

Neandertal Man the Hunter: A History of Neandertal Subsistence

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ABSTRACT

The history of Neandertals has been examined by a number of researchers who highlight how historical biases have impacted popular and scientific perceptions of Neandertals. Consequently, the history of Neandertals is relevant to current debates about their relationship to modern humans. However, histories of Neandertal research to date have focused on changes in beliefs regarding the Neandertals' relationship to modern humans and correlated shifts in perceptions of their intelligence and anatomy. The development of ideas about Neandertal subsistence has generally not been discussed. This paper intends to correct this oversight. Through an historical overview of Neandertal subsistence research, this paper suggests that ideas about Neandertal subsistence have been affected by historical trends not only within archaeology, but also in anthropological and evolutionary theory.

Introduction

As our close relatives and the first recognized fossil hominid, the Neandertals have been a subject of controversy among both academics and the public since their discovery and recognition. Accordingly, the history surrounding Neandertals is relevant to current debates about their relationship to modern humans. Neandertal history has been examined by a number of researchers who highlight the historical biases that have impacted perceptions of Neandertals (Brace 1964; Graves 1991; Stringer and Gamble 1993; Trinkaus and Shipman 1993; Tattersall 1995). These histories focus on changes in beliefs regarding the Neandertals' relationship to modern humans in addition to shifting perceptions of their intelligence and anatomy, while discussions relating to Neandertal subsistence and ecology have generally been left out. This paper will examine the historical development of ideas about Neandertal subsistence in order to determine whether ideas about Neandertal subsistence have been affected by the same historical biases identified in other histories of Neandertal research.

Scientific discovery and early history of the Neandertals

The Neandertals' ongoing "image problem is rooted in their history" (Tattersall 1995:74). The first fossils to be identified as Neandertal were recovered in a German valley in 1856 (Stringer and Gamble 1993; Trinkaus and Shipman 1993), before the introduction and scientific acceptance of Darwin's theory of evolution. The German scientist Hermann Schaaffhausen, who first presented the remains to the scientific community in 1857, believed that the Neandertal bones were the remains of a member of an ancient and primitive, but nevertheless human, tribe that drowned in the biblical flood (Tattersall 1995). Many researchers agreed with this interpretation, arguing that the Neandertal material represented a savage antediluvian *Homo sapiens* (Trinkaus and Shipman 1993). In 1863, the British geologist William King argued that the Neandertal material belonged to a separate hominid species, the brutish *Homo neanderthalensis*, but his was the minority opinion (Trinkaus and Shipman 1993). Other scientists were more reluctant to accept the possibility of other human species (Tattersall 1995). Thus, an interpretation of the Neandertal remains as the bones of a horseman with rickets (whose brow ridges were created by constant frowning due to pain) was popular during this time, especially because it was endorsed by the German physician Rudolf Virchow, who was highly respected for his expertise in pathology (Stringer and Gamble 1993; Trinkaus and Shipman 1993).

The discovery of additional Neandertal specimens from the 1860s onwards gradually dispelled the notion that the original remains were pathological. The discovery of another fossil hominid species (*Anthropopithecus javanensis*, later *Pithecanthropus javanensis*) by Eugene Dubois in 1891 was crucial in the acceptance of Neandertals as a distinct hominid species possibly ancestral to modern man (Tattersall 1995). Respected biologists, geologists, and anthropologists, including Ernst Haeckel (1898) and Gabriel de Mortillet (1883), argued that Neandertals were the link between *Pithecanthropus* and *Homo sapiens* (Trinkaus and Shipman 1993). Although the more 'primitive' *Pithecanthropus* made the Neandertals seem considerably less threatening (Trinkaus and Shipman 1993), they continued to be portrayed as 'savages.' For example, it was argued in 1906 that the Neandertal material from Krapina, Croatia, showed evidence of cannibalism (Tattersall 1995).

Not long afterwards, Marcellin Boule's (1911-1913) reconstruction of the 'old man' from La-Chapelle-aux-Saints, France, was published. Boule's reconstruction portrayed the Neandertals as "beetle-browed, bent-kneed, sloping-necked, shuffling slouches with grasping feet and inferior brains" (Tattersall 1995:92). This reconstruction, in conjunction with the discovery of a hominid skull at Piltdown, England, in 1912, dealt the image of Neandertals a devastating

blow. The Piltdown skull, which had a large brain and large jaw (relative to *Pithecanthropus* and Neandertals) fit the pre-sapiens ‘brains before brawn’ model of human evolution favored by many researchers at the time (Trinkaus and Shipman 1993). This model presupposed a very early split between the ancestors of modern humans and Neandertals. The location of the Piltdown discovery also fit well with contemporary Euro-centric attitudes. Although the skull was later proven to be a fraud (a modern human skull fitted to an orangutan mandible), the combination of these events resulted in Neandertals being left on the evolutionary sidelines for the next thirty years.

Despite the stifling influence of Piltdown man and the pre-sapiens theorists, some research on Neandertals did take place between the discovery of Piltdown and the discovery that it was a forgery in 1953. Unlike the majority of his colleagues, American physical anthropologist Aleš Hrdlička was skeptical of the authenticity of Piltdown and believed instead that Neandertals were human ancestors (Trinkaus and Shipman 1993; Tattersall 1995). Hrdlička (1927) argued that Neandertals evolved in Europe during the cooling periods of the last glaciation, eventually becoming modern Aurignacian man. However, interpretations of Neandertal ritual behavior during this period continued to contrast and distance the Neandertals from ‘civilized’ modern humans. For example, in 1921, cave bear remains found at Drachenloch, Switzerland, were touted as evidence for Neandertal ritual and sacrifice involving cave bears, hence the myth of the Cult of the Cave Bear (Tattersall 1995).

The perception of Neandertals as primitive savages only distantly related to modern humans may have been encouraged by racist thinking prevalent in physical anthropology during the early part of the twentieth century. During the 1920s and 1930s, physical anthropology in North America developed primarily as the study of race, partially due to substantial political pressure related to the eugenics movement (Caspari 2003). Races were considered to have evolutionary significance and were represented in trees along with fossil hominids (Caspari 2003; Proctor 1988). Diagrams emphasizing the differences between modern human groups gave the impression of great biological distance between Neandertals and modern humans. By the end of the 1930s, however, political and scientific backlash against the Holocaust, eugenics, and ‘scientific’ Nazism began to place pressure on anthropologists to reject the race concept (Caspari 2003; Hooton 1936; Proctor 1988). The emergence of the new evolutionary synthesis in the 1940s (Huxley 1942) would soon give physical anthropologists the means to redefine their discipline (Caspari 2003).

The new evolutionary synthesis, by combining Mendelian genetics with natural selection theory, emphasized the variability within species and encouraged lumping rather than splitting of taxonomic categories. The introduction of the synthesis, along with the debunking of Piltdown man, cleared the way for

Neandertals to be considered as a candidate for modern *Homo sapiens*' closest ancestor. The German anthropologist Franz Weidenreich (1940, 1943, 1947) argued that Neandertals and modern *Homo sapiens* were all part of a single, ancient polytypic species. Weidenreich's work may have been misinterpreted by contemporaries who, due to the continued influence of racial and typological thought, failed to understand the gene flow component of his model, due to the continued influence of racial and typological thought (Caspari (2003). However, Weidenreich's *rapprochement* of modern humans and Neandertals was foreshadowed by changes in the interpretation of Neandertal ritual behavior. In 1939, the Italian archaeologist Alberto Blanc interpreted fractures on a Neandertal cranium from Italy as evidence for murder and ritual cannibalism, because the cranium was placed in a crown of stones. These were later discovered to be in a natural arrangement (Trinkaus and Shipman 1993). Blanc suggested that this disposal indicated complex ritual, care for the dead, and a belief in the afterlife. According to Trinkaus and Shipman (1993:258), this interpretation redeemed Neandertal cannibalism through religious belief and made Neandertals more 'human.'

During the 1950s and 1960s, there was continued political pressure to de-racialize public thought, as exemplified by the UNESCO statement on race (1950), the civil rights movement, and desegregation in the American south (Caspari 2003). Concomitantly, the influence of the new evolutionary synthesis increased, as demonstrated by the development of New Physical Anthropology (Caspari 2003; Delisle 1995). The New Physical Anthropology, like the evolutionary synthesis, focused on populational rather than individual or typological variability (Caspari 2003; Delisle 1995; Washburn 1951). These trends may have been responsible for the continued 'humanizing' of the Neandertals during the mid-twentieth century. The influence of the synthesis on interpretations of human evolution can be seen in the works of F. Clark Howell (1952, 1957) and C. Loring Brace (1964). Both Brace and Howell emphasized variability between known Neandertal remains and concluded, contrary to the pre-sapiens model, that Neandertals and modern humans were descended from a recent common ancestor. Howell (1957) suggested that both late Neandertals and early modern humans were descendants of early Neandertals in the Near East (e.g., Mount Carmel). He suggested that Neandertals evolved in isolation in Europe during the Würm I glaciation, and were subsequently replaced by modern humans in Western Europe. Brace (1964) argued for four main stages of human evolution, with Neandertals being the penultimate stage. Hrdlička (1927) and Weidenreich (1943) had proposed this idea prior to the Second World War, but Brace (1964) suggested that it had been overlooked because Hrdlička and Weidenreich had no students and the normal process of scientific discourse had been interrupted by the War. Brace rejected the possibility of multiple hominid

species after the Middle Pleistocene (Howell 1964), emphasizing instead the transitional nature of some Neandertal and early Upper Palaeolithic skeletal forms. The trends seen in the work of Weidenreich, Brace, and Howell would usher in the development of theoretical models under which many anthropologists studying Neandertal evolution still operate today.

Other developments in the late 1950s and 1960s also emphasized similarities between Neandertals and modern humans. Neandertal anatomy was re-examined in 1955 by Camille Arambourg, who determined that Neandertal locomotion was similar to that of modern humans, and was not a bent-kneed shuffle, as proposed by Boule in the early part of the century (Tattersall 1995). Excavations at Shanidar, Iraq, were also particularly important in shaping the new image of Neandertals. Pollen discovered in a Neandertal burial at Shanidar was interpreted as evidence of flowers placed in the graves (Leroi-Gourhan 1968), while the age and disabilities of the Shanidar 1 skeleton were interpreted as indications of a system of social support (Solecki 1971). The title of Solecki's (1971) publication of the Shanidar findings, *Shanidar, the First Flower People*, summarized the general attitude towards Neandertals in this period: behaviorally modern but anatomically primitive (Trinkaus and Shipman 1993).

Emerging evolutionary models: continuity and replacement

During the early 1970s, Milford Wolpoff continued in the tradition of Weidenreich and Brace, arguing for what later became known as the multiregional model. This model suggests that ancient regional populations of hominids evolved into modern humans *in situ* through gene flow and selective pressures (Brose and Wolpoff 1971). However, as the political and cultural movements that defined the 1960s declined, the image of the Neandertals as intelligent ancestors trapped in a primitive body was challenged. British palaeoanthropologist Christopher Stringer (1974) advocated a replacement of late Neandertal populations by invading modern humans. The discovery of very early (older than 40 kya) anatomically modern humans at Omo in Ethiopia lent support to this position (Trinkaus and Shipman 1993). German anthropologist Günter Braüer formulated the 'Out of Africa' hypothesis, which argued that all modern human populations originated in Africa (Trinkaus and Shipman 1993). At the time, Braüer did not exclude the possibility of mixing between expanding modern human populations and existing regional hominid populations, although other researchers supporting this theory would later exclude the possibility of large amounts of genetic exchange between modern and archaic populations (Trinkaus and Shipman 1993; Mellars 1999). The debate between the multiregional and replacement camps intensified during the late 1970s (Trinkaus and Shipman 1993).

DNA analysis was introduced to anthropological studies in the 1980s, intensifying the debate over modern human origins and *Homo sapiens*' relationship to Neandertals. Cann, Stoneking, and Wilson (1987) added vigor to the replacement hypothesis, when they suggested that all modern humans had a common origin in Africa around 200,000 years ago on the basis of mitochondrial DNA diversity in modern humans. However, the 'mitochondrial Eve' hypothesis was highly criticized, particularly for the methods used to calculate genetic trees and the estimation of the rate of genetic change (Trinkaus and Shipman 1993).

By the late 1990s, research on Neandertal DNA emerged, with Neandertal mtDNA first sequenced by Krings et al. (1998), and nuclear DNA first sequenced by Green et al. (2006). Although Neandertal DNA is quite distinct from modern human DNA, the actual meaning of the DNA data for Neandertal/modern human relationships remains unclear (Green et al. 2006; Relethford 2001). Although replacement theorists such as Christopher Stringer have integrated the DNA data into their models, other researchers, notably Milford Wolpoff, have continued to defend the multiregional hypothesis (Trinkaus and Shipman 1993). The view that Neandertals were not completely replaced by modern populations has also found support in the archaeological record (e.g., Morin 2008). Although most researchers have conceded that the Neandertal to modern human transition is more complex than originally imagined, the multiregional/replacement debate continues to be a major focus of Neandertal research.

Historical influences on anthropological interpretations of Neandertals

Scientific thought about Neandertals and their relationship to modern humans has changed significantly over the past 150 years. The ways in which thought about Neandertals has somewhat mirrored greater historical processes have not been lost on scholars in the discipline. Brace's (1964) argument that Boule's (1911-1913) interpretation of the Neandertals was an expression of Cuvier's theory of catastrophism is an early example of this type of reflection. Other scholars have noted how the dark, savage image of the Neandertals that pervaded during the early 1900s, and up to around 1940, echoed both the dark political times as well as the prominence of racial thinking in anthropology at the time (Graves 1991; Trinkaus and Shipman 1993). The alignment of anthropologists with the populational thinking of the New Physical Anthropology and the new evolutionary synthesis roughly coincided with the repudiation of race by anthropologists after WWII and the subsequent re-positioning of Neandertals within the human lineage and even within the human species. Popular portrayals of Neandertals, such as H.G. Wells's 1921 short story *The Grisly Folk*, in which Neandertals are depicted as monsters, and William Golding's 1955 novel *The Inheritors*, in which they are depicted as innocents, also reflect a major shift in

attitudes towards Neandertals after WWII (Graves 1991; Stringer and Gamble 1993). Graves (1991) argues that attitudes towards Neandertals up to the end of WWII are best explained using a colonial metaphor, while after the war, they can be explained using a metaphor of indigenous development. According to Graves, this shift in theoretical attitudes was a reaction against imperialism. These arguments suggest that historical patterns of thought may have had a real impact on scientific discourse concerning Neandertals. Such processes may continue to work today, but without the benefit of substantial hindsight it is difficult to determine the trends shaping recent work and the possible biases introduced by these perspectives.

Neandertal subsistence: early ideas to the 1960s

Until Neandertals were recognized as a distinct type of hominid, questions of Neandertal diet and behavior were immaterial. Even after the general acceptance of Neandertals as a distinct type of hominid in the late 1800s, research focused heavily on anatomy. Studies attempted to place the Neandertals in their proper position in relation to modern humans (including different races of humans) and eventually to other fossil hominids. Discussions of Neandertal behavior were limited. Boule's 1923 textbook, *Fossil Men*, makes only this mention of Neandertal subsistence: "[the structure of the jaw] points to a dentition more employed for biting than chewing, and implies a vegetarian rather than carnivorous diet" (Boule 1923:212). Boule and many of his contemporaries evidently did not consider subsistence to be an important factor shaping the course of hominid evolution. One notable exception to this pattern is Hrdlička's (1927) paper on the Neandertal phase of man. Hrdlička contrasted the subsistence patterns of Neandertals and subsequent Aurignacians. According to Hrdlička, Neandertals were chiefly hunters, who used fire to roast meat, lived in caves and shelters, broke the bones of animals to extract brain and marrow, and who did not use any form of storage. Excluding fishing and the use of molluscs, Hrdlička considered the subsistence habits of Neandertals to be essentially the same as those of Aurignacians. Using this and other evidence, Hrdlička argued that Neandertals were the most likely candidate for modern *Homo sapiens*' most recent ancestor. For Hrdlička, the study of Neandertal adaptation was directly relevant to the study of the evolution of modern humans, whereas for other researchers at the time, Neandertals represented only a primitive side branch of the human family tree.

The general absence of subsistence studies until 1950 is probably also related to the focus of archaeological studies during this time. Archaeology in the late nineteenth century was essentially evolutionary in approach: archaeologists were preoccupied with determining the stages of development of archaeological cultures, and hence both artifacts and animal remains were primarily used as

indicators of chronology and technological development (Trigger 1968). By the first half of the twentieth century, evolutionary approaches had been repudiated as racist and imperialist, and the cultural-historical approach emerged in both European and American archaeology (Trigger 2006). This approach identified material culture with actual cultural groups and attempted to explain the development of cultures through processes such as migration and diffusion (Trigger 1968, 2006). Both the evolutionary and cultural-historical approaches had “little concern for the individual cultural contexts in which artefacts were being found” (Trigger 1968:530), and focused on the relationships between cultures rather than on the characteristics of the cultures themselves. This bias could explain the absence of early studies focusing on Neandertal culture and behavior.

Brief mentions of Neandertal subsistence practices began to appear more frequently during the second half of the twentieth century. This trend may reflect the increased interest in Neandertals as potential human ancestors after the Second World War and the demonstration of the Piltdown fraud. Howell (1952) argued that Neandertals were primarily gatherers who engaged in a limited amount of hunting, mostly of large herbivores. He suggested that Neandertals would have been restricted to areas with higher densities of plants, berries, nuts, and small forest animals. Conversely, in 1954, Nougier argued that collection of plant foods would have been rare in the cold environment in which the Neandertals lived and that Neandertal technology would not have permitted fishing or the capture of birds. Nougier suggested that Neandertals lived almost exclusively on meat, especially that of large ungulates. Weckler (1954) suggested that the first modern *Homo sapiens* who entered Europe learned specialized cold climate hunting techniques and possibly even religion from Neandertals. Brues (1959) argued that based on the Neandertals’ powerful build, they could not have pursued mobile prey, but must have captured prey by surrounding them or by using traps. According to Brues, this type of hunting required co-operation and intelligent planning by Neandertals, but ultimately they were out-competed by swift and more efficient modern humans. Although these mentions of Neandertal subsistence may reflect increased interest in Neandertals due to their reincorporation by some anthropologists into scenarios of human evolution, they also precede major developments in archaeological thought during the 1960s, which would bring a new set of theoretical and methodological considerations into play.

Neandertal subsistence: 1960s and 1970s

The 1960s represent a turning point in archaeological subsistence studies, a change related to a number of major developments in archaeology at the time. Cultural-historical approaches waned as interest in past cultures declined and

interest in past behaviors increased (Trigger 2006). Lewis Binford spearheaded the New Archaeology, which explicitly rejected the cultural-historical approach in favor of a processual approach dedicated to understanding how cultures functioned. Under the New Archaeology, cultures were understood primarily as adaptive systems and the relationship between culture and the environment was considered the primary cause of cultural change (Trigger 2006). The emergence of zooarchaeology and subsistence studies as an important aspect of archaeological research in the 1960s was correlated with this change in research focus. Animal remains were accepted as a means of interpreting cultural change and human relationships with the environment (Reitz and Wing 1999). The development of the ecology movement in the 1960s onwards also stimulated greater interest in the relationships between human groups and their environments (Trigger 2006).

An example of the influence of the New Archaeology on subsistence studies of Neandertals is illustrated in the work of Lewis and Sally Binford. They argued that “the form and composition of assemblages recovered from geologically undisturbed contexts are directly related to the form and composition of human activities at a given location” (Binford and Binford 1966a:291). This meant that faunal assemblages could be analyzed to determine the activities that took place at a site. On the basis of faunal remains from the Levant, Binford and Binford (1966b) suggested that early Mousterian (Neandertal) subsistence was characterized by a generalized hunting strategy, in which all game resources in the environment were exploited. As ‘sapiensized’ Neandertals appeared in the terminal Mousterian, there was a switch to systematic predation on a single prey species, a ‘specialized’ hunting pattern that the Binfords argued was characteristic of modern human groups. Sally Binford (1968) elaborated this argument, suggesting that a ‘predatory revolution’ (a switch from generalized to specialized hunting) occurred during the Middle to Upper Palaeolithic transition, and pressured hominid groups to aggregate. This aggregation would have encouraged gene flow and evolutionary change in Neandertal populations.

Despite the efforts of the Binfords, subsistence studies of Neandertals did not take off in the mid-1960s. This false start was probably linked to the hominization theory dominant at the time, and promoted by the ‘Man the Hunter’ symposium in 1966. The general consensus about the importance of hunting in hominid evolution that emerged from the symposium can be summarized as “biology, psychology, customs that separate us from the apes – all these we owe to the hunters of time past” (Washburn and Lancaster 1968:303). With the belief that even early Australopithecines had been hunters (Howell 1965; Lee and Devore 1968), there could be little doubt that Neandertals were efficient hunters. For instance, in his popular science book *Early Man*, Howell (1965) depicted

Neandertals as clever and co-operative hunters, who used drives and camouflaged pits to capture animals such as ibex, reindeer, woolly rhinoceros, and mammoth.

The relationship between the focus on hunting as an evolutionary prime mover and perceptions of Neandertal subsistence is illustrated in a number of works from the 1960s and 1970s. For instance, in *Emergence of Man*, Pfeiffer (1969) argued that meat eating, specifically big game hunting, gradually transformed the hominid brain and physique beginning with *Homo erectus* approximately 1.5 million years ago. According to Pfeiffer, Neandertals were efficient hunters, but due to the cold, relatively unproductive environment they inhabited, they had to live and hunt in small groups. Their small group sizes meant that they could kill only individual animals. In contrast, Pfeiffer suggested that modern humans lived in large groups and was a more effective predator than Neandertals because large numbers of animals could be killed simultaneously through co-operative effort. Neandertals were thus driven to extinction through competition with modern *Homo sapiens*.

During the 1970s a greater number of researchers began to acknowledge the possibility of scavenging among early hominids, but the general consensus that hunting had been an important factor in human evolution continued to prevail. Washburn and Moore (1974) argued that life on the savanna forced the australopithecines to turn to meat rather than fruit or herbs as a primary food source. Hunting caused increases in travel (hence, bipedalism) and tool use. Similarly, Wood (1976) depicted *Australopithecus africanus* and *Homo habilis* as meat eaters, and *Homo erectus* as a competent hunter. His view of Neandertals was a logical progression: they were skilled hunters of large game including mammoth, rhinoceros, and bear.

The changes in perspectives on the Neandertals' relationship to modern humans that took place during the 1970s (the beginning of the multiregional/replacement debate) also had an effect on reconstructions of Neandertal subsistence. For example, Mellars (1973:271) argued that "a broadening of the subsistence base to include both fish and (less certainly) birds" was an important development of the Upper Palaeolithic that contrasted modern humans from Neandertals. Geist (1978) argued that in the cold climate of Late Pleistocene Europe, Neandertals could only have survived in a supercarnivore niche because plant foods would have been lacking and the niche of carnivore was already occupied. In order to survive, Neandertals would have had to hunt megafauna such as mammoth and rhinoceros, which were too large to be hunted by most carnivores. This argument was incorporated into a broader adaptive and evolutionary scenario in which Neandertals were adapted to "close-quarters confrontation hunting" (Geist 1978:294). According to Geist, Neandertals depended on slow, gregarious megafauna, as they required large amounts of meat to create sufficient fat stores between kills. Smaller game did not provide an

adequate net energy return to sustain Neandertal groups. Dependence on the Pleistocene megafauna led to the Neandertals' extinction with the onset of climate warming between Würm glaciations I and II. Geist's extinction scenario fit well with replacement hypotheses that were being articulated at the time.

Neandertal subsistence: 1980s

The early 1980s marked a long overdue change in opinions on hominid subsistence, including Neandertals. The feminist critique of the late 1970s helped to outline the failings of the Man the Hunter hominization theory (e.g., Zihlman 1978). However, the major impetus for change in perceptions of hominid subsistence can probably be attributed to the work of C.K. Brain (1981) and Lewis Binford (1981). Their studies on the role of carnivores in bone accumulation processes provided strong evidence against the Man the Hunter theory (Straus 1982). Brain and Binford showed that early hominids were not necessarily efficient hunters, but may have been scavengers and, in some cases, the hunted. This work forced many archaeologists and faunal analysts to recognize the importance of taphonomy in understanding archaeological sites.

As a result of Brain and Binford's work, there was a major debate over hominid scavenging from 1981–84 and a general shift forwards in time (at least to *Homo erectus*) of hunting as a major means of hominid subsistence (Binford 1985). Researchers studying Neandertals began to take taphonomy into account as well. Dennell (1983) summarized the problems faced by researchers studying Neandertals in the 1980s: due to the lack of taphonomic studies, it was unclear whether carnivores such as hyaenas and wolves were hunted by Neandertals or occupied cave sites separately. Important aspects of subsistence such as prey age and sex, seasonality, methods of capture and kill, and butchery also had been inadequately investigated.

Binford (1985) added to the hunting/scavenging debate when he argued that the cut marks and gnawing patterns on faunal remains from Hoxne and Swanscombe, both in England, and Abri Vaufrey, France, indicated scavenging of large, and occasionally, moderate-sized prey by Neandertals. Binford suggested that Neandertals were unable to hunt large game and that instead they scavenged, indicating a lack of planning, cooperation, and sharing. In Binford's view, big game hunting was a uniquely modern condition.

By suggesting that Middle Palaeolithic subsistence may not have been as similar to modern subsistence as previously thought, the hunting/scavenging debate brought ecology and subsistence directly into the controversy over the Middle to Upper Palaeolithic transition. However, there was little agreement on the nature of subsistence differences between Neandertals and modern humans. For example, Chase (1989) argued that Middle and Upper Palaeolithic subsistence practices (in Europe) were essentially the same, and could not be used to explain

the Middle to Upper Palaeolithic transition. In contrast, Trinkaus (1986) argued that based on their lower limb morphology, Neandertals were adapted for endurance and extensive locomotion. The idea that Neandertals were highly mobile, in combination with their technological limitations, suggested to Trinkaus that Neandertals had low subsistence efficiency. Ogilvie et al. (1989) observed high incidences of dental enamel hypoplasia in Neandertals. These authors suggested that dietary fluctuations were common among Neandertal populations, and that individuals were frequently nutritionally deprived, a possible indication of lower foraging efficiency and of unpredictability in Neandertal diets. These discussions reflect attempts to delineate a boundary between modern human and Neandertal behavioral adaptations within the multiregional/replacement framework characteristic of 1980s research on Neandertals. If early hominids and Neandertals could not be considered hunters, then defining Neandertal subsistence practices was critical for defining truly 'modern' behavior.

The focus of research on Neandertal subsistence during the 1980s is illustrated in the 1986 conference *L'Homme de Néandertal*, which was held for the one hundredth anniversary of the discovery of the Spy Neandertals. The published works stemming from the conference included an entire volume dedicated to Neandertal subsistence (Otte 1989). In the introductory paper to the volume on subsistence, Patou (1989) outlined the main questions concerning Neandertal subsistence that were important at the time. These included taphonomy, site function, hunting versus scavenging, opportunism versus specialized hunting, and mobility.

Neandertal subsistence: 1990s to present

Since 1990, studies of Neandertal subsistence have proliferated and become more specialized. Four strains of research on Neandertal subsistence can be identified as important sources of evidence: zooarchaeology, palaeobotany, osteology, and stable isotope analysis. All of these branches have contributed different evidence, sometimes complementary, sometimes contradictory, to the reconstruction of Neandertal subsistence practices. Therefore, it is not surprising that a trend towards increasing complexity in reconstructions of Neandertal subsistence emerged over the last twenty years.

Zooarchaeological analyses are the primary field of research on Neandertal subsistence and have been the core component of the debate over Neandertal hunting and scavenging, which continued until the early 1990s. Mary Stiner's contributions to the hunting/scavenging debate have been of particular importance. Stiner (1991) examined the transport behaviors of hunting and scavenging animals and argued, following Binford, that head and horn elements, rather than meat-bearing parts, dominate assemblages resulting from episodes of scavenging. Based on these criteria, Stiner determined that Middle Palaeolithic

hominids in west-central Italy hunted and scavenged prior to 55 kya, after which time Neandertals and, later, modern humans in the region only hunted. Stiner pointed out, however, that although prior to 55 kya Neandertals occasionally scavenged opportunistically, they were also competent hunters.

In response to Stiner's work, Marean and Kim (1998) argued that the head-and-horn or head-and-foot dominated assemblages that Stiner considered to be indicative of scavenging were in fact a result of identification procedures that ignored long bone shaft fragments and/or of selective discard of long bones during excavations (see also Pickering et al. 2003). Marean and Kim suggested that there is no evidence for regular scavenging in the Middle Palaeolithic. Instead, they argued that Neandertals were not scavengers and were capable of a focused hunting pattern. Regardless of whether Neandertals did or did not engage in scavenging, it finally became clear during the 1990s that they were certainly not obligate scavengers, as Binford had suggested in 1985.

The debate over Neandertal hunting abilities strongly characterized zooarchaeological research on Neandertal subsistence during the 1980s and 1990s. However, by the start of the new millennium, the focus of research had shifted to when and how Middle Palaeolithic hominids chose to hunt (Burke 2000). Research on Neandertal hunting leading up to the year 2000 indicated that there were many similarities in Middle and Upper Palaeolithic subsistence and that Middle Palaeolithic subsistence was highly sophisticated. These realizations forced a broadening of the conceptualized Neandertal niche (Burke 2000) and supported the conclusion that anatomic modernity cannot be exclusively equated with behavioral modernity (McBrearty and Brooks 2000). Burke (2000) suggested that research on Neandertal hunting in the early 2000s would focus on the diversity of regional patterns in Middle Palaeolithic subsistence and the decision-making processes involved in subsistence strategies. Grayson and Delpech (2003) agreed that zooarchaeological research on Neandertal hunting has entered a new phase in which research focuses on Neandertal choices rather than limitations.

The Middle to Upper Palaeolithic transition has continued to be a question of major interest in zooarchaeological studies of Neandertal subsistence. In particular, since the conclusion of the hunting/scavenging debate, the question of diet breadth (the variety of foods included in the diet) has assumed particular importance. It has been argued that broad-spectrum diets (diets incorporating a broad range of resources, including difficult to obtain foods such as rabbits, birds, and fish) are a distinguishing characteristic of modern humans, who were therefore able to outcompete Neandertals (O'Connell 2006). Broad-spectrum resource exploitation by Neandertals under different ecological conditions has therefore been an important focus of recent research (e.g., Laroulandie 2004; Speth and Tchernov 2002; Stiner 1994; Stringer et al. 2008). Stiner et al. (2000) argued that a broad-spectrum revolution in subsistence began to take place before

the Upper Palaeolithic. They highlighted the use of small fauna, such as marine molluscs and tortoises, by Neandertals in Italy even during the early Middle Palaeolithic. Towards the end of the Middle Palaeolithic, Stiner and colleagues noted size decreases in tortoise bones and molluscs found at archaeological sites, which they argued was a result of increased predation. Consequently, Stiner et al. considered population increases, instead of Neandertal hunting abilities, to be the reason for the addition of prey with lower return rates (such as birds and lagomorphs) to the diet during the Upper Palaeolithic.

In contrast, a number of zooarchaeologists have found little evidence for subsistence change at the Middle to Upper Palaeolithic boundary in Western Europe that cannot be explained by climate change (Faith 2007; Grayson and Delpech 2003, 2008; Grayson et al. 2001; Morin 2008). Grayson and Delpech (2003) suggest that major changes in subsistence patterns do not occur until the Magdalenian, long after the Neandertal to modern human transition. These authors point out, however, that although there were no significant changes visible in the archaeological record, return rates and failure rates may have differed in the Middle and Upper Palaeolithic periods.

In general, zooarchaeological studies have demonstrated that patterns of resource use among Neandertals are complex and variable (Burke 2000), although they may have been strongly conditioned by local prey availability (Bar-Yosef 2004). However, as pointed out by Bar-Yosef (2004), many analyses of Neandertal ecology have had a tendency to homogenize Neandertal behaviour during the entire Middle Palaeolithic, instead of recognizing the potential for behavioral change during this extended period.

The study of plant remains is helping to correct the “meat fixation” of past subsistence studies (Madella et al. 2002:704). Madella and colleagues examined phytoliths from Amud cave in Israel and determined that Neandertals used plant materials extensively, not only for fuel and bedding but also for food. Palm and Moraceae phytoliths suggested consumption of palm fruits and figs, while the morphology of many herbaceous phytoliths suggested that Neandertals might have gathered wild cereals. Lev et al. (2005) identified carbonized plant remains from Kebara Cave, Israel. They concluded that Neandertals at Kebara were probably consuming a significant amount of legumes. Acorns, pistachios, and fruits may also have constituted a significant part of the diet, at least in the fall. There was no evidence of root plant foods and very little evidence for the use of cereals. Overall, Lev et al. concluded that subsistence at Kebara included broad-spectrum plant foraging and that the occupants may have been able to live at the site year round. These analyses of plant remains suggest considerable complexity in Neandertal foraging, including extensive use of a variety of plant materials when these were available.

Osteological analyses have also made contributions to the study of Neandertal subsistence. Comparisons of Neandertal and modern human teeth (Spencer and Demes 1993) have suggested that, like the Inuit, Neandertals had powerful bite forces and used their incisors intensively. Thus, Neandertals may have consumed frozen meat, crunched bone, and used their teeth as tools in a number of day-to-day activities as do the Inuit. The large molar size in Neandertals also suggested that their diet caused more attrition than the Inuit diet, possibly indicating a greater proportion of plant food in the Neandertal diet (Spencer and Demes 1993). Berger and Trinkaus (1995) analyzed patterns of traumatic injury in Neandertals and determined that their patterns of injury were highly unusual in comparison to most human groups (including some ancient groups), and were in fact most similar to those of modern rodeo riders. Based on this similarity, Berger and Trinkaus concluded that Neandertal subsistence involved close contact with angry medium-sized ungulates, and that Neandertal technology may have limited them to close range hunting. Although not as exclusively focused on subsistence as zooarchaeological and palaeobotanical studies, these examples demonstrate that osteological analyses have yielded interesting data worth examining in conjunction with more direct evidence for subsistence.

Chemical analyses of Neandertal bone have also made an important contribution to studies of Neandertal subsistence since 1990. Carbon and nitrogen stable isotope analyses of Neandertal remains were first carried out by Bocherens et al. (1991) on a 40000-year-old specimen from Marillac, France. They determined that the Neandertal had a high $\delta^{15}\text{N}$ (nitrogen fifteen) level but a terrestrial $\delta^{13}\text{C}$ (carbon thirteen) signature, indicative of a diet containing substantial amounts of herbivore meat. Since that time, additional stable isotope studies of Neandertal remains have been carried out (Richards et al. 2000; Richards et al. 2001) and these studies have also suggested that the diet of Neandertals' was dominated by herbivore meat. Richards et al. (2001) and Richards and Trinkaus (2009) used stable isotope data to argue that Neandertals did not and probably could not exploit freshwater marine resources, in contrast to Upper Palaeolithic modern humans who appear to have done so. Richards et al. (2001) suggested that Neandertal populations were vulnerable due to their reliance on large mammals and that a broad-spectrum diet including fish and small game was associated only with fully modern humans. This argument illustrates the ongoing debate concerning the onset of 'modern' behavior and the nature of the Neandertal to modern human transition.

In summary, research on Neandertal subsistence has grown increasingly complex since 1990, with numerous disciplines making significant contributions. Generally, it is now agreed upon that Neandertals were competent hunters, but the extent to which they exclusively pursued large game is debated. Plant foods and

small game, as well as scavenged carcasses, may have been significant dietary components under favorable circumstances. The overall importance of these additional elements and the conditions under which they were included in Neandertal diets is an increasingly important question. The interest in the spectrum of Neandertal diets is tied to the ongoing interest in the Middle to Upper Palaeolithic transition, as researchers attempt to determine whether modern humans had a competitive edge over Neandertals. However, the complexity now proposed for Neandertal subsistence reflects the complexity that is increasingly recognized in the Neandertal to modern human transition.

Discussion

Disciplinary boundaries are blurred in the study of Neandertals. The broader disciplines engaged in the study of Neandertals include palaeoanthropology and zooarchaeology, but also the domain of evolutionary biology in which palaeoanthropology is embedded. The history detailed here indicates that the study of Neandertal subsistence may have been affected by some of the historical biases in physical anthropology and evolutionary theory that affected views of Neandertals more generally. However, theoretical developments specific to the discipline of archaeology and changes in hominization theory appear to have been more important influences on the development of Neandertal ecology as a subject of study. Until the 1940s, the perception in palaeoanthropology of Neandertals as an evolutionary dead end turned interest away from Neandertals as archaeologists focused their efforts towards other potential candidates of modern *Homo sapiens*' ancestor, notably Piltdown man. After the emergence of the new evolutionary synthesis in the early 1940s, which encouraged the placement of Neandertals within the evolutionary lineage of *Homo sapiens*', studies of Neandertal subsistence continued to be inhibited by cultural-historical perspectives in archaeology. These paradigms focused the attention of archaeologists on typologically definitions of cultures rather than on adaptation or behavior.

Despite the emergence of the New Archaeology, which placed greater emphasis on behavior and adaptation, the dominance of 'Man the Hunter' hominization theory in the 1960s meant that Neandertals were often automatically considered to be efficient large game hunters. This outlook persisted despite criticism well into the 1970s, and was certainly assisted, at least during the 1960s, by the view that Neandertals were direct ancestors of modern man. As a result, concerted efforts to study Neandertal subsistence during this period were scarce.

By the early 1980s, taphonomy had developed as an essential component of archaeological research, helping to disprove the Man the Hunter theory. Scavenging assumed a greater role in hominid evolution, to the extent that Binford (1985) suggested that Neandertals were obligate scavengers. It was

partially as a result of this scientific stimulus that studies of Neandertal subsistence flourished in the 1980s. By questioning the hunting ability of Neandertals, Binford questioned their humanity as it had been defined in the Man the Hunter paradigm. This questioning of the Neandertal's modernity resonated well with the accelerated development of replacement models during the 1980s, which once again suggested that Neandertals might have been an evolutionary dead end. Subsequently, other researchers questioned Neandertal foraging abilities, while some argued that their subsistence practices were essentially identical to those of later human groups. The search for differences and similarities between Neandertal and modern human subsistence fit well with the polarized attitudes of the continuity/replacement debate.

Since the 1990s, the study of subsistence has been a major focus of research on Neandertals, and an increasingly important component of the continuity/replacement debate. Although Neandertals are once again perceived as hunters, main research foci, such as Neandertal diet breadth, are still questions through which researchers hope to resolve the debate concerning the Middle to Upper Palaeolithic transition.

Conclusion

This paper has provided a brief overview of the history of Neandertal subsistence research and its relation to broader trends in archaeology and anthropology. This research confirms that zooarchaeological interpretations of subsistence are influenced by their historical and disciplinary context. However, our knowledge of Neandertal subsistence should not be considered simply as historically-situated prejudice. The archaeological data has, on occasion, resisted certain interpretations and directed the course of future research. The outcome of the hunting/scavenging debate, in which faunal remains eventually provided a strong disproof of the scavenging hypothesis, serves as a prime example. Nevertheless, it remains clear that "interest in Neanderthals is [...] as much in ourselves and where we draw the line of humanity as in them" (Stringer and Gamble 1993:38). Neandertals provide the opportunity for anthropologists to search for the exact characteristic that define the modern condition, and this search not only includes art, anatomy, and toolkits but also the ways in which we go about procuring the necessities for survival.

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