotiate a working social life in this larger group (Stanford 2001a, 135-137). However, as shown by Kaplan *et al.* (2000) some sort of provisioning of women with children is needed in AMH and probably in Neanderthals too. Therefore, with Neanderthal carnivory in mind, we can hypothesize that whatever sharing conventions were in place in Neanderthal society, one of their functions must have been provisioning the children. The role of meat as social currency should not be underestimated and will be explored further in chapter 4. We must keep in mind that such patterns will probably remain archaeologically invisible and the biological approximations as sketched above will remain an important avenue to approach this subject.

Neanderthals were thus hunter/gatherers with life-histories resembling our own. However, their life was more dangerous than that of AMH, probably resulting in shorter average lifespans. Higher energetic needs in order to cope with the cold climate and differences in the mechanics of locomotion are other important differences between Neanderthal and AMH hunter/gatherers. The implications of these differences for Neanderthal foraging strategies will be examined in chapter 4.