Chapter 30

Heading North: an Africanist Perspective on the Replacement of Neanderthals by Modern Humans

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The previous ‘Human Revolution’ conference focused much of its attention on debating the relative strengths of early versions of the single origins and multi-regional continuity models, and seeking explanations for the so-called ‘Human Revolution’ that occurred in Europe between 40,000 and 30,000 years ago. The 2005 ‘Rethinking the Human Revolution’ conference stood in contrast in several ways that mark both a consensus coupled to new directions in research and debate. These consensuses include the following. It is now clear that the multiregional continuity model is for the most part untenable and that some version of the single origins model remains as the best explanation for modern human origins. Marine isotope stage (MIS) 6 is a critical time for the origins of modern humans. A ‘Human Revolution’ at 40,000–30,000 years ago may have occurred in Europe, but not in Africa, and the former was likely due to the migration into Eurasia of anatomically modern humans. Neanderthals as a recognizable population go extinct shortly after 35,000 years ago. Many of the material culture markers that we once looked to as indicators of modern human behavior appear earlier in Africa than in Eurasia.

Consensus on the major issues goes no further. Some would say that we can discard the term ‘Human Revolution’. Certainly its use as a pan-Old World phenomena is falsified (McBrearty & Brooks 2000), but if one restricts the use to Europe then it is likely still viable. There is much debate around the timing and process of the introduction of modern people into western Eurasia, and that is tightly entwined with the dating of the Aurignacian. There is widespread debate on the behavioural characteristics of Neanderthals, but at this conference at least much of that debate took a narrow archaeological view, ignoring for the most part evidence from physical anthropology, human biology and bone chemistry. That approach works at cross-purposes with the palaeoanthropological approach, and ignores the fact that organisms have a suite of related bio-behavioural adaptations that, to be understood, must be integrated. The integrative bio-behavioural approach is a core principle in this chapter.

As some variant of the single origins model has gained prominence, archaeologists have struggled to understand the implications for behavioural evolution, and much of this has been framed around a debate over the origins and timing of ‘modern human behaviour’. The Africanists are divided on the timing and nature of the appearance of ‘modern human behaviour’ in Africa. Some see evidence for its appearance sometime after 130,000 years ago (Watts 1999), while others argue for a gradual appearance over a wide span of time (McBrearty & Brooks 2000). I believe the record is still too thin to resolve either argument. The term ‘modern human behaviour’ continues to bedevil us, largely because it is poorly defined, but there is growing consensus around a definition that has symbolic capacity at its core (Henshilwood & Marean 2002).

This means that ultimately the concept of ‘modern human behaviour’ and symbolic capacity will likely fuse and the former term will become redundant. The search for the timing and context of the appearance of symbolic behaviour in the archaeological record is, without doubt, an important research topic. However, when we address the issue of the expansion of modern humans and the replacement of Neanderthals, symbolic behaviour may or may not be a significant part of the process. Symbolic behaviour is one, albeit important, component of the adaptive strategy of Homo sapiens, which is the sum total of adaptations of a species to its abiotic, biotic and social environment (Lincoln et al. 1982).

All species have a definable adaptive strategy. When we open a guidebook to mammals, such as A Field Guide to the Mammals of Africa (Haltenorth & Diller 1977), we find a synopsis of each species’ adap-
adaptive strategy as reflected in its biology and behaviour. No two are the same. The burden is on us to resolve such definitions for hominins as well. I think Neanderthals and modern humans had differing adaptive strategies that can ultimately be resolved in a succinct manner that will lay the foundation for understanding their relations and the former’s extinction. The core of these strategies is now becoming clear, and provides an explanation for why Neanderthals went extinct in western Europe following the arrival of modern humans. To highlight the differing core adaptive strategies, I will focus below on differences between western Europe and Africa, since it appears likely that the former was the evolutionary core area for Neanderthals, and therefore crucial to the final shape of their adaptive strategy.

Differences revealed in similarities

Perhaps the best evidence for fundamental differences between modern humans and Neanderthals is, counterintuitively, the basic similarities in material culture complexity between Africa and western Europe between 200,000 and 35,000 years ago. There is little doubt that lithic technology was the core of the technological system of these hominins. Basic core-preparation and reduction technology was rather similar between Africa and Eurasia but there are some differences (Marean & Assefa 2005). Blade technology is far more common and sophisticated in Africa, as is the production of backed pieces from those blades. The production of finely shaped and flaked lanceolate and foliate bifaces is more widespread in Africa — many of them rival European bifacial technologies that occur far later in time. So, based on these measures, African lithic technology does appear to be somewhat more complex, but not decisively so, and certainly not as different as that between the Middle and Upper Palaeolithic of Europe. But that is the problem, and here is why it is so critical to contextualize the evolution of modern humans and Neanderthals.

In a book published in 1976, Oswalt (1976) quantified the complexity of technology of foraging peoples. His measure of complexity was what he called techno-units — the number of individual parts of a technology. His result is well known — the colder the climate, the more complex the technology (Fig. 30.1). This result was later expanded in reach and sophistication by Binford (1980; 1982) and Torrence (1983; 1989). This pattern of increasing complexity with latitude is driven by several challenges posed by colder climates. In colder climates a hominin needs to provide itself with a warm microclimate of clothing, shelter, and warm air created by more complex hearths. Plant foods are for the most part absent during fall through spring, and thus there is a greater emphasis on hunting large mammals, with a consequent increase in the complexity of hunting technology that takes the form of reliable and effective technologies. These are often composite technologies. We also often see greater complexity to symbolic expression in the form of portable artefacts. Tropical hunter-gatherers generally have very light technologies designed for high residential mobility.

Following this general pattern, we should see in the archaeological record differing technologies between western Europe and Africa, and more specifically we would expect western Europe to be far more complex than Africa in material culture at any particular point in time. If we compare the post 35,000 yr records in Africa and western Europe, this expectation is met. Western Europe early in the Upper Palaeolithic has a plethora of highly complex technological systems with extreme symbolic expression. This is not true in Africa except in very special situations and these generally occur rather late, often in the Holocene. This is not the pattern seen prior to 35,000 yr. The archaeological records at this time in Africa and Western Europe are both lacking in material culture complexity, and one could argue that Africa surpasses Western Europe in complexity (Marean & Assefa 2005).

So, our question should not be ‘are the African Middle Stone Age and western European Middle Palaeolithic similarly complex’, it should be ‘is the western European record more complex than the African record, as we would expect’. Obviously, it is not. But, when modern humans enter western Europe, that complexity explodes. The most parsimonious hypothesis for this explosion of cultural complexity is that these modern humans had the adaptive

![Figure 30.1. The relationship between tool complexity as measured by technounits (Oswalt 1976) and effective temperature.](image-url)
system documented in Oswalt’s work and were thus pre-adapted to this expression of complexity given the proper environmental stimuli. Neanderthals were not, and this suggests they had a different adaptive system. It highlights the significance of evolutionary context — the environment is a prime mover of the evolution of technology, behaviour and biology. And the ecological differences between Africa and Eurasia must figure into the replacement.

The replacement event

At this point I will make the assumption that modern humans evolved in Africa, spread out of Africa, and replaced Neanderthals and any other remnant populations of near-modern humans.

I think this debate is essentially resolved, and that we now need to focus on the details of how and why replacement happened. A recent volume of Quaternary International was devoted to this topic, and many of the papers there offer interesting ideas as to the nature of this replacement. Unlike that volume, which is dominated nearly exclusively by Europeanists, I will examine the issue with an Africanist perspective.

Replacement of one species by another, or of one ethnic group by another, is not an unusual event from an evolutionary perspective. The palaeontological and ethnographic record provides many useful examples for us to draw on for understanding the process. One key lesson to be learned from this record of replacement is that the replaced species was typically well adapted to its environment and often highly successful. Therefore arguing for a replacement event does not suggest that Neanderthals were poorly adapted. Rather, the replacing species is just better at doing something that ultimately allows it to survive and reproduce better than the other. The ethnographic and historic records illustrate that replacement can occur through many processes, and in human history direct conflict, both through subtle and dramatic differences in technology, was common. Bettinger & Baumhoff (1982) were one of the first to develop an ecologically grounded evolutionary theory for ethnic spread (or replacement as discussed here) among hunter-gatherers, and many of the ideas advanced here benefit from their discussion.

The palaeontological record provides numerous examples of replacement as a result of resource competition, and one that is instructive here is the Great American Interchange and the eventual extinction of South America’s top carnivores. Prior to 3.5 million years ago, North and South America were separated by ocean, and then after 3.5 myr the Isthmus of Panama rose and connected the two land masses. The dominant carnivores of South America prior to this event were large predaceous birds, often called ‘terror birds’ because of their large size and awesome armory of talon and beak. Entering South America from North America were the ancestors of the modern carnivore guild such as mountain lions and wolves. No one would argue that these large predaceous birds were poorly adapted, since they lasted for about 26 million years. It is unlikely that mammalian carnivores hunted these birds since the birds were vastly larger and stronger. One widely supported interpretation is that mammalian carnivores usurped their feeding niche, and thus lowered the foraging return rates of the birds, eventually driving them to extinction (Marshall 1994).

The replacement of Neanderthals could easily fall into competition or conflict scenarios, could be a combination of the two, and might be regionally variable. It may be a very long time before we can narrow down the most likely explanation(s), but I think the place to start is to try to identify the parameters of each scenario so that we can generate test implications from which to work. In this paper I want to investigate replacement by usurping feeding niche. In a recent paper (Marean 2005) I developed this argument more fully, particularly in regards to the biological background for Neanderthals. Here I want to update that argument and place it more directly in the context of western Europe. The argument that modern humans replaced Neanderthals by usurping their feeding niche has a rather counterintuitive correlate — that modern humans quickly became better than Neanderthals at procuring food in temperate and cold environments. This seems even more counterintuitive when we consider that Neanderthals must have had several biological and behavioural advantages by means of their long evolutionary history in these environments, and as suggested by their anatomy. I think there are some very good reasons as to why modern humans may have rapidly turned the tables on Neanderthals, and I develop those below.

The context for the evolution of differing adaptive systems

The Neanderthal lineage and the mosaic of features that define it appear to have evolved in an accretionary manner beginning as early as 450,000 BP (Hublin 1998). By the beginning of oxygen isotope stage (OIS) 5 (~130,000 years ago) there is widespread agreement that Neanderthals as a recognizable biological population existed throughout western Eurasia. Climates over the span of Neanderthal evolution were generally far colder than they are today (Van Andel & Tzedakis
1996). OIS 6 was long and very cold, and while OIS 5e may have been as warm as current conditions, even the less cold sub-stages of 5 (5c and 5a) were colder than current conditions. OIS 5d and 5b were substantially cooler than current conditions and OIS 4 through 3 much colder, with the latter being temporally variable. Locations that are today temperate woodland were steppic and/or tundra during OIS 4 and 3, and the colder sub-stages of OIS 5 saw the development of coniferous forests that could tolerate colder conditions than are present today. If the final stages of Neanderthal evolution occurred in OIS 6 and western Europe was a centre for this evolution, then they evolved in conditions that were some of the coldest that Europe has ever experienced.

Modern people evolving in Africa faced a very different environment. Most of Africa currently falls within the tropics, while the far northern and southern areas are in sub-tropical to mild temperate climates. While all of Africa experienced temperature drops during glacial periods, they were less dramatic than those in the temperate and cold latitudes. African climates fluctuated between 3–5°C colder during glacial periods, while Europe was much colder (Deacon & Lancaster 1988). With some regional exceptions, most of Africa was drier during glacial periods, and saw dramatic expansions of grasslands, arid grasslands, and deserts.

Temperate and cold latitudes, unlike tropical environments, have prolonged cold seasons, generally lasting from late fall through early spring (Grove 1988). This difference has a profound impact on floral and faunal diversity and biomass, and therefore food for evolving populations of hominins. Holding rainfall constant, biomass and net primary production is greater in the tropics and decreases steadily from the temperate to the cold latitudes (Pianka 1966: De Vos 1969; Whittaker & Likens 1973; Krebs 1978; Coupland 1979; Rosenzweig 1992). The result is that tropical African ecosystems have a greater biomass and diversity of plants and animals and less seasonal punctuation to these resources. Reflecting these differences, modern hunter-gatherers in tropical environments rely more on plant foods for subsistence (Lee 1968; Kelly 1995; Binford 2001).

Several studies have shown that plant foods can be found in abundance all year even in the most arid of African habitats, mostly as a consequence of the abundance of below ground tuberous plants that are still harvestable in dry seasons. Plants with underground storage organs, which pack large amounts of carbohydrates, are abundant in African ecosystems, far above temperate environments. However, these plant foods typically occur in spatially diverse patches, often in short bursts of productivity, scattered in a complicated way across the seasons (Sept 1986).

Faunal resources in the tropics are also more abundant and less seasonally punctuated than in cold temperate and cold environments. Tropical Africa differs significantly from temperate and cold environments by having large numbers of both migratory and residential ungulates (see discussion in Marean 1997). The tropics also have far more species of small animals, particularly reptiles and amphibians, as well as edible insects such as locusts and termites that swarm in very high densities. These differing systems provided radically divergent contexts for later human evolution and, I think, produced selective pressures that resulted in different adaptive strategies.

The biological adaptations of Neanderthals

A long history of research into human biological adaptations shows that modern humans with prolonged histories in extreme environments typically have genetically-based anatomical and physiological adaptations to these environments (Moran 1982). The Inuit are one of the most commonly cited examples. However, it is important to note that the vast majority of modern humans in such extreme environments, such as the Inuit, have inhabited these environments for a relatively short period of time, in the range of several thousands of years. Neanderthals evolved in a primarily glacial-period western Europe over hundreds of thousands of years. This means that Neanderthals may have evolved biological adaptations to these environments that far exceed those observed among modern humans, and may have even included adaptations that have not been observed among modern humans.

Neanderthals have various anatomical and material cultural characteristics that I think signal this, and collectively suggest a unique adaptive system with no modern analog. Many of these are well known in the literature on Neanderthals, and in Marean (2005) I discuss them more extensively. Here I summarize them briefly:

1. Neanderthals had thick and dense bones relative to modern humans in similar environments (Ben-Itzhak et al. 1988; Kennedy et al. 1990). This is made even more surprising given that Inuit, a group often used for anatomical comparisons to Neanderthals because they lived in similarly cold environments, have the thinnest and least dense bones on record for modern hunter-gatherers (Lazenby 1997). Northern latitudes have very low vitamin D levels resulting from low UVB (Jablonski & Chaplin 2000). Neanderthals evolved in...
locations with similarly low UVB levels, and they likely evolved a totally new physiological strategy to deal with low UVB (Marean 2005).

2. Neanderthals had very large muscle mass relative to modern humans in similar environments (Trinkaus 1983; 2000; Trinkaus et al. 1998) and therefore must have burned greater amounts of energy. The importance of this is exhumed by the fact that Neanderthals lived in energy-poor environments where the best sources of energy, calories from plant foods and fat from animals, was in very short supply the majority of the season (Marean 2005).

3. The Neanderthal bony labyrinth was highly derived and unique (Spoor et al. 2003). Spoor suggests that it signals an ambulatory system distinct from modern humans, probably slower.

4. Neanderthals have high trauma rates, far outside the range for modern humans (Berger & Trinkaus 1995).

5. Neanderthals show no signs of having developed hot-rock technology for bone boiling. All modern human hunter-gatherers in cold to temperate environments possessed hot-rock technology for rendering grease from spongy bone, and this forms an essential element of energy extraction from the environment. The lack of this technology, posed against the evidence for a high-energy physiology, is quite surprising (Marean 2005).

6. The most recent dietary evidence from isotopes suggests a pattern that can only be considered stunning. Neanderthals dating to MIS 3 from an area stretching from northern Belgium to southern France all show enriched nitrogen values that, when posed against fauna from the same sites, suggests they received the majority of their calories from mammoth and wholly rhinoceros to the near exclusion of other mammals (Bocherens et al. 2001; 2005).

There are at least two surprising aspects about these isotopic results. First, the vegetation reconstructions for OIS 3 (following the summary in Van Andel & Tzedakis 1996) suggests that these sites would have sampled conifer forest through tundra, so despite the vegetation variation the Neanderthals all have the same isotopic signature. And second, these isotopically identified diets do not match the faunal assemblages, which should show dominance by mammoth and other megafauna, but do not (see summary in Mellars 1996). The faunal assemblages from similar times and environments, which are dominated by cave assemblages in France, show a diverse species representation, and a nearly complete lack of mammoth and wholly rhinoceros.

So either the zooarchaeological assemblages from these cave and rockshelter sites are failing to show us what Neanderthals are eating, or the isotope data is fundamentally flawed. I think the answer is the former, and there are at least two reasons why we would expect caves and rockshelter species abundance not to accurately correspond to the representation of species in the diet.

**Isotope and zooarchaeological discrepancies**

Zooarchaeologists regularly use the relative representation of species in faunal assemblages to interpret animal exploitation patterns in the past. Until recently the only source of knowledge on what animals were exploited and eaten by prehistoric people was the relative representation of species in zooarchaeological assemblages. To date there has been little discussion over the correspondence between species as represented in archaeological deposits and their representation in the diet of ancient people. The increasing use of isotope studies to reconstruct past diet present us with a way to check our zooarchaeological interpretations, and perhaps discover some incongruities.

Any such comparison needs to ask several questions that target the comparability of the isotopic and zooarchaeological data, as the two are quite different. Isotopes provide proxy measures of diet as reflected in a rather narrow set of isotopes such as carbon and nitrogen. So, except in very rare circumstances, isotopes cannot estimate the relative contribution of individual species to the diet. Since zooarchaeologists can routinely identify particular skeletal elements to species, zooarchaeologists can attempt to resolve species abundance in the diet, and therefore make estimates of relative contribution of individual species.

Isotopes are typically measured and provided on the basis of an individual organism, and thus provide a proxy measure of an individual’s diet, which typically represents the mean of a span of time that is long relative to human ontogeny, perhaps a decade, but is short in geological time. So, unless there is a large population that has been measured, the isotopic evidence is mostly at the individual level and short in geological time, and thus subject to potential sampling problems that could unduly emphasize individual distinctions or temporally short (in geological time) anomalies from a diet typical for a taxon or slice of time. Zooarchaeologists examine faunal assemblages that represent the discard behaviour of an unknown number of individuals, typically over very long periods of time because the discard unit is typically some type of meaningful stratigraphic unit that can represent hundreds to thousands of years. So the
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Evidence is highly time averaged and group representative. One might argue that these distinctions serve to the advantage of zooarchaeology, but these advantages are trumped by two serious disadvantages that plague the zooarchaeologist.

Selective skeletal element transport and its impacts on species abundance

Studies of skeletal element abundance in zooarchaeology have been the source of a great deal of debate in the last decade, but most of this debate has focused on how to quantify skeletal element abundance and what the relative representation of skeletal elements means for behaviour. Ethnoarchaeological studies of skeletal element transport were designed partially to address these issues, but they have had an ancillary benefit that bears on a variety of zooarchaeological issues. There are several axioms of skeletal element transport among hunter-gatherers that these studies have identified. I review them here briefly, but more detailed syntheses can be found elsewhere (Monahan 1998; Marean & Cleghorn 2003).

Transport completeness can vary in both the number of anatomical units that are transported, as well as in how much bone rides or is shed prior to that transport. The zooarchaeologist is interested in the correspondence, or lack thereof, between bone transport and dietary significance. Assuming we are discussing transport from an encounter and butchery location to a residential site (such as the caves and rockshelters that dominate the western European record), and holding all other things equal, these basic patterns seem to hold:

1. Completeness of transport is a function of carcass size. Smaller animals are more likely to receive more complete levels of transport.
   a. Individual hunters can typically transport whole animals in the size range of 1 and 2 using Brain’s categories (1981), which is roughly equivalent to juvenile and adult goats, respectively.
   b. Above size 2, it then becomes necessary to either shed bone, choose to leave behind anatomical units, or enlist the assistance of more people.

2. Completeness of transport is a function of distance between the encounter site and the residential site. The farther the distance, the greater the filter on transport or anatomical units and bone.

3. Larger groups can result in more complete transport.

4. Really large carcasses, ones above size 4 (this would include giraffe, elephants, and so on) rarely receive significant transport of bone. Rather, they receive heavy filleting so that only meat is transported, or the entire group moves to the carcass.

These results pose significant problems for the zooarchaeologist attempting to utilize zooarchaeological assemblages to infer the importance of species in the diet. The main problem is the impact of carcass size on transport. The ethnoarchaeological data suggest that completeness of transport, and therefore visibility in archaeological assemblages, is strongly influenced by body size. To illustrate the problem, I have taken the entire Hadza bone transport data set from the independent studies of the O’Connell (O’Connell et al. 1988a,b; 1990) and Bunn (Bunn et al. 1988; Bunn & Ezzo 1993; Bunn 1993) groups, and transformed the data into a transport completeness index by size (Fig. 30.2). As is clear, the number of bones transported per encountered carcass is entirely dependent on body size, and drops to four bones per carcass with size 5 — these are mostly giraffe in this data set.

This problem is likely compounded by zooarchaeological method. Species abundance is typically developed from studies of the most taxonomically diagnostic body parts, and these are typically teeth and antlers and horncores (Klein & Cruz-Uribe 1984). Both of these reside on the head, and the head is an element that receives extremely biased transport. In smaller species that are transported whole, it commonly rides back with the carcass. However, in the...
case of larger species the horn and antler, which have no nutritional value, pose enormous loads that are quickly shed for transport.

The mammoth and wholly rhinoceroses that are indicated by isotope data as being dominant in the Neanderthal diets are large animals which were probably only occasionally transported into the caves and rockshelters that dominate the western Europe record. If these animals were a common prey item, as suggested by the isotopes, it is likely that their large size and consequent lack of transport would result in their being virtually invisible in the zooarchaeological assemblages that currently exist.

The impact of multiple accumulating agents on overall species abundance

Studies of cave taphonomy have become increasingly sophisticated over the years, but the interpretation of Palaeolithic faunal assemblages has yet to catch up. One of the axioms of cave taphonomy is that accumulations of fauna in caves and rockshelters are almost never the result of a single accumulator. Caves and rockshelters are natural magnets for animal occupation (Brain 1981), many of which are accumulators of bones. These include people, bears, large felids, hyaenids, canids, rodents, a large selection of small carnivores (such as mongoose and badgers, and so on) and raptorial birds. Our observational units in caves and rockshelters are typically lithological units that often represent very long spans of time and may not even correlate well with human occupation (Shannon et al. 2005). It seems naïve to assume that these lithological units in caves and rockshelters, often representing hundreds to thousands of years of time, would have been occupied by only one species of bone accumulator. Detailed studies of taphonomy, when applied to these assemblages, have begun to document the multiple accumulator nature of these assemblages. To illustrate this, I will refer to a case study from Die Kelders Cave 1 in South Africa (Marean et al. 2000a).

DK1 is in the Western Cape of South Africa, and is currently along the coast. During its occupation, it was probably at least 7–10 km inland from the sea (Marean et al. 2000b). Figure 30.3 shows the large mammal species representation at DK1 compared to a slice of the Klasies River sequence, taken from Klein (1976). I have narrowed the Klasies River sample to a time slice that is roughly comparable with DK1 in basic species composition, both assemblages look reasonably similar, being dominated by size 1 and size 4 animals. In the Klasies River sample the Cape Buffalo (*Syncerus caffer*) and extinct Giant buffalo (*Pelorovis antiquus*) are split into young and old individuals, since the representation is strongly bi-model. The published Klasies River sample derives only from the Singer and Wymer excavations in the late 1960s (Singer & Wymer 1982), and is highly biased by the coarse screening that was used and the discard of all but the most complete teeth, horn cores and articular ends of bones (Bartram & Marean 1999). It has been argued that people were virtually the sole accumulators of the fauna in all of the layers in this sequence (Klein 1976; Milo 1994; 1998). I do not dispute the fact that the presence of vast numbers of stone artefacts and human modification on the bone clearly signals that people were significant to the accumulation of the fauna. However, the human-induced surface modification frequencies are quite low, and there are strong signs of other agents of bone accumulation, such as

![Figure 30.3. The large mammal species representation as a percentage of total MNI at DK1 the Klasies River Howieson’s Poort layers, taken from Klein (1976; 1978). The time slices represented are roughly comparable in age. In the Klasies River sample the Cape Buffalo (*Syncerus caffer*) and extinct Giant buffalo (*Pelorovis antiquus*) are split into young and old individuals, since the representation is strongly bi-model.](image-url)
complete skeletons of leopards, and high frequencies of small mammals. The argument that people were the sole accumulator, and that the species representation can be taken as fully reflective of human behaviour, warrants concern. DK1 shows why.

At DK1 we examined every faunal fragment under a microscope regardless of size. The screening went down to 1.5 mm mesh, so very little was lost. Our study of this finely screened, very small material, revealed a surprising result. Many of the size 1 bovid bones are gastrically etched, as is the distal first phalanx of a small bovid illustrated in Figure 30.4a. Figure 30.4b portrays the frequency of gastrically etched fragments as a percentage of the total number of fragments at DK1 MSA layers 10 through 14.

Patterning in the spatial distribution of gastrically etched bone helps identify the agent of this etching as raptorial. Figure 30.5B shows the frequency of gastric etching for size 1 bovids by square in Layer 10. Interestingly, there is a cluster of very high gastric etching in the northwestern area of the excavations. Today, just above this area, there are degraded joints in the limestone that form crevices in which raptors nest (Fig. 30.5A). These features likely have great antiquity, and even 70,000 years ago were producing ideal nesting sites for raptors. The gastric etching frequencies combined with the spatial data strongly suggest that raptors, not people, were the primary accumulators of the small bovids. Figure 6 shows that, due to the small nature of the fragments, few would survive the ½ mesh screen used at Klasies and other sites.

Without the taphonomic analysis, we would conclude from the species abundance data that the DK1 MSA people hunted eland (size 4) and grysbok (size 1) equally. However, the taphonomic analysis clearly shows that many if not most of the size 1 bovids were accumulated by raptors, while the eland were accumulated by people. When we combine this result with the strong transport filter that would have been placed on eland (see discussion above), then the conclusion is that MSA people at DK1 targeted eland, the largest bovid on the landscape, nearly to the exclusion of all other species. The lesson here is clear — disentangling the agent of accumulation is a difficult task, and very likely the signal will not be clear. Without detailed taphonomic analysis of unbiased collections, species abundance data cannot be taken as reflective of hunter-gatherer diet.

Evolutionary foundations for the replacement of Neanderthals

To summarize my points so far, the evolutionary context in Africa versus Eurasia was very different. We should expect different evolutionary trajectories in later human evolution that produced differing adaptive systems. Neanderthals have several anatomical and behavioural patterns that are unusual, and certainly suggest an animal with a different adaptive system to that of modern humans, and this of course fits our expectations. The isotope data suggest a specialized diet focusing on megafauna for Neanderthals, and there are good reasons to expect the zooarchaeological signal for Neanderthal diet to be insensitive to the presence of these megafauna. This sets the context for exploring a foraging niche replacement model.

One way in which modern humans could have outcompeted Neanderthals was if their hunting abilities were more effective. There are at least three areas
where abilities can vary. One is success rate, and we might think of this as hunting efficiency — the amount of labour invested can decrease or increase, and thus a predator’s net return rate can vary. Predators vary widely in their success rates. Unfortunately it may never be possible to resolve hunting success rates in the zooarchaeological record.

A second component of hunting ability is killing ability — whether or not the predator can kill particular prey. This has perhaps received the most attention in the literature. Binford (1981; 1984; 1985) argued that Neanderthals were restricted to scavenging large mammals, what has been termed the ‘obligate scavenging model’ (Marean & Assefa 1999). Stiner (1991a;b; 1993) has argued for a more flexible scavenging behaviour pattern. Klein (Klein & Cruz-Uribe 1996; Klein 1998; 2000) has argued that modern humans in southern Africa could not hunt the most dangerous prey in what has been termed the ‘less effective hunter model’ (Marean & Assefa 1999). As has been show elsewhere, the scavenging arguments are based on spurious patterning that results from selectively retained or studied assemblages (Marean & Kim 1998; Marean 1998; Marean & Assefa 1999). The pattern found in the less effective hunter model has a more parsimonious explanations, and at this time remains unsubstantiated (see Marean & Assefa 1999; Minichillo & Marean 2000; Henshilwood & Marean 2002). Thus, to date, we have no firm evidence that Neanderthals or near modern humans could not hunt any particular prey item. It seems likely that zooarchaeology can eventually help resolve the question of killing ability, but the task is not simple and will require detailed taphonomic studies of unbiased collections.

A third component of hunting ability is trauma rate — a predator could be very successful, but if there is a high rate of trauma this decreases its fitness. Studies of hominin anatomy and trauma rates seem likely to provide excellent evidence on trauma rate during hunting. It has been shown that Neanderthals had high rates of trauma (Berger & Trinkaus 1995) and died young (Trinkaus 1995), suggesting to these researchers that Neanderthals hunted with close-combat types of techniques. While this is plausible, there is another explanation that has less to do with preferred hunting technique and more to do with preferred prey.

Specialized hunting strategies are ones where the predator tends to focus on a narrow set of prey. In these strategies, predators develop specialized anatomical features, functional sets, and behaviours for the killing of that prey; the prey meanwhile respond with their own adaptations, resulting in an evolutionary arms race (Bakker 1983). Specialized adaptations often evolve at the expense of other features and behaviours, and can ultimately become a liability when conditions change such that preferred prey is no longer available. Specialized predators can focus on eating large volumes of small prey (anteaters eating ants) or small numbers of...
large prey (sabertooths eating mammoths). A classic example of the latter specialized predators is sabertooth cats, such as *Homotherium*. They had specialized crania, dentition and postcrania, all devoted to killing large prey and focusing on their flesh to the exclusion of within-bone nutrients. Their co-association with large numbers of mammoths in Freisenhahn Cave suggests that they focused on young mammoths (Graham 1976; Marean & Ehrhardt 1995), and this is supported by a recent isotope study that shows that *Homotherium* δ15N values are the most enriched of all the predators in a rich predator guild, and fall near a set of juvenile mammoths and hippo (Palmqvist *et al.* 2003).

There are several characteristics of Neanderthals that are consistent with a large mammal specialized predator adaptation. Neanderthals have a very expensive muscular and bony system. Neanderthals had high rates of trauma that could have resulted from regularly hunting large prey, not from choosing to use close combat encounter strategies. Importantly, the isotope data strongly suggest a narrow diet focusing on a set of mammals that were quite large, and the similarity of the Neanderthal nitrogen results to those of *Homotherium* further supports this interpretation.

In contrast to specialized predators, *generalized predators* have flexible adaptations that can do lots of things. Their anatomy is generalized so that they can hunt in a variety of contexts and eat widely from the carcass. Leopards are a classic generalized predator. It is also interesting to note that generalized predators move between habitats better than specialized because they can switch prey quite easily; the wide distribution of leopards illustrates this well. One could also argue that generalized predators should be able to migrate well due to their expansive home ranges and the ability to switch prey items. Modern humans are a classic generalized predator.

*Generalized replaces the specialized*

In the discussion above I have developed an argument that posits that Neanderthals evolved as a specialized predator with a high risk, high return and physically risky foraging strategy. They focused on the pursuit of the largest mammals available with the highest return rates, and eschewed smaller mammals like birds, fish and small mammals. Modern humans in Africa evolved a low risk, regular return strategy similar to that seen among modern tropical hunter-gatherers in arid environments. Prey choice was broad and focused on plants supplemented by animals, including everything from small to large items. This put strong selection on a flexible strategy with the ability to map onto the spatial and temporal appearance of hundreds of differing food resources.

Betinger & Baumhoff (1982) argued for a similar distinction between Numic and pre-Numic speakers in the Great Basin in North America. They argued that invading Numic peoples practised a foraging strategy with a wider diet breadth (processor) than pre-Numic peoples (traveller), and that when juxtaposed in the same habitat, and when in competition for limited resources, the former will nearly always prevail. This is for two reasons. First, competition increases search and travel times for both groups, but more for those with the narrower diet breadth (the travellers) since their smaller diet breadth requires greater amounts of time spent searching. Second, the generalized predator will compete for all of the resources of the specialized predator, but the specialized predator will only compete for a small list of food items typically taken by the generalized predator because it will ignore the lower ranked food items.

Moving into the upper latitudes of western Eurasia, modern humans practised a strategy that was, relative to Neanderthals, more generalized and low risk. By necessity the economic emphasis switched from plants to animals, but modern humans incorporated a broader range of food items including fish and small mammals when these were available. This new strategy allowed modern humans to displace Neanderthals by usurping the narrow range of food items targeted by Neanderthals, depressing the productivity of those food items, and increasing search and travel time for Neanderthals. The result was the eventual replacement of Neanderthals by modern humans.

**Conclusions**

In the pages above I have outlined a basic hypothesis for the extinction and replacement of Neanderthals by modern humans. Clearly it is just one of many hypotheses for this event. It has several advantages as a hypothesis. It encompasses and accommodates a wide range of archaeological and physical anthropological evidence. It explains the rather unusual anatomical specializations of Neanderthals in a way that is consistent with our understanding of other modern and palaeontological predators. Importantly, it is testable and I have outlined in detail elsewhere some of the test implications (Marean 2005).

To conclude, the disparate characteristics of Africa and Eurasia provided contrasting evolutionary contexts that resulted in very different animals representing two adaptive strategies. Neanderthals evolved a specialized strategy that was high risk but high gain when successful. They had several anatomical adaptations designed to enhance that strategy, but ones that could also work to their disadvantage.
Modern humans evolved a much more generalized and diverse strategy that arose out of their focus on a wide range of plant foods in Africa. When they entered Eurasia, they were pre-adapted to broaden their niche to include smaller mammals, birds, and fish, while still competing with Neanderthals for their primary food items. When these two foraging adaptations inhabited the same space, the broader more generalized strategy of modern humans lowered the return rates for Neanderthals, in precisely the same manner that generalized foragers have usurped the feeding niche of specialized foragers at other times and places in evolution. The result was the eventual extinction of Neanderthals and their replacement by modern humans.

Acknowledgements

I thank the conference organizers for inviting me to participate and contribute to the published volume. The conference was outstanding; a tribute to their thoughtfulness and organizational abilities. I thank the following for helpful comments on an earlier version of this paper: Francesco d’Errico, Donald Grayson, Jim O’Connell and John Shea. The financial support of the National Science Foundation (USA) (grant # BCS-9912465 and BCS-0130713) and the Hyde Family Trust are gratefully appreciated.

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Journal of Archaeological Science 17, 301–16.