A study of Neanderthal physiology, engetics and behaviour

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ABSTRACT - A STUDY OF NEANDERTHAL PHYSIOLOGY ENERGETICS AND BEHAVIOUR

GRANT STIRLING

The general context of Neanderthal existence in Europe and Southwest Asia is assessed from a physiological perspective, based on studies of living populations experiencing certain roughly analogous circumstances. Various aspects of the fossil, archaeological, and paleoenvironmental records relevant to the discussion of energy balance among the Neanderthals were investigated.

Within living populations exposed to cold climate, subsisting on energy deficient diets, or participating in strenuous exercise regimes, various metabolic and physiological responses are evident. These relate to an attempt to maintain energy balance under such stresses, and are mediated by the action of thyroid hormones. It is proposed that the Neanderthals, who endured similar conditions, must have adapted to a low level of circulating active thyroid hormones in the face of an energy imbalance (negative) and sacrificed linear growth (of the legs/limbs primarily) as an energy sparing mechanism, so that other more essential body functions could be maintained to enable survival.

Given that the Neanderthal physique was skeletally robust and highly muscled (and that a significant degree and frequency of trauma is evident) it logical that they were engaging in very specific and stressful activity patterns. The Neanderthal physique would have prohibited certain activities but facilitated others. It is clear that modern athletes who share these attributes take part in power and speed events, involving intermittent bursts of high intensity exercise, rather than more stamina orientated ones. This information is used, in conjunction with archaeological and paleoenvironmental evidence, to develop a theory of the daily subsistence practices of the Neanderthals, involving the ambushing of game in a closed environment.

Such start-stop activities in a cold environment would have had a bearing on metabolism and energy balance, but also exerted pressure on thermoregulatory mechanisms. In light of this a new theory is developed to explain the evolution of the Neanderthals' exceptional cranial capacity and morphology. The elongated and unflexed basicranium is proposed to have arisen in order to accommodate an expanded cavernous sinus at the base of the brain. This would have provided a mechanism for regulating brain temperature under oscillating periods of heavy physical exertion and rest in a cold environment.

The points outlined here are made with reference to previously suggested notions of ecogeographic patterning of body morphology and differential mobility at the time of the 'transition'. Finally, the aspects of Neanderthal existence discussed are placed in a broad ecological and evolutionary context alongside the contemporaneous Early Anatomically Modern Humans (EAMH).

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CHAPTER 1

Introduction:

The Neanderthals have been a source of great contention from the moment they were first recognised as an ancestral human group, and they will doubtless continue to be controversial into the foreseeable future. Initially they were caught up in the Evolutionist versus Creationist debate, but since then have come to occupy the central role in the issues surrounding the origin of anatomically modern humans. Linked to this debate are questions about the Neanderthals themselves regarding their physical, behavioural and intellectual properties. Besides a plethora of academic studies, these particular hominids have came to be the epitome of our past in popular conceptions, ranging from fictional novels to films and cartoon strips.

Over time our views of the Neanderthals have undergone numerous shifts and reversals, bringing them closer or pushing them further from our modern selves. Early visions of them as apish brutes with a stooped posture and little intellect (based on Boule's description of the Neanderthal skeleton from La Chapelle-aux-Saints in 1911) have largely been replaced by a more favourable picture of fully-erect and large-brained individuals. But just how alike or dissimilar early modern and living human populations were they?

A great deal of this systematic reinterpretation of the Neanderthals by different workers relates directly to the modern human origins debate. Studies which reveal the Neanderthals to be more human, for whatever reason, tend to come from or be rapidly absorbed as fact by those favouring regional continuity. In contrast, studies finding disparities between Neanderthalness and humanness are usually associated with replacement arguments. Indeed, popular conceptions of the Neanderthals change roughly accordingly to which model of modern human evolution is in vogue within the scientific community, at the time.

The fate of the Neanderthals or their particular morphology is an intriguing question and still occupies a key position in the ongoing discussions about the origins of modern humans. Wolpoff (1980; p289) describes it as "one of the most vexing problems in the history of modern palaeontology". Although this statement is now nearly twenty years old it is as applicable today as it was then. Indeed, possibly more so as an increasing number of genetic studies and techniques (e.g. the extraction and analysis of Neanderthal DNA by Krings et al 1997) seem to be throwing more fuel onto the fire, rather than dowsing it!

1.1 - The Phylogenetic Relationship Between Neanderthals and Anatomically Modern Humans:

It has been widely accepted that numerous anatomical features of the Neanderthals are derived and highly specialised. Brauer (1989) sees a 'morphological gap' between the Neanderthals and early moderns in Europe. Rak (1986; in Brauer 1989) states that the functional morphology of the Neanderthal face represents a distinct 'departure' from the generalised fundamental architectural pattern that characterises all the species of the genus *Homo*. A similar, but less extreme, statement could also be made regarding their skeletal morphology and its robustness (chapter 5). As such they are clearly distinct as a group, whether recognised at the species or sub species level, from those specimens classed as Early Anatomically Modern Humans (EAMH).

From the outset it should be made clear that the ensuing thesis will not enter into the replacement versus continuity debate. Throughout the paper references may be made to Neanderthal extinction, replacement or other phenomena in a similar vein. Such terms are only used for descriptive ease, rather than to promote Neanderthal displacement by EAMH and dispel the possibility of Neanderthal contribution to the living gene pool. The rapid 'de-selection' of the Neanderthal physical morphology is believed to have been equally feasible. Due to a combination of phenotypic plasticity and genetic control the chance for such a quick morphological change among the Neanderthals (as is apparent in the fossil record) is possible, particularly if some degree of hybridisation is recognised. For concise insights into the extreme and oppositional arguments behind the discussion over the emergence of modern humans by the main protagonists see Stringer (1990), Thorne & Wolpoff (1992), and Wilson & Cann

(1992); or alternatively pick up any of the plethora of general human evolution texts on the subject for a brief overview of the current state of affairs.

The 'Classic' Neanderthal stage was between 110-35,000ya (Mellars 1996; Ch. 1), but their various features can be traced back to 250-200,000ya or further in the 'Pre-Neanderthal' specimens from Swanscombe, Petralona, and other European sites. Mellars (1996) states that Neanderthals were 'replaced' 40-35,000ya by anatomically and behaviourally modern humans. However, at the French site of Arcy-sur-Cure a fossil temporal bone fragment (with bony labyrinth in tact) dated to 34,000ya can now be accorded Neanderthal status (Hublin 1996) and the Neanderthal specimen from Zafarraya in southern Spain has been tentatively dated to only 25,000ya, and as such would be the youngest known Neanderthal specimen. EAMH appear in western Europe around 30,000ya and in central areas 36-34,000ya, respectively (Zubrow 1989). This evidence supports the idea of Neanderthal-EAMH co-existence in Europe. The two populations also appear to have been contemporaneous in Southwest Asia for a significantly longer time than they were in Europe, with Neanderthal specimens dating from 120,000ya (Tabun) to 60,000ya (Kebara) and EAMH presence noted within this time frame at Skhul and Qafzeh (Stringer 1990). All that needs to be appreciated here is that the two populations were morphologically distinct but contemporaneous.

1.2 - Aims:

To set the scene, the paleoenvironmental context of Neanderthal existence and details of the distinctive Neanderthal post-cranial morphology will be reviewed. Authors have attempted to distinguish Neanderthals and EAMH on the basis of intellectual capabilities. Naturally EAMH superiority in fields such as game acquisition and lithic production is assumed since they out-lived the Neanderthals, despite the fact that the latter had a larger cranial capacity (up to 1800 cubic centimetres). A brief techno-cultural comparison between Neanderthals and EAMH will be outlined based on recent interpretations and revelations, and it will become evident that the Neanderthals had very similar abilities to their EAMH contemporaries.

Subsequently, the bulk of the thesis will take the form of an assessment of the Neanderthal morphology and behaviour from a physiological viewpoint. This will be based on inferences derived from studies of living human groups suffering analogous stresses to those the Neanderthals experienced. Energy balance, metabolism, and thyroid hormone status will be investigated under conditions of cold, nutritional, and biomechanical stresses. In relation to these physiological factors, influences on and consequences of Neanderthal growth and activity patterns will be discussed. A theory to explain the unique basicranial morphology will also be proposed in these terms. Points will be raised concerning the relative contributions of phenotypic plasticity and genetic control to Neanderthal skeletal morphology.

These data will be reconciled with the archaeological and environmental records (on which the majority of other theories of this kind have been based). Finally, drawing together all of this information, a picture of Neanderthal subsistence within a specific ecological niche will be produced, and a possible account for the disappearance of the Neanderthal physique will be given in these terms.

CHAPTER 2

The Neanderthal World - Environmental Context:

"It is likely that Mousterian social groups were composed of relatively small and mobile populations of highly adaptable individuals. Some of them managed to survive for at least 80,000 years in western Europe in environmental circumstances that varied from conditions little different to the present to a near permafrost tundra" (Jelinek 1988; p 207).

Turner (1991; in Gamble 1993) notes the relatively late arrival of hominids in Europe at 500,000ya. Coinciding with this several new species appear in the faunal record of Europe (deer, bovids, rhino, and horse); and carnivore species seem to dwindle there (cheetah, sabre-tooth tiger, and dirk-tooth cat). Prior to 500,000ya limited prey species and heavy competition from scavenging carnivores would have made it difficult for hominids to enter Europe and survive. From 700,000 the archaeological record only shows intermittent hominid occupation; while from 400,000ya occupation is more permanent by archaic *H sapiens* forms.

In the Eurasian Middle Palaeolithic hominid groups localised into discrete regional patches and are only continuously present in regions with vertical differentiation and proximal resource diversification. Upper Palaeolithic groups successfully colonised more open biomes (Soffer 1992; Velichko 1988; in Soffer 1994). In Europe Middle Palaeolithic occupation was restricted to the southern parts.

2.1 - The European Environment:

The 'classic' Neanderthal period in Europe coincides with the latter stages of the Eem interglacial and the early-middle Wurm glaciation. The landscape was dominated by steppe and tundra conditions which would have produced a highly seasonally variable food resource base. A scarcity of plant material in the winter months would have necessitated a seasonal shift in order to include greater proportions of meat in the diet, via ungulate carcass acquisition.

"The glacial landscape of Europe [in the later Pleistocene] was continuous, however, in neither geographic nor temporal distributions, and therefor the environmental stressors that purportedly formed the basis of Neanderthal living conditions were not uniform in time or space" (Hutchinson et al 1997; p 905). Hayden (1993) describes the habitat of this time as possibly being the most physically demanding one ever populated by hominids.

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Mellars (1996; Ch. 2) summarises the environmental background to the Neanderthal occupation of Europe (in particular France) as follows:

- 126-118,000ya - The last interglacial; commonly called the Eem or Riss-Wurm. Average temperatures were 2-3 degrees centigrade higher than today. Massive, dense forests dominated the European landscape.
- 118-75,000ya - Early last glacial. Temperature oscillations with 2 warmer interstadials. During colder periods Europe was covered by more open vegetation with patchy birch/pine forests.
- 75-25,000 - The middle glacial period.

Butzer (1971; p274-275) gives a detailed account of the middle glacial and start of the late glacial in mid-latitude Europe:

- 75,000ya - end of Eem interglacial and onset of early Wurm. Inception of Scandinavian glacier. Cold climate dominates, but temperate phases of early Wurm are recognised at 65 and 60,000ya (Amersfoort and Brorup, respectively). Possible total deglaciation in Scandinavia.
- 58-40,000ya - first cold maximum of the Wurm with full glacial conditions (lower pleniglacial). Ice front possibly farther south than Baltic Sea.
- 40-29,000ya - cool-temperate interval of the Wurm interpleniglacial (Paudorf Interstadial). Brief temperature maximas at 37 and 30,000ya (Hengelo and Denekamp, respectively) interrupted by longer cold interval. Partial deglaciation.
- 29-13,000ya - second cold maximum (upper pleniglacial). Maximum glaciation occurred about 20,000ya (Brandenburg interval), followed by recessional halts at the Frankfurt (18,000ya) and Pommeranian (15,000ya) morraines.

- 13-12,000ya - rapid glacial retreat initiated at the beginning of the late glacial.

"....while the prevailing temperatures of the last 100ka remained well below those of the present day and the environment in northern and western Europe was one of essentially polar desert conditions, significant ameliorations of climate developed at quasi-regular intervals" (Bell & Walker 1992; 56).

Mellars (1996) describes northern Europe as an open tundra/polar desert and southern Europe as a 'steppe' environment (drier due to the 'continental' effect), during the middle glacial period. Sea levels were lowered and the Northern European Plain extended across the North Sea and 30-40km into the Atlantic Ocean from the current French coastline.

Evidence presented by Roberts (1984) from southern Europe indicates that interglacial (and shorter temperate spells) vegetation was dominated by trees (e.g. oak). During glacial stages the boreal, mixed deciduous and Mediterranean woodland of Pleistocene Europe were reduced to southern refugia. They were replaced by grasses, which dominated the landscape under glacial conditions creating a steppe environment. "...the vegetational zones were not simply displaced but were reduced to isolated refugia or eliminated completely as the climate changed" (Roberts 1984; 44).

Birk's (1984 in Bell & Walker 1992) four stage model of vegetational changes in response to such climatic oscillations:

1. *Cryocratic phase* - during a glacial stage when climate is cold and dry (and continental in extra-glacial zones) sparse, species-poor, arctic-alpine or steppe-herbaceous vegetation exists.
2. *Protocratic phase* - the first stage of an interglacial (temperatures beginning to rise) when steppe/tundra vegetation is progressively replaced by species-rich grassland, scrub, then open woodland.
3. *Mesocratic phase* - during the interglacial optimum there is the establishment and expansion of closed temperate deciduous woodland. (species diversification progresses throughout this time).

4. *Oligocratic phase* - As the climate begins to deteriorate once more the mixed woodland is replaced by conifer-dominated woods, ericaceous heaths and bogs. As the woods open up some potocratic phase plants expand and with continued climatic deterioration the cryocratic phase returns.

In the Perigord of France varied and diverse ecological conditions are recorded, from sheltered valleys to exposed limestone plateaux (Mellars 1996). The former would have been on the major migratory routes of many herds, adding to species diversity by funnelling externally based animals through the region. Bosinski (1967; in Roebroeks et al 1995) noted that Middle Palaeolithic sites in western and central Europe are always associated with a cold fauna, which includes reindeer, woolly rhino, and mammoth.

In Germany the evidence points to hominid adaptation to a cold open environment during the Middle Palaeolithic, similar to that occupied by their Upper Palaeolithic successors (Muller & Beck 1988; in Roebroeks et al 1995). Middle Palaeolithic levels at Upper Danube sites contain cold living fauna (musk-ox, reindeer, horse, woolly rhino). But certain small- and large-scale mammals testify to the presence of gallery forest (Hahn & Kind 1991; in Roebroeks et al 1995), which may have been the essential element as far as the Neanderthals were concerned.

Gamble (1986; in Shea 1989) noted that while the Neanderthals abandoned central Europe under polar desert conditions of low terrestrial productivity during glacial advances 70-50,000ya. EAMH persisted there in the face of similar conditions 30-12,000ya.

2.2 - Environmental Shifts and Hominid Migrations to/from Southwest Asia:

Wiley (1981; in Simmons 1994) defined a 'contact zone' as a region of hybridisation or intergradation of different populations or species. The recognition of discrete species in such a situation depends upon the degree of contact in spatial terms as well as its temporal duration. In terms of modern human evolution, Southwest Asia is a crucial and highly contentious contact zone. Here EAMH appear in the fossil record by 100,000ya, and their subsequent coexistence in the region with the Neanderthals lasted 50-60,000 years.

This southwards migration or gene flow into Mediterranean coastal regions possibly coincides with the onset of cold/dry conditions in western Europe in isotope stage 4. This would have altered availability, reliability and accessibility of food resources there, as ice sheets expanded south and east preceded by tundra and polar desert conditions (Cordy 1984; in Bar-Yosef 1989b). The changing European environment would have challenged existing adaptations of the Mousterians, forcing them southwards. Neanderthals may have reached the Levant following the southward migrations of vegetation and fauna during the early stages of the Last Glacial 75-65,000ya. The need to adopt new technologies or adapt behaviour would probably been minimal since the Neanderthals moved with an entire bio-community (Shea 1989). Although Chase (1986; in Bar-Yosef 1989b) claims that hominids in the region replaced their game of red and roe deer, and horse with reindeer.

The Neanderthals may not have persisted in the Middle East for the whole of the time under question. It is feasible that they expanded into and retreated from the region more than once, coinciding with colder phases as glacial extent fluctuated in Europe altering conditions there. Common sense denotes that the Neanderthals would have tracked their preferred environment as other species migrated according to the prevailing climatic conditions.

Faunal evidence from the Mediterranean basin correlates with the 'fragmentary' pollen record, indicating "extensive open vegetation or parklands" during the early Wurm (Butzer 1971; p). During this time woodland species migrated south into northern Africa, where a forest-steppe mosaic had developed fringing the northern coasts of Lybia. Sub-tropical woodlands were replaced by temperate species in southern Europe, as the climate became cold and dry. Temperate genera became important along the north African coast and in the Levant. Alpine meadows, montane steppes (possibly cold temperate woodlands), forest-steppe mosaics were widespread in the hill country of southern Europe, which supported significant populations of cold-tolerant mammals. The Mediterranean zone was characterised by montane steppe and forest-steppe mosaics. During the Wurm pleniglacials the dry season was extended to up to eight months in some areas. (Butzer 1971)

Between 40-30,000ya there was an increase in global temperature of 5-6 degrees centigrade (the Wurm interpleniglacial). In response to this temperate woodland spread northwards once again into the previously periglacial and tundra landscapes of Europe. This would have aided the expansion of the Neanderthals back into Europe since they were already well adapted to such conditions.

Over the duration of the Neanderthal and EAMH occupation, two ecological zones existed in the Levant (Shea 1998): Mediterranean woodland which covered northern and coastal areas; and the Irano-Turanian steppe across southern and interior areas (the Saharo-Arabian desert is a more recent development).

In the Upper Pleistocene the climate was generally cooler and more humid, particularly along the coast, than today (Shea 1998). There was a year round pattern of rainfall, as opposed to the highly seasonal rains experienced today. The onset of glacial conditions to the north in Eurasia would have affected the Levant in two ways: making the interior cold and dry; and aiding the spread of woodland southwards (to currently desertified regions) along the hills of southern Israel and the western escarpment of the Trans-Jordan plateau. Corresponding to global climatic shifts these zones of woodland and steppe would have shifted across the landscape. Evidence from biotic residues shows that the majority of Levantine Mousterian sites were occupied when the predominant habitat was a mixture of steppe and woodland. Lebanon and northern Israel were more consistently covered with woodland, while Jordan, Syria and southern Israel were more often under steppe conditions.

From the geographical distributions of sites in Southwest Asia there is a tendency for Mousterian locations to be preferentially located in wetter conditions. By the late Mousterian the Irano-Turanian vegetational belt was being exploited (e.g. Douara

Cave), possibly enabled by the development of hunting techniques. During both the Middle and Upper Palaeolithic caves above 1,400m are thought to have been only summer camps, which implies seasonal vertical movements Bar-Yosef (1989b).

2.3 - Game Available to Hominids:

There is painfully little of the plant content of hominids' diets preserved in the archaeological record. Relative vegetable/meat proportions can be compared between past and present populations via inferences based on tooth morphology, tooth-wear patterns, and isotope levels in bone collagen (section 2.4). This is unfortunate because the importance of the contribution of vegetable material in the hominids' diets cannot be accurately assessed and consequently their relative reliance on animal tissue is unknown. Seasonal disparities in the relative reliance on each food type would be most enlightening, but will be difficult to determine. Reliance on the faunal record produces an unavoidable bias in deciphering the diet of any hominid, and has possibly lead to too great an emphasis being placed on the inclusion of animal material in their diets. However, in the case of the Neanderthals there is some justification in this as they are believed to have been heavily reliant on meat for subsistence.

The hominids at Kobeh Cave, Iran, appeared to have concentrated on the wild goats of the rocky mountain slopes. The Mousterian layers at nearby Warwasi are dominated by equids, which would probably been abundant on the grassy plains of the valley (Turnbull 1975; in Marean & Kim 1998). At another site in the area, Bisitun, there is much greater diversity; red deer (whose presence is suggestive of woodland habitat) then equids being the more numerous (Coon 1951; in Marean & Kim 1998). These faunal disparities could represent either the times of occupation under different climatic regimes (e.g. Kobeh Cave - glacial stage; Bisitun - interglacial; Warwasi - similar conditions to today); or the occupation of the sites at different seasons. In these two scenarios the taxonomic variation is accounted for by shifts in the dominant species available in accordance with general (global) climatic circumstances or more short-term seasonal migrations.

Shea (1998) notes the distinct lack of the largest woodland animals in the Levantine Mousterian faunal assemblages believing them to have been too dangerous to hunt. Bar Yosef (1989b) records the relative abundance of a wide range of small-medium sized species, such as aurochs, various deer species, ibex, and gazelle. These are small group or solitary species which would have been dispersed and difficult to predict their movements as few had seasonally regulated movements.

2.3.1 - Open Vegetation:

In tundra regions the extreme cold reduced the available vegetation food sources. Herbivorous reindeer and caribou were most common. Also present were woolly mammoth herds and open country species, such as bison and wild horse. In fewer numbers were the giant elk, woolly rhino, and saiga antelope. "....Pleistocene low-latitude tundras had a tremendous carrying capacity, somewhat greater than the recent, high-latitude tundras" (Butzer 1971; p 141).

Mid-latitude grasslands and steppes were home to a "limited variety of swift-footed, gregarious herbivores" (Butzer 1971; p 145). Varied, rich, and nutritious grasses gave such are as high carrying capacities. Wild horse and also pronghorn and saiga antelopes were common in Europe.

Late Pleistocene low-latitude tundra and loess environments had greater carrying capacities than modern high-latitude tundras. The substantial size of the faunal records at sites associated with hominid occupations is testimony to this. Examples include Solutre in France (1000ds of wild horses) and Predmost in what was Czechoslovakia (600 woolly mammoths) as determined by Woldstedt (1954; in Butzer 1971).

?

2.3.2 - Wooded Areas:

During the interstadial stages forest-tundra, scrub, or boreal woodlands were able to re-occupy most of the former tundra belt in a relatively short time (Butzer 1971). Boreal (dense coniferous) forests of higher latitudes did not offer much herbaceous vegetation; so gregarious herbivores could not be supported. Species present included deer and Old World aurochs, as well as reindeer on a seasonal basis. "....the variety of big game is small, and their number limited" (Butzer 1971; p 145).

Deciduous and mixed forests of a cold-temperate climate provided better, and almost all year round, grazing for large herbivores. Red deer, bison, and aurochs were common and widespread. Roe deer were present in Europe, while fallow deer occupied the Near East. (Butzer 1971)

2.3.3 - The Condition of Game Available to Neanderthals:

"....important resources available for human use - both plants and animals - were undoubtedly altered by rapidly changing climates and oscillating landscapes....periodic reduction may well have resulted in stresses that would have profoundly affected nutritional health during the late Pleistocene" (Hutchinson et al 1997; p 912).

Fat reserves in birds and terrestrial mammals have several constraints: dietary abundance, biomechanical needs of flight, and the selective pressures for adaptive advantage via agility (Cachel 1997). Terrestrial mammals become seasonally obese; the quantity, timing and anatomical location of which is under tight physiological control. Fat only accumulates just prior to mating, birthing, hibernation, or migration (Pond 1978). Sea mammals consistently maintain much higher subcutaneous levels of fat as an insulating mechanism (Gaskin 1982; both in Cachel 1997). The inclusion of fish (notably salmon with its predictable seasonal movements) into the hominid diet only occurred on a significant scale in the late Upper Palaeolithic (section 4.3.2).

Past vegetation reconstructions on the local level are hard, but plants would probably have provided hominids with carbohydrates at least on a seasonal basis (Speth 1989). In temperate/northern latitudes today plant resources decline in availability and quality during winter and spring. Hunting increases to supplement stored plant food reserves, and the hunter-gatherers suffer weight loss and possibly starvation. Ungulates are also particularly susceptible to these phenomena and experience fat (subcutaneous, visceral, and even marrow varieties) depletion by late spring. Throughout the dry season ungulates may subsist on a 'sub-maintenance' diet (Speth's term 1987). Total fat levels in temperate/northern latitude ungulates commonly drop to 2-3%, or lower. This factor would have been critical for the Neanderthals occurring just when they would have needed fat the most (i.e. when carbohydrate sources were sparsest).

Fat mobilisation in ungulates adheres to a fixed sequence: back fat first, then deposits in the body cavity, and finally the fat in the marrow and brain. Thus, the body part selection by hominids should alter systematically over the stressful period. Marrow fat in the distal limbs is the most resilient fatty deposit and contains the highest proportions of oleic and steric acids. These give the deposits a desirable taste, reduced susceptibility of turning rancid, greater digestibility, and a low melting point. In general fatty foods produce a feeling of satiety, and are rich in easily metabolisable energy (i.e. are calorie dense), fat soluble vitamins, and essential fatty acids (Guthrie 1975; in Speth 1989). Thus, fat is likely to be the primary target during the dry season.

Hunter-gatherers are forced on a seasonal basis to increasingly subsist on such lean meat. If, in order to maintain adequate total caloric intakes, this continues for significant periods associated deleterious effects arise (section 8.3).

2.4 - Determining the Neanderthal Diet:

Several recent studies have concluded that the Neanderthals included significant quantities of meat in their diet. These studies, based on different lines of inquiry, have also identified a degree of nutritional stress among the Neanderthals.

2.4.1 - Microwear Patterns on Tooth Enamel:

153 molar teeth from museum collections of modern hunter gatherers, pastoral and agricultural groups with different diets were studied by Lalueza et al (1996) using a Scanning Electron Microscope. The length and orientation of every striation on the

buccal surface of the teeth was determined using a semi-automatic program of an image analyser program (IBAS). Intergroup variability was found to be greater than intragroup variation. The predominantly carnivorous groups are characterised by fewer striations overall and a higher proportion of vertical striations, when compared to vegetarian groups. According to Lalueza et al (1996) these results are compatible with studies looking at chewing biomechanics (when eating meat vertical chomping predominates) and the phytolith content of plants (making vegetarian diets more abrasive).

Some of the Neanderthals fall with the carnivorous hunter gatherers (i.e. Eskimos, Vancouver Islanders, and Fuegans) but others fall with the mixed diet groups. Only Tabun 1 was clearly classified within the carnivorous group (with a 91% probability). The samples of both archaic and modern *H sapiens* (Africa, Southwest Asian and European) show signs of having had more abrasive diets, probably due to their inclusion of more plant materials (Lalueza et al 1996). No apparent dietary trends are observed across these two samples. The variability seen within the Neanderthal group is put down to their extensive geographical and temporal distribution, hence members living in somewhat varied environments (Lalueza et al 1996).

Looking at the contexts of the Neanderthal specimens studied here it seems that the variability noted does have some patterning. The carnivorous Neanderthals are from Southwest Asian and earlier European sites (e.g. Amud 1 and La Quina V), while the mixed diet group are essentially late European specimens (e.g. St Cesaire and Marillac). Alternatively this could in fact be the result of distinct seasonal shifts in the Neanderthal diet. However, Perez-Perez et al (1994; in Lalueza et al 1996) claim that buccal striation patterns take a long time to become established, and propose that slight seasonal fluctuations in dietary intake may not affect the surface patterns significantly.

2.4.2 - Neanderthal Carnivory and Weaning Practices:

Wolpoff (1980) identified an increase in deciduous tooth size among late Neanderthals. He interprets this as signifying earlier weaning and a possible reduction in birth spacing. Skinner (1989; in Soffer 1994) notes that this trend continues into the Upper Palaeolithic. If birth spacing reduced among Neanderthals; it may be that weaned infants were not receiving supplementary nutrition from their mothers. Stress on juveniles would have increased and hence so would infant mortality. According to Soffer (1994) food sharing and biparental provisioning practices among EAMH would have reduced the stresses on juveniles and young adults.

Gibraltar 2 Child was found in Mousterian deposits (Garrod et al 1928), and its age at death is estimated at 5 years by tooth eruption stage (Tillier 1982; both in Fox & Perez-Perez 1993). Striation patterns on the vestibular surfaces of the first and second deciduous molars were studied by Fox & Perez-Perez (1993). Anterior teeth were omitted from the study due to the various non-dental uses of them among Neanderthals. The Gibraltar 2 Child is shown to have a more abrasive diet than a Medieval sample from Spain, but the wear patterns are similar to those displayed by modern Eskimos (from Greenland) and Fuegans (Tierra del Fuego). A low total number of striations, with predominantly vertical striations and low number of horizontal, seems to be related to a large meat intake. This could be interpreted to mean that, like these two populations, the specimen could have been mainly carnivorous. However a greater number of striations than in these two modern populations suggests a higher contribution of abrasive particles (from whatever source?).

2.4.3 - The Chemical Composition of Neanderthal Bone:

Bocherens et al (1991) and Fizet et al (1995) conducted research at the site of Marillac in Charentes, France. Layers 9 and 10 had previously yielded Neanderthal remains, which have been dated to the end of the Wurm Glaciation around 40,000ya.

The 13C and 15N natural isotope abundances in bone collagen can be used to distinguish different categories of resources in a specimen's diet. The carbon isotope ratios (13C/12C) reflect corresponding isotopes found in the plants at the base of the food chain. This ratio is influenced by and varies with the environment; such as aerial versus marine.

The 13C and 15N values of collagen extracted from the bones of fossil mammalian species were calculated and compared them with values obtained from living representatives of their species with known diets. Broadly matching results demonstrated that these values are preserved in bone during the fossilisation process. This data was then used as an 'ecological reference' in order to position the Neanderthals in the past food web.

Even when the Neanderthal 15N values are corrected according to their low glycine amino acid levels (which otherwise would be artificially high according to Tuross et al 1988; in Bocherens et al 1991) they were still within the carnivore range of variation at +8.6 0/00. The Neanderthal 13C values (and the lack of suitable implements in the associated industrial assemblages) do not support the theory that they might have been including marine sources in their diet, even on a seasonal basis (Fizet et al 1995). Both 13C and 15N values have lead Bocherens et al (1991) to conclude that the Neanderthals at Marillac were 'mostly carnivorous'. Fizet et al (1995) agree with this interpretation but also claim the Neanderthals to have been 'less specific' in their prey selection relative to the carnivore species present, such as wolves. Other recent studies of collagen geochemistry also infer that Neanderthals had a highly carnivorous diet including a wide range of species (e.g. Dorozynski & Anderson 1991; in Cachel 1997).

2.4.4 - Dietary Change at the Transition:

Trace element analysis can determine the amount of strontium in bone, which reflects the amount of strontium in the individual's diet. Plant materials naturally contain higher levels compared to animal soft tissues. Therefor the level of strontium in the bone will e vary depending on the relative proportions of plant and animal material in the diet. (Alexander et al 1956; Comar et al 1957; in Schoeninger 1982)

Schoeninger (1982) calculated and compared strontium:calcium ratios in human and faunal bone in Israel. Samples of bone from archaic modern humans (Tabun, Skhul, Qafzeh) and fully modern humans (Kebara, el-Wad) were analysed. The use of ratios, as opposed to absolute strontium values, controlled for potentially unequal soil strontium values between sites.

Schoeninger (1982) concluded that a change in the proportion of animal protein in the diet only occurred 20,000 years after the appearance of the modern (i.e. skeletally gracile) form. Therefor, it does not follow that the skeletal changes across the transition occurred due to behavioural alterations associated with obtaining different types of foods. If there was a coinciding behavioural shift then it only involved different ways of securing and/or processing the same foods as previously. The food base remained unmodified throughout this time within the Levant, although alterations in procurement strategies are not ruled out by this study and may have occurred.

2.4.5 - Dental Identification of Nutritional Stress:

Hypoplasias are serial pits or horizontal circumferential banded grooves on tooth crowns, which arise due to irregularities in 'amelogenesis' (enamel matrix formation and deposition) due to ameloblast death, and 'dentinogenesis' (dentine formation). Among recent populations, they are usually more pronounced on the anterior dentition. (Scott 1991)

Hypocalcifications are opacities or bands of discoloration that contrast with normal enamel and result from a disruption of the process of enamel matrix mineralisation (Hutchinson et al 1997).

Both of these conditions have been shown to reflect stress episodes during the growth and development of tooth crowns (Goodman & Rose 1990; Yaeger 1990; in Hutchinson et al 1997). The two pathologies are closely associated, and therefor likely to represent parallel metabolic stress experiences. The factors determining which of the two manifests seem to be linked to the timing of the stress event in relation to that of enamel development and maturation (Yaeger 1990; in Hutchinson et al 1997).

Experimental and clinical data show that a wide range of causes exist; but environmental stress (i.e. nutritional deficiency/disease morbidity) is the prime culprit among past populations. Since matrix formation and calcification seem to follow fairly universal scheduling, the age of the individual at which these bands can be estimated. (Scott 1991)

2.4.6 - Contrasts in Frequency of Dental Indicators Across the Transition:

Ogilvie et al (1989; in Skinner 1996) found no skeletal evidence of infectious disease in Neanderthals; but a high proportion (78%) of individuals (those with ≥ 2 analysable teeth) showed enamel hypoplasia. It was concluded that the causative trauma and nutritional stress commenced at weaning. Only 3.9% of the milk teeth studied were affected, so the health status of Neanderthal infants was deemed to have been good. At Krapina Molnar & Molnar (1985; in Skinner 1996) noted enamel hypoplasia (concentrated on the third molar) as being evidence for late childhood stress (peaking at around 11 years of age).

Hutchinson et al (1997) recognise a higher frequency of defects in anterior teeth in certain modern (i.e. Holocene) humans, and state that "The unusually high frequency of enamel defects in posterior teeth, especially the third molar, appears to be unique to Neanderthals" (Hutchinson et al 1997; p909). However, no explanation for this contrast is proposed.

"....our study suggests that at least with regards to the Krapina population, nutritional stress was not especially elevated compared with that affecting several other world populations....the late Pleistocene Krapina hominids may have experienced stresses roughly analogous to those affecting at least some modern foragers" (Hutchinson et al 1997; p 913).

For example, the pre-agricultural foragers from the North American Atlantic Coast appear to have been particularly stressed relative to other recent populations. They show a greater frequency of enamel defects (and other skeletal indicators) than the Krapina Neanderthals (Hutchinson et al 1997)

Despite this Hutchinson et al (1997) still concede that: "They [the Krapina Neanderthals] show....an extreme level of what appears to be periodic nutritional stress" (p904)

Neanderthals are at the top end of the modern range for the frequency of hypoplasias; the patterning of which appears to indicate nutritional stress from weaning onwards and peaking in adolescence (Ogilvie, Curran & Trinkaus 1983; in Trinkaus 1989). The frequency of hypoplasias among Upper Palaeolithic Europeans is substantially lower, indicating better nutritional status (Trinkaus 1989).

2.4.6 - Localised Hypoplasia of the Primary Canine:

LHPC is absent in the Middle Palaeolithic. Its highest prevalence anywhere either at present or in the past occurs in the Upper Palaeolithic of western Europe (Skinner 1986). Within only a few months of birth the suffering infants have insufficient facial bone mass. Skinner et al's (1994) study implicated the lack of dietary vitamin A (all in Skinner 1996)

Natural availabilities of provitamin A and preformed vitamin A are likely to have been similar in the two periods. It is possible that the Neanderthals could have had better access to pigmented vegetables of preformed vitamin A (in liver), or evolved a physiologically more efficient means of extracting the required retinol. Rodriguez &

Irwin (1972; in Skinner 1996) found that the conversion rates of beta-carotene to vitamin A varied by up to four times across different species.

Storage may have played a part in the contrast according to Skinner (1996). If the Neanderthals lacked the ability to store foods, as is deduced from the fossil record, they would have been forced to rely on a supply of fresh meat (and the vitamin A rich liver). The drying process for meat preservation during storage in the Upper Palaeolithic would have reduced the carotene/vitamin A content substantially. Despite this slight dietary inadequacy, it is apparent that the nutritional status among EAMH was generally superior in balance and quantity to that of the Neanderthals.

2.4.7 - The Question of Cannibalism Among the Neanderthals:

The possibility of cannibalistic practices among Neanderthals is intermittently debated and remains unsolved. If accepted, then the question of ritual versus dietary cannibalism will be harder to determine, although the evidence for dietary stress may provide a strong motive (sections 2.4.5 & 2.4.6).

"A review of the purported evidence for cannibalism at Krapina (craniocervical fragmentation, diaphyseal splitting, 'cut marks', patterned preservation and breakage, burnt bone, and disassociation of the skeletons) indicates that none of the damage patterns present in the Krapina Neanderthal sample can be explained solely as the products of cannibalism" (Trinkaus 1985; 203).

According to Trinkaus (1985) most of the damage patterns seen at Krapina are simply the normal effects of sediment pressure on bone or the results of post-depositional disturbances (human or animal activity in the cave, geological processes, and the excavation practices of the time).

However, fragmentary remains, judged to have several Neanderthal autapomorphies, from the small site of Abri Moula, in Southeast France, from layers C (dated at 49,000ya), D, and E offer conflicting evidence. Three of the cranial fragments and a proximal radius epiphysis bear clear cut marks "undoubtedly from a flint tool" (Defleur et al 1993; 214), which are associated with indicators of fresh bone breakage (v-shaped and bevelled break pattern at an oblique angle).

"Although our new osteological data cannot prove the practice of cannibalism among the Neanderthals, they constitute an important argument in favour of the hypothesis that such practices could have occurred among the Middle Palaeolithic inhabitants of Western Europe" (Defleur et al 1993; 214).

2.5 - Cold Grasslands and Eskimo Subsistence Strategies Today:

Cold grasslands are found above 60 degrees latitude today. Examples today include the Barren Grounds steppe on the Northwest coast of Hudson Bay, and the arctic prairie/tundra along the flanks of the Brooks Range in Northeast Alaska. These ecosystems are inhabited by the Asqamuit or Caribou Eskimos and the Nunamiut Eskimos, respectively. They are dominated by sedges of grasses with significant lichen and moss representation, while migratory caribou predominate the large mammalian community (Pielou 1994; in Marean 1997).

The plant food content of the Eskimo diet is negligible. The Tuluaqmuit Nunamuit use twelve species of plants (Campbell 1968), and the Caribou Eskimo use only six (Smith 1929; both in Marean 1997). In cold (and temperate) grasslands few, if any, plant foods are available from early winter to early spring, and during warmer months only patchily distributed, unpredictable small items (e.g. nuts, berries, seeds) are available, which would require intensive collecting and processing. Thus there is a "striking seasonal dearth of carbohydrate so typical of temperate or cold grasslands" (Marean 1997; 200).

A heavy reliance on animals is an obvious strategy. Pray animals are usually migratory and thus only available in quantity for short seasonal periods. Many are in a poor and lean condition, lacking the necessary fat to compensate for the lack of carbohydrate in their hunter's diet (Speth 1983; in Marean 1997).

Firson (1991; in Marean 1997) points to several risks relating to a dependence on seasonal migratory species:

- They are prone to 'boom-and-bust' oscillating demographic patterns involving sudden population crashes. Burch (1972) noted Alaskan caribou herds had undergone several such crashes. This puts considerable stress on their hunters' communities.
- Such migratory patterns only offer a brief window of opportunity in which the Eskimos can hunt the animals. This means any unsuccessful activities will use up valuable and limited time. Tactical/communal techniques are quite time consuming but are still the optimal strategy available in open high-visibility environments.

In ecosystems where plants are highly seasonal and extremely limited and animals are only passing through along migration routes the above techniques employed by the Eskimos offer the maximum likelihood of success and consequent acquisition of surplus. Such a surplus could be their greatest appeal (Frison 1991; in Marean 1997). Such ecological conditions are seen as broadly similar to those experienced by the Neanderthals, namely the cold environment with a seasonal scarcity of carbohydrates demanding a reliance on meat for subsistence.

2.6 - The Approach of Full Glacial Conditions in Europe and Neanderthal 'Replacement':

An earlier climatic shift around 55,000ya (coinciding with the first cold maximum of the Wurm) has been linked to alterations in hominid foraging strategies and technological practices in Italy (Stiner 1994). In mid-latitude Europe an increase in aridity is noted as open vegetation spread over unglaciated terrain (grasses, lichens, scrubs, etc.). Although in certain areas of 'upland foothill country' significant tree cover is recorded. (Butzer 1971)

At the glacial maximum (20,000ya) southern (i.e. along the Mediterranean coast) Europe was dominated by forest-steppe, the north west by permafrost, and the north west by loess-steppe and/or permafrost. The main glaciers were the Scandinavian and British ones further north, but in southern reaches the Alps and Pyrenees were glaciated. The loess-steppe (e.g. in France) was essentially a herbaceous tundra. Some pine and birch were present but the pollen record is primarily non-arboreal. Non-glaciated Russian Europe was covered with steppe-tundra and parkland vegetation, with only scattered tree growth. Here the climate was dry and extremely continental. In the late Upper Palaeolithic of western Europe reindeer were the most important game. In central Europe it was mammoth (on the loess steppe by Gravettian hunters), and central Russia a mixture of reindeer (on the tundras by Magdalenian hunters) and horse. In Spain gregarious ungulates were few or absent, and game resources were more diversified. (all in Butzer 1971)

"One of the ironies of full glacial conditions in Western Europe is the fact that despite substantially lowered temperatures and a dearth of arboreal vegetation, the pervasive, and often now extinct, open vegetation communities (low latitude periglacial 'steppe-tundra', heath, grassland, parkland, etc.) provided vast expanses of lush pasture for a wide variety of medium to large ungulates....These pleniglacial habitats supported ungulate biomasses resembling those of modern African Savannahs in terms of size and diversity more than those of Holocene European woodlands" (Straus 1987; 150).

"Ironically, the European centre of accelerated cultural innovation during the last glacial was found in the then prevailing forest-tundra and cold loess steppes, rather than in the warmer, temperate woodlands of the Mediterranean region....the forest tundra of Europe had displaced the African savannahs as a centre of innovation" (Butzer 1971; p 454).

However, after paleoenvironmental analysis Butzer concludes that "Glacial Europe was consequently *not* a marginal resource base for sufficiently advanced hunting populations" (1971; p 463 emphasis added). Perhaps with this in mind the irony noted in the above statements diminishes. However, despite an apparent abundance of available game, the Neanderthals must have been ill equipped for survival as the climate cooled and the European ecosystem altered accordingly.

CHAPTER 3

The Techno-Cultural Transition - Evidence from Europe and Southwest Asia:

Details of the techno-cultural transition are far from clear and it was certainly not completed in one all-encompassing step. In fact the notion of all the aspects of the transition occurring simultaneously resulting in the completion of 'hominisation' (Rigaud's term 1989; p 153) appears to have been largely dropped, with different authors citing different factors occurring at different times either side of the so called transition. The various elements converge to produce the transition in the human condition via an "accumulation of relatively independent, multiple but convergent factors....[which] took place over a period of time considerably longer than that of the last (Riss/Wurm) interglacial" (Rigaud 1989; p 153).

The process began in the early Mousterian and continued well into the Aurignacian. Gamble (1986; in Clark & Lindly 1989) stated that the archaeological evidence for the appearance (i.e. the convergence which Rigaud speaks of) of fully modern/sapient behavioural patterns post-dates both the Middle-Upper Palaeolithic transition and the anatomical shift from archaic to modern *H sapiens* by 15-20,000 years. What follows is a brief assessment of the varying opinions concerning the relative cultural, technological, and mental capabilities subsistence capabilities of these two groups, relating to subsistence and the acquisition of game

3.1 - The Archaeological Evidence for the Lithic Characteristics of the Transition:

The Middle Palaeolithic spanned 200,000 years and was technologically stable. Both Levallois (hallmark methodology of the Mousterian) and non-Levallois techniques were employed in tool manufacture. Rare typological and technological oscillations are noted however, taking the form of isolated premature and transient appearances of Upper Palaeolithic-like industries with a preponderance of blades in the Middle East (Amudian) and southern Africa (Howieson's Poort), only to be subsequently replaced by a reversion to typical Middle Palaeolithic flake industries (Tuffreau et al 1986; in Mellars 1989). Thus, it would appear that Middle Palaeolithic hominids had the capabilities to manufacture such 'advanced' implements; but for whatever reason selected not to do so on a regular basis. Shifts between generalised and specialised animal exploitations are also noted. Nowhere is a directional change towards the Upper Palaeolithic apparent according to Mellars (1996).

Traditionally recognised characteristics of the Upper relative to the Middle Palaeolithic lithics (adapted from Mellars 1996 & 1989):

1. Increase in blade, relative to flake, frequencies. Mellars claims that there is an associated shift in manufacturing methodology from hard to soft hammer technique. Bilsborough (pers. comm.) recognises it as the development of 'punch striking', but these two descriptions are not mutually exclusive.
2. Appearance and abundance of new tool forms, such as multifaceted burins and nosed scrapers. Some technologically simpler and less varied burins are recorded in the Middle East during the Middle Palaeolithic.
3. Appearance of morphologically new artefact types, qualitatively different from preceding tools (e.g. Chatelperronian points in France; Uluzzian crescents in Italy; Emireh points and chamfered blades in the 'transitional' industries of the Middle East).
4. The dynamic and innovative nature of the technological change in the Upper Palaeolithic, created the phenomenon of rapid appearance of new types and the rapid succession/replacement by the next new ones; whereby clearly defined techno-chronological phases can be discerned.
5. There is a more discrete separation between different artefact categories due to a more tightly ordered pattern of standardisation and deliberately 'imposed form'; i.e. where modification and working is so extensive that the end product bears little resemblance in shape to that of the original piece. Examples include Upper Perigordian truncated elements and Magdalenian microlithic forms (Brezillon 1968).

However, Harrold (1989) categorically states that the generally agreed differences between the Middle and Upper Palaeolithic are only obvious when considering late Upper Palaeolithic industries, such as the Magdalenian (of France and Spain) or the

Epigravettian (of Italy), not the ones immediately after the transition (i.e. the early Aurignacian). Sackett (1988; in Mellars 1989) claims that the perceived increased complexity of forms in the Upper Palaeolithic merely reflects the temporal and spatial extent of the period. Looking at individual assemblages, a significantly broader range of morphologically discrete types would not be discerned in an Upper Palaeolithic assemblage relative to a Middle (or even Lower) Palaeolithic one.

3.2 - The Industrial Sequence in Western Europe:

Harrold (1989) concentrates on the evidence from the region stretching from Cantabrian Spain to north central France. In this region the Mousterian was succeeded by the Chatelperronian which co-existed with and then gave way to the early Aurignacian in a 'time-transgressive' manner from southeast to northwest. There are no instances of the Mousterian overlying either or being interstratified between the Chatelperronian or Aurignacian industries. Harrold (1989) describes the Chatelperronian as a true Upper Palaeolithic industry with knives, end-scrapers, burins and truncated pieces; although it also still contains some Mousterian 'types', such as notches and denticulates. Roughly contemporary to this is the early Aurignacian, within which a sequence of stages are sometimes recognised, but their temporal ordering and development are usually unclear. Aurignacian 'type' tools include split-base bone points and Aurignacian blades.

It is widely believed that production of the Chatelperronian was exclusively by Neanderthals, and Aurignacian by EAMH. The early Aurignacian assemblages are actually not associated with any human remains (Rigaud 1989), but later ones are only associated with anatomically modern humans, such as at Cro Magnon. There is also the possibility that the anatomically modern man from Combe-Capelle may have been from a Chatelperronian level (Rigaud 1989). Although it cannot be proved that each group could/did not produce the assemblages assigned to the other, the available evidence is highly suggestive that such a distinct association existed. Indeed, d'Errico et al (1998; S2) recognise that the "Neanderthals may therefore have been producers of all the pre-Aurignacian Upper Palaeolithic technocomplexes of western and central

Europe (Chatel, Lincombian, Uluzzian, Szeletian and others)". Despite the fact that there are no diagnostic human remains with the earliest Aurignacian assemblages, such as at Bacho Kiro level 11 which is termed 'protoaurignacian' (Kozolowski 1982; in Rigaud 1989), these industries are accepted as being EAMH constructs.

3.2.1 - The Mousterian - Chatelperronian Interface:

The technological sophistication demonstrated by Mousterian bifaces, Levallois points and cores are testimony to the well developed mental and kinaesthetic abilities above and beyond those necessary to produce blades (Hayden 1993). The production of a simple prismatic blade is far easier than the procedure for making a Levallois point. Bordes (1961; in Hayden 1993) noted that blades even occur in the Acheulean, and comprise up to 40% of certain Mousterian assemblages. Although blades are present before the Upper Palaeolithic; in the Chatelperronian they are struck from prismatic cores which are largely absent in the Mousterian (Harrold 1989).

38,000ya a process of 'leptolithisation' (a shift to thinner tools - Rigaud's term 1989) occurs and blades become dominant over flaking technologies and the Mousterian gave way to the Chatelperronian (37-35,000ya). There are three traditional views (in Harrold 1989; and in Clark & Lindly 1989):

1. The Chatelperronian as an intrusive industry introduced from elsewhere; being clearly distinct and no transitional industries being recognised. This option has been largely rejected now.
2. Alternatively as an independent development from local Mousterian variants (Mousterian of Acheulean according to Bordes 1972; Mousterian of Acheulean Type B in Pyrenean France by Bahn 1984 and the Dordogne heartland by Tuffreau 1976; and/or from Denticulate Mousterian in certain areas, such as Arcy-sur-Cure in Girard's opinion 1980).
3. Or possibly as a heavily acculturated Mousterian derivation via cultural diffusion from the industries accompanying the EAMH migration into the region (Klein 1973).

Unfortunately the evidence in the archaeological record for any one would not be mutually exclusive relative to the other two!

Rigaud (1989) claims that there is no conceptual difference between the Levallois blade technique and the blade core reduction of the Upper Palaeolithic. The Chatelperronian involved the systematisation of blade production and a type shift to Upper Palaeolithic forms (having been rare in previous assemblages), built on a 'substrate' of Mousterian technology. "Arcy[-sur-Cure, France] is consistent with the hypothesis of an original and independent cultural evolution of western Europe's late Neanderthals" (d'Errico et al 1998; S4). Such a theory does not demand (but equally does not eliminate the possibility of) Neanderthal - EAMH socio-cultural interaction.

Flakes and the discoid/irregular cores from which they are produced continue throughout the Upper Palaeolithic. However, Harrold's analysis found "no support for the notion that the late Mousterian tended toward higher blade production" (1989; p 691). Thus, flakes imply continuity, and blades discontinuity between the Mousterian and Chatelperronian. Overall typological discontinuity between the two industries is apparent. Late Mousterian assemblages, such as at Combe Grenal, Pech de l'Aze 1, and Le Moustier, are not particularly 'evolved' nor do they show a trend towards a Chatelperronian kind of typology. La Ferrassie E and Le Moustier K, formerly viewed as transitional industries, are now recognised as being artificial admixtures. Vectored change within the Chatelperronian away from the Mousterian is only evident at Grotte du Renne and Grande Roche where the oldest levels are the most typologically primitive/regressive.

The widely perceived evidence for lithic continuity is seen is merely due to the preceding Middle Palaeolithic period providing a technological and typological base on which later industries could build. In other words there was not a strict directional evolution towards the Chatelperronian/Upper Palaeolithic; the Middle Palaeolithic permitting rather than determining later developments. Following this, Harrold (1989) concludes that the Chatelperronian is most likely an indigenous development of the local Mousterian under the impact of diffusion and possible migration from elsewhere. This theory certainly implies a significant degree of Neanderthal - EAMH interaction.

3.2.2 - The Chatelperronian - Early Aurignacian Interface:

Chatelperronian lithic technology is distinct from that of the Aurignacian in both the procedure for producing blades and the way blanks were transformed (Guilbaud 1987 &1996; Bodu 1990; Pelegrin 1990 & 1995; in d'Errico et al 1998); but the two are at least partly contemporary. Claims of the Chatelperronian being entirely earlier than the first typically Aurignacian assemblages are 'unconvincing' (Mellars 1998). The Chatelperronian at Arcy-sur-Cure is the latest known occurrence persisting beyond 33,000ya (Hublin 1996). Two hypotheses are recognised (in Harrold 1989):

1. They are different cultural traditions associated with different ethnic/tribal groupings with mutually exclusive tools, such as Chatelperron knives and Aurignacian blades (Sonnerville-Bordes 1960; Howell 1984)
2. Or they reflect functionally differentiated behaviours at different sites possibly due to seasonal or environmental variations (Sally Binford 1972; Ashton 1983).

Both industries are characterised by blades, and there is no indication that early Aurignacian assemblages are more heavily laminar than the Chatelperronian. Scalar Aurignacian retouch (characterised by broad and overlapping flake scars) is incorporated into several type definitions of Upper Palaeolithic industries. It is totally lacking in the Chatelperronian. Early Aurignacian assemblages are more typologically diverse, on average having 8.5 more tool types than Chatelperronian assemblages (Harrold 1989). Rigaud (1982; in Harrold 1989) stated that the very rare occurrence in one industry of characteristic types and retouch forms in the other is insufficient to infer typological continuity. With this in mind, it is noted that the early Aurignacian has fewer Mousterian-type artefacts than the Chatelperronian.

Harrold (1989) concludes that in general there seems to be considerable continuity, or at least similarity between the two industries, with the same basic Upper Palaeolithic production techniques and artefact morphology repertoire. The evidence points towards separate material culture traditions. While some are willing to accept that certain, but limited, Aurignacian technical practices appear to have been adopted in the Chatelperronian via acculturation; d'Errico et al (1988) are less permissive in summarising the situation:

"Analysis of the stratigraphic, chronological, and archaeological data from the key site of Grotte du Renne (Arcy-sur-Cure, France) shows that the notion of acculturation, as commonly understood, is inconsistent with the evidence....the site is not an exceptional case and is best explained by models of independent development that are supported by re-evaluations of the Chatelperronian technology and by the patterns of chronological and geographical distribution of Aurignacian, Chatelperronian, Uluzzian, and late Mousterian settlements" (1998; S1).

However, in commenting upon d'Errico et al's article Mellars (1998) raises the issue that the independent evolution of the Chatelperronian and Aurignacian has an 'extraordinary level of historical coincidence'. Thus, the likelihood that two distinct populations could have developed Upper Palaeolithic tool kits separately is brought into question.

3.3 - The Industrial Sequence in Southwest Asia and Associations with Hominids:

The scraper assemblages from La Quina and Tabun are distinct in spatial and (probably) temporal terms, and are very unlikely to have been produced by culturally related peoples. However, in terms of the processes of reduction and absolute form of the pieces they are almost identical. From this Dibble (1989) deduces that, at this stage in human evolution, technological constraints were exerting a greater effect on tool morphology than cultural patterns.

If physical variability of Upper Palaeolithic hominids does reflect differences in evolutionary ecological strategies, then there should be a correlation between artifactual traces of those strategies and morphological variation (Shea 1989). The archaeological record in the Levant challenges this idea since both archaics and moderns are associated with the same Levalloiso-Mousterian technology. Major behavioural discontinuities are not apparent in the archaeological record linked to morphologically distinct hominids. In functional terms the assemblages at Qafzeh and Kebara cannot be separated (Shea 1989). The ranges and relative frequencies of activities, selections of tool shape, and manufacturing techniques are the same. The only disparity is in the proportion of used artefacts, as identified by the presence of retouch: Qafzeh having 64%; Kebara only 20%. However, this may represent a scarcity of raw materials at Qafzeh, and not necessarily a cultural or technological disparity between the populations at each site (section 3.4.3).

The Levantine Mousterian sequence may have begun as early as 128,000ya or as late as 80,000ya (and disappeared around 44/43,000ya); later than the Middle Stone Age in southern Africa, the Saharan Mousterian, or even early appearances of the European Mousterian. Without evidence for a pre-Mugharan Levantine Mousterian, the separate evolution of early Mousterian in both Europe and Africa, with its avoidance of the Southwest Asian cross-roads, must be explained (Bar-Yosef 1989a; 1898b). The Levantine Mousterian is characterised by the Levallois technique, although the classic radial core preparation is rare at most sites (Bar-Yosef 1989b).

Tabun is the 'type' site for the three phases of the Levantine Mousterian (Clark & Lindly 1989): Phase I (layer D: 90-80,000ya) is characterised by elongated Levallois points and limited Upper Palaeolithic tool forms, such as end-scrapers, blades and burins; phase II (layer C: 60-50,000ya) is dominated by broad oval Levallois flakes and classic Mousterian forms; and in phase III (level B: c. 50,000ya) narrow point and blade forms predominate. Here there is a trend towards thinner flakes, but due to variations in raw materials and an erosional incident that occurred across areas of the Levant about this time, the documentation of such a sequence is less prevalent at other sites.

Transitional industries are noted at the start of the Upper Palaeolithic in the Levant at Ksar'Akil (central) and Boker Tachtit (southern). Change is autochronous as the typological shift predates the technological one (Bar-Yosef 1989b). The Upper

Palaeolithic is dominated by the Ahmarian blade/bladelet tradition from 35,000ya; although it is interrupted by the Levantine Aurignacian around 22,000ya (a period characterised by flake production, nosed and carinated scrapers, bone and antler artefacts).

There is no simple relationship between the lithic and hominid types in the Levant region. A linear lithic developmental pattern does not correspond to the morphological ordering of the fossil hominids (e.g. the EAMH sample from Qafzeh recently dated to 92,000ya, rather than 40,000ya as originally believed). Both Neanderthals and EAMH are found with similar Mousterian industries. Also, evidence at different sites of hearth structures, burials, and similar tool use patterns (identified by edge ware damage) associated with both hominid forms means that behavioural differences between the two populations cannot be traced from the current archaeological evidence (Bar-Yosef 1989a).

A direct correlation between environmental change and lithic core reduction strategies cannot be established in Southwest Asia. The major cultural changes are not linked to climatic fluctuations; although a time-lag could be possible. Shifts seen in the faunal assemblages indicate the evolution of hunting during the Middle Palaeolithic allowing temporary occupation of semi-arid areas. (Bar-Yosef 1989b)

"....[there is] no corresponding difference between patterns of Levalloiso-Mousterian industrial variability which is not otherwise explicable as the effects of regional variation in the circumstances of tool use [with anatomical contrasts between hominid populations in the Levant]." (Shea 1989; p 622)

3.4 - Industrial Variation:

Most industrial assemblages could contain hundreds or even thousands of years worth of discarded tools. A clear picture of individual short-term occupations is hard to discern; particularly in terms of day-to-day activities. Different (types of) sites and materials will have differential survival rates. Differences in the size of assemblages and the time scale over which they accumulated will affect the industrial variation recorded between them; the spatially and/or temporally more expansive the site the more likely it is that it will contain a wider range of artefact types. Bias views into the past are therefor unavoidable.

3.4.1 - Functional Determination:

No strict one-to-one correlations between lithic morphology and function have been established. Leading theories include (in Mellars 1996):

- Geneste (1985) notches/denticulates made as needed and immediately discarded. Other forms made from better quality material and these valued tools are transported which implies a degree of planning or forethought.
- Binford (1992) notches/denticulates used in immediate vicinity of source for plant processing. Scrapers, points, and bifaces are made from better quality materials from more distant sources, and used for carcass processing. There are no clear or simple correlations of industrial types and faunal assemblages; although in some instances Quina Mousterian is associated with high frequencies of reindeer, and Mousterian of Acheulean with predominantly red deer or bovid remains.
- Mellars (1996) suggests that there is a selection of better quality material for the tools which are more intricate and wanted to have a long use-life. Better quality material is able to be reworked more often.

While Binford advocates a functional model to explain variation in industrial composition; Dibble & Rolland place all recognised forms along a continuum of the reshaping/resharpening process of a basic tool form - called 'lithic reduction' (in Mellars 1996). They state that heavy retouch reflects either a scarcity of suitable raw material or permanence of occupation at the site (for whatever reason). Dibble (1984; in Mellars 1996) also states that discard was initiated when a minimum width was reached, relating to prehension of the actual artefact rather than cultural rules. This reduction model is not to account for defining types or underlying technological contrasts, but for varying frequencies of different tools between sites. Non-functional explanations for industrial variation have also been proposed:

3.4.2 - Social Distance and Isolation:

Isaac (1972; in Mellars 1996) suggested that in isolation, a scenario of inaccurate replication of tool production techniques passed between generations within a particular group may accumulate, resulting in technological drift. Demographic fluctuations or changes in spatial distribution causing a thinning of the population on the ground, possibly in response to environmental changes, would lead to such isolation of groups.

For Example, in the Iberian Peninsula nothing is observed to have changed in the Neanderthal material culture, whereby they maintained a traditional Mousterian/Middle Palaeolithic form. They were replaced there suddenly, as late as 30-28,000ya. Blade debitage is unknown from any Neanderthal associated assemblages on the Iberian Peninsula. The 'Ebro Frontier' is a valley across northern Spain, which acted to isolate the Iberian Neanderthals. Neither other European Neanderthals nor EAMH could apparently cross this ecological divide. The resultant phenomenon is termed a case of "uneven independent development" (d'Errico et al 1998; S21).

3.4.3 - Technological Adaptation:

This is related to the character, availability, or accessibility of raw materials in the area (e.g. for satisfactory control of flaking when using the Levallois technique, fine grained materials are required). Intensive or sedentary occupations could have led to more intensive reworkings or a shift to the more economical non-Levallois technique (Mellars 1996).

For example, side scrapers and tools with low Levallois indices dominate the Pontinian (Italian Mousterian) industry (Bietti 1980; Taschini 1972; in Stiner & Kuhn 1994). The only workable raw materials within 50km of the cave sites are mostly less than 10cm across and come from beach deposits. The Pontinian uses two techniques of flake production: 'centripetal' working around the edge; and 'platform' working parallel to the long axis. The former maximised the size of flakes and blanks produced, while the latter maximised the number of flakes produced per core. At Moscerini and Guitari (early Mousterian) the centripetal technique dominates. The products are large with considerable retouch and sharpening, having prolonged use and transport frequencies. In contrast, at Sant'Agostino and Breuil (late Mousterian) it is platform core reduction that dominates. Large numbers of small unmodified flakes were produced with little evidence of transport over significant distances. The small size of the pebbles precluded the production of blades (Kuhn 1990; in Stiner & Kuhn 1994).

Stiner (1994) concludes that the variation observed in the Pontinian is not necessarily an evolutionary trend but more likely adjustments within a single subsistence system relating to changing resource opportunities. Geneste (1990; in Hayden 1993) claimed that such evidence for the management of lithics demonstrates that the anticipation of needs and situations both temporally and spatially was manifest in the realms of acquired habits amongst the hominids of the Middle Palaeolithic period.

3.4.4 - Technological Convergence:

This is defined as the recurrence of basic industrial features in different times and places under the 'law of limited possibilities' (Rolland 1981; in Mellars 1996). In other words, similar tool types will appear simply because only certain shapes can be produced given the basic structure of the raw material under consideration. Such creative constriction would have occurred whether using lithic, bone or antler starting points. The Quina Mousterian's initial appearance and re-emergence during the last glacial sequence in Southwest France, and the Quina-like Yabrudian industry in the Middle East (characterised by a high frequency of thick, heavily retouched racilloir forms - 50-55%) are quoted as examples of such a phenomenon (Mellars 1996).

3.5 - Lithic Raw Material Procurement Strategies and their Implications for Hominid Behaviour:

The 'provenancing' of tools determines their geological source. Secondary sources include rivers which transport material from geological source to the point of procurement by hominids.

The territories of lithic acquisition (60 square km zones around sites) in the Dordogne valley are identical from the Middle Riss to the start of the later Wurm (200,000-25,000ya). No major changes are apparent in the general economy coinciding with the arrival of modern humans. Geneste (1988; in Hayden 1993) observed no major break in patterns of raw material procurement between Mousterian and Upper Palaeolithic assemblages; indicating similar conceptual capacities to plan economic and technological activities. Larick (1983; in Rigaud 1989) showed that the first significant shift in raw material exploitation occurred much later at the maximum of the Last Glacial.

Geneste (1986; in Mellars 1996; Ch. 5) states that there is an exponential decline in material quantity with increasing distance. The materials transported over greater distances are generally of a better quality in terms of flaking superiority. Associated with this, the intensification (reflected in the degree of systematic retouch) of use increases with the distance material is transported. According to Mellars (1996) southwestern French Middle Palaeolithic sites derive the majority of raw materials from local sources within 4-5km; with only around 5% of the material coming from the 80-100km range.

Butzer (1986; in Clark & Lindly 1989) and d'Errico (1998) noted that in areas where geography restricted mobility and raw material acquisition has remained constant, overall assemblage characteristics have remained constant over the transition period. An example is northern Spain where the ongoing use of fine grained quartzite has produced assemblage homogeneity, regardless of cultural input. In general however, the Middle Palaeolithic industries (and Chatelperronian where developed) make use of local often poorer quality materials relative to the Aurignacian in which a greater proportion of exotic, better quality blanks are utilised.

The presence of tools made from non-local sources in the Italian late Upper Palaeolithic implies the anticipation of prolonged cold season stay. Mousterians used local materials and adapted their reduction techniques as appropriate. The opportunity to gain raw materials is dependant on the foraging or seasonal migratory range of the group. It could be that the Mousterians were 'improvisers' and the late Upper Palaeolithic hominids 'advance-planners' (Stiner 1994).

Wobst (1974) and Gamble (1983; both in Mellars 1996; Ch. 5) suggest the operation of trading networks. However, Mellars (1996) suggests the materials were collected during seasonal movements. The former places limits on Neanderthal group mobility, while the latter proposes greater mobility.

Hayden states that "It is difficult to imagine that regional alliances would not have existed in Mousterian or even previous periods" (1993; p 137) claiming some Mousterian artefacts were derived from sources beyond 'expectable' ranges of groups lacking transport aids (as calculated by Roebroeks et al 1988; Geneste 1989). Hayden (1993) proposes that Mousterian lithic procurement territories reached 6,000-12,000 square km (Ellis in 1989 placed the absolute maximum range at only 5,000 based on modern ethnographic studies) implying that substantial regional interactions were taking place. Exactly what and how much is supposed to have moved such distances is omitted from his discussion.

3.6 - Bone, Antler and Ivory Artefacts:

Simple and limited bone working is known from Mousterian contexts, and even the Acheulean (Rigaud 1989). But although, the materials may have been 'used' during the Middle Palaeolithic, standardised and highly shaped bone, antler and ivory artefacts only appear in the Upper Palaeolithic. For example, the Chatelperronian needles at Arcy-sur-Cure 33-34,000ya (Leroi-Gourhan & Leroi-Gourhan 1964); and Aurignacian split-base bone points across western and central Europe (Leroy-Prost 1975; both in Mellars 1996). Only in the Aurignacian do bone (especially in the form of *sagaies* projectile points) and antler artefacts comprise a significant proportion of the tool kit. A large variety in techniques developed during the Upper Palaeolithic; such as sawing, polishing, and perforating, produced form variation across Europe (Rigaud 1989).

Mousterian examples of bone technology are unstandardised, lacking significant re-working/shaping, and sporadic in occurrence. Within the Chatelperronian they are more numerous, use several Upper Palaeolithic working techniques (e.g. grove-and-splinter extraction, whittling, polishing), and show a variety of forms (e.g. poincons, baguettes). The contrast between the Mousterian and Chatelperronian is more obvious here than in lithic terms.

Hayden (1993) suggests that the increased investment in the manufacture of bone tools (due to the difficulty in working this material) meant that they were primarily used as status symbols. Evidence such as the antler digging pick and awl from Regourdou (Bonifay; n.d.; in Hayden 1993) shows that Mousterian groups were capable of making such tools but seen to have chosen not to most of the time, probably as such status competition was not a significant consideration for the hominids of the time.

The overall range and complexity is comparable between the two early Upper Palaeolithic industries (Harrold 1989). However, less than half of the Chatelperronian industries studied contained bone artefacts; whereas all but one early Aurignacian did. Split-base bone points are totally lacking in the Chatelperronian. Bhaltachaya (1977) says that early Aurignacian assemblages have few, if any, worked bone objects; while Harrold (1981) states that the Chatelperronian assemblages usually contain at least one or two (both in Clark & Lindly 1989). However the experts phrase their findings, relative to later assemblages these early Upper Palaeolithic ones are not particularly rich in bone artefacts. There does appear to be a clinal change during the Upper Palaeolithic towards a high proportion/diversity of bone and antler industries and art objects; but those early post-transition variants are relatively underdeveloped. The implication is one of in situ development well after the transition. Indeed, bone technology is so sparse in the Levant prior to 20,000ya that its documentation cannot be used to distinguish the Middle from the early Upper Palaeolithic at the transition (Clark & Lindly 1989).

Hublin (1996) notes that the archaeological context of the Neanderthal temporal fragment from Arcy-sur-Cure suggests the population it represents used a rich bone and ivory industry and personal ornamentation (pierced/grooved animal teeth and ivory rings). But "Evidence from France and Italy seems to indicate there was no adoption or absorption of Aurignacian bone technology by the Neanderthals....The same is true of lithic technology....independent development becomes the most parsimonious explanation for the evidence" (d'Errico et al 1998; S15).

3.7 - Projectile Points and Ancient Wooden Hunting Spears:

In recent years the discussion of big game hunting by hominids has became confined to after the appearance of EAMH 40,000ya; with scavenging being the most acceptable assumption regarding hominid activities prior to this event (section 4.2). The new discovery at Schoningen in Germany of "....complete, unambiguous throwing spears 380,000 to 400,000 years old...." (Dennell 1997) has thrown fuel onto the fiery debate over the contrasts/similarities in hunting capabilities of the anatomically archaic and modern humans.

Before this discovery many had limited the Neanderthals and other archaic forms to the stabbing of game using cumbersome thrusting spears (Trinkaus 1989), such as the yew wood one with a fire hardened tip from Clacton, England (350,000ya) or that from Lehringen, Germany dated to the last interglacial (125-115, 000ya). Binford claims they were used in close contact situations with injured animals due to sickness or carnivore attack - not a very enterprising form of hunting. Gamble (1988; in Mellars 1996) suggests they may have been used as probes to detect carcasses buried beneath the snow. Most deductions were made from studies of faunal assemblages. For example Delpech (1983; in Rigaud 1989) showed those associated with the late Mousterian to be close in species diversity and body part representation to those of the early Aurignacian; the major shift to specialised hunting only happening within the Magdalenian.

In northern Europe the earliest well-documented archaeological sites are dated to 500,000ya, so the spears relate to the time of initial colonisation. The spears are complete, measuring two metres in length, and are "....unquestionable spears, and....must have been used for hunting large mammals" (Dennell 1997). The spears are made from the trunk of a 30-year-old spruce tree. The tip end comes from the trunk's base where the wood is hardest. Each has the same proportions and its centre of gravity 1/3 of the way down from the tip, as in a modern javelin. They therefore represent a considerable investment of time, effort and skill, and imply considerable depth of planning, design sophistication and patience in carving, in Dennell's opinion. Such spears could have been the key to northern European colonisation in the cold climate and harsh winter conditions that existed at the time. Efficient hunting technology would have given hominids distinct advantages where game was relatively scarce and daylight hours in which to obtain it were short. Judging by the weight of the spears, the throwers would have needed to have been large and powerfully built (such as Neanderthals).

Chase (1989; p 332) clearly states that there is no evidence of projectile points of any material in the European Middle Palaeolithic. On tools of these industries the 'bulb of percussion' is not removed which would have inhibited the hafting of Mousterian or Levallois points. In the light of the above wooden spears it should be asked whether this fact, if agreed upon, actually matters in terms of hunting success? If the spears are as well constructed as Dennell suggests then they would appear to be perfectly adequate for the task in hand on their own.

Evidence, in the form of impact damage 'microfractures', shows that Levantine stone points were hafted projectiles. This phenomenon is noted at Kebara, Tabun, Qafzeh, Heyonim, and Tor Faraj (Shea 1988, 1991, 1993, 1995, 1997 in Shea 1998) where the marks are said to be indistinguishable from those on experimental spear points; and very similar to those on authentic North American stone spear and arrow points

(Dockall 1997; Odell & Cowan 1986; in Shea 1998). Plisson & Schmider (1990) have identified such impact marks in certain Chatelperronian contexts; while Anderson & Gerfaud (1990) state that damage of this kind is absent from the European Mousterian context (both in Shea 1998). The presence of impact-damaged and hafted projectile points in similar frequencies at these sites shows that both Neanderthals and EAMH had similar predatory capacities, with both populations showing a degree of planning and foresight in their tool manufacture. Therefore, according to Shea (1989) there was not a behavioural discontinuity coinciding with the anatomical one in Southwest Asia. The distribution of projectile points and butchery tools supports a central place model for the provisioning of meat procurement here.

Marks (1983; in Mellars 1989) demonstrated that the shift in tool form preceded the shift from flake to blade technology at the transition (e.g. at Boker Tachtit in Israel; and the Bohunican industry in Czechoslovakia). Clark (1983; in Mellars 1989) suggests that the increased complexity of technology in the Upper Palaeolithic corresponds with the appearance of 'hafting'. Although there is limited evidence for this practice in the Middle Palaeolithic, it is proposed that the blade blanks of the Upper Palaeolithic were better than the earlier flake-based tools which accounts for the massive proliferation of hafting. So what was the impetus for the proliferation of composite spears and tools? If it related to damage and repair, as has been suggested (i.e. only having to replace the broken section as opposed to the whole implement), this shift would not have affected hunting success only preparation time and effort. As such the use of haftable projectile points of any material cannot be implicated in any changes in hunting strategy or competence.

Alternatively, it is noted by Bilsborough (pers. comm.) and Shea (1998) that that hafted points could have been important in impeding the escape of game. Smooth javelin style spears may have fallen out, whereas hafted points (the much later development of the barbed harpoon tip is an elaborate example of the point being made) would have stayed in prey longer and caused greater damage to/laceration of muscles and increased blood loss, thus slowing the animal's flight. There is ethnographic evidence that heavily tipped weapons (often metal points today) are reserved for dispatching large prey at close quarters, where the risk of injury to the hunter is greatest (Churchill 1993; Geist 1981; in Shea 1998).

CHAPTER 4

Faunal Assemblages and their Implications for Hominid Subsistence Patterns

The 'shrewd omnivory hypothesis' of Hartwig (1997) assumes that at the time of hominid emergence from Africa no niche for specialisation on a single dietary domain was available. Earlier and subsequent hominids lacked the physical attributes necessary to displace resident highly specialised niche dwellers (e.g. predators, scavengers or browsers). The shrewd omnivory hypothesis states that hominids cultivated a novel composite niche defined by opportunistic levels of gathering, hunting, scavenging, harvesting that collectively were antagonistic to established, specialised niche dwellers and were as such unlikely to provoke confrontation and the process of competitive exclusion.

Discussions concerning methods of acquiring meat, and possibly more importantly fat (section 8.3) among Neanderthals and EAMH fall into two categories. The first attempts to establish the magnitude of the contribution made to each group's subsistence by scavenging. The second is aimed at elucidating the time when general hunting practices gave way to a more specialist brand. In practical terms it is the different species represented in what age cohort(s) and by which body parts that has to be discerned. Accurate achievement of this is problematic and the interpretation of the data is contentious.

4.1 - Body Part Representation and Age Mortality Profiles:

Assemblages at Combe Grenal (Mellars 1996) and other Middle Palaeolithic sites in Europe, are generally dominated by the skull/jaw and distal limb bones (the least meaty parts), and there is an under representation of proximal limb bones and scapulae (most meaty). Although occasionally periodic proportional increases in these latter parts are noted.

Binford (1981; in Fernanda Blasco 1997) devised the Modified General Utility Index (MGUI) which rates the 'profitability' of different prey species according to the proportions of meat/fat/marrow to be gleaned from their fleshiest parts (i.e. scapula, humerus, pelvis and femur). These are the parts which are transported away from the kill site most often.

Explanations proposed to account for the observed differential body part representation (not all are mutually exclusive):

- *Pure scavenging* - of least meaty parts after carnivores have consumed the meatiest parts. Dismissed by Chase (1986, 1988; in Mellars 1996) since cut mark and breakage patterns are not consistent with the utilisation of desiccated or frozen carcasses. Stiner (1994) states that there is no convincing evidence at Italian sites for hominids scavenging carnivore kills here, although it is accepted as a feasible opportunistic scenario.
- *On site butchery and carcass processing* - at a safe haven near the kill site where carcasses taken for initial butchery. Chase (in Mellars 1996) suggests the less meaty parts are consumed while this process takes place and the meatier parts are taken to be consumed/shared at occupation sites elsewhere.
- *Differential processing time* (Binford 1984; in Mellars 1996) - whereby the most represented parts are those which contain the highest proportions of fat (tongue, brain, marrow) which are hardest to extract. Meatier, more easily butchered parts done at the kill site with only the meat transported, while these less accessible reserves brought back unprocessed so can be done safely and at leisure later.
- *Schlepp Effect* (Perkins & Daly 1968; cited by Mellars 1996) - the dead animal's hide is turned into a make-shift sack to carry its own butchered meat, which is dragged back to occupation sites using the foot bones as handles.

Stiner (1994) recorded a natural/complete balance of parts, corresponding to hunting or early access to carcasses, in the Upper Palaeolithic and in some instances in the late Middle Palaeolithic. Head part dominance is thought to indicate either scavenging/late access, or the unworthiness of other parts for transport due to fat depletion and is thus a seasonal phenomenon. This situation generally characterises the Middle Palaeolithic of Italy.

Mortality Profiles allow the comparison of the different age ranges of the different species present at a site. Theoretical 'yardstick' profiles are: Catastrophic (death of all age classes) and Attritional (death of the weakest - i.e. the very young and very old). Specialist literature indicates certain human hunting strategies have mortality profiles with biases towards adult animals. This is true of certain past and present human groups (e.g. Stiner 1994; Auguste 1995 in Fernanda Blasco 1997). Other groups concentrate on the very young of medium-large sized species which may be linked to seasonal site occupation (Klein & Cruz-Uribe 1984; in Fernanda Blasco 1997) or exploitation during the breeding season (Stiner 1994). This latter explanation would correlate with Cachel's (1997) claims for the need to maximise fat acquisition, since the breeding season is one marked by a fattening process (sections 2.3.3 and 8.3.2).

The age ranges of equids at Combe Grenal (Levine 1983; in Chase 1989) and elands at Klasies River Mouth (Klein 1986; in Chase 1989) show the Middle Palaeolithic hominids to have been capable of killing prime-age animals. If these earlier hominids were relatively less technologically complex then it did not inhibit their ability to hunt large prime-age game. (Chase 1989; p 331)

In Italy Stiner (1994) recorded the mid-sized ungulate remains (red and fallow deer, ibex) in Mousterian levels tending towards anatomical completeness at Grotte Breuil and Grotta di Sant'Agostino, but that the assemblages at Grotta di Moscerini and Grotta Guattari are head-dominated. In the former age profiles are prime adult or non-selective, while in the latter there is a bias towards old adult prey. All four Italian caves are in similar topographic settings. Mortality patterns show more diverse ungulate acquisition strategies in the Mousterian than in later humans in Italy. Evidence at different Mousterian sites identifies domination by either hunting or scavenging, whereas in the Upper Palaeolithic hunting is seen to be dominant at all sites. This trend towards increased hunting specialisation in Italy appears to have been realised prior to the Upper Palaeolithic.

In Southwest France it is widely accepted (including Binford and Chase) that systematic hunting of reindeer occurred during the Wurm II phase. Neanderthals are shown to have targeted young females in late spring/early summer at calving grounds;

a time when the pickings are easy and animals are fattest (Mellars 1996). The acquisition of other species is more hotly contested.

4.2 - Scavenging Versus Hunting:

The parameters of scavenging in the cold/temperate environments of Europe and Southwest Asia during the Pleistocene are unknown; such as the seasonality of carcass availability, persistence of carcass preservation, and the habitats in which carcasses were likely to have been found. So it is difficult to say whether obligate or regular scavenging in such environments would have been a viable hominid subsistence strategy (Marean 1998).

Binford (1984) rejected any ideas of hunting by hominids prior to about 40,000ya. His analysis of large animal remains in Middle Stone Age levels at Klasies River Mouth Cave indicated that they were scavenged. In 1985 Binford stated that by the Wurm II stage hominids in south-central France hominids were regularly hunting medium-sized animals but still having to scavenge larger carcasses, such as aurochs and horses. (all in Chase 1988). Thus, the archaic members of our lineage were behaviourally and intellectually distanced from their modern successors. Support for opportunistic scavenging taking the place of the traditional view of the big-game archaic *H sapiens* hunter was considerable (e.g. Bunn et al 1980; Shipman 1983; in Speth 1989). However, it now seems that the debate has gone full-circle. Once again hunting has become the in vogue strategy among archaic *H sapiens* groups.

Gamble (1993; 139) suggests that natural and non-human caused mortalities frozen within the ice would have provided a 'substantial larder', particularly if carcasses were frozen while they still contained significant quantities of fat and marrow. Previously, Gamble (1987; in Gamble 1993) had proposed a winter niche for hominids after the carnivores disappeared form Europe, involving the following migratory ungulate herds and searching for carcasses along water courses. Reasonable group sizes would have been necessary in order to make the searches efficient, and would have been sustainable since a single carcass could have fed many individuals. He postulated that the wooden implements usually regarded as spears were actually probes for searching out these carcasses under the snow. This theory, as the sole means of Neanderthal meat acquisition, would now appear to be disproved if Dennell's (1997) assessment of the ancient wooden spears is accurate (section 3.7). It is also possible that the use and control of fire (unavailable to carnivores) was an important means of accessing frozen carcasses. The lack of built up fires in the Middle Palaeolithic archaeological record testifies to their temporary nature, being used for the immediate job in hand then abandoned.

It is very hard to imagine scavenging being the primary subsistence practice of the Neanderthals given their highly specialised skeletal morphology (chapter 5), and their large brains. Such phenomena do not reconcile with visions of these hominids wandering about the landscape in search of another animal's left-overs. The only feasible way in which the physical presence of the Neanderthals could be envisaged to have adapted for scavenging would be if they were practising a highly confrontational form. Chasing packs of carnivore predators off fresh kills would have been dangerous and favoured a robust physique. It could also account for some of the trauma noted on Neanderthal skeletons. It is interesting that in all modern non-human social predators, such as hyenas, scavenging is not confrontational.

Stiner (1994) says that the hunting/scavenging debate is not a clear dichotomy, but variation in proportion combinations. The difference between Middle and Upper Palaeolithic being in how these methods were integrated into the wider foraging systems, geographical scales of movement, and the degree to which application was sensitive to choice and timing of shelter use.

4.2.1 - Behaviour Patterns of Modern Non-Human Scavengers:

Blumenschine (1988; in Marean & Kim 1998) claimed that defleshed bones discarded in the Serengeti, of East Africa, are usually scavenged within a day by hyenas or jackals. Carnivores regularly scavenge at San (Bartram et al 1991) and Hazda (Lupo 1995) hunter gatherer camps (both in Marean & Kim 1998). This has been shown to significantly alter the composition of the bone assemblages discarded by these human populations.

Blumenschine and Marean (1993; in Marean & Kim 1998) conducted experiments whereby captive scavenger carnivores were given access to carcasses/bone assemblages on a post-hominid (hominid-first model) and primary-access (carnivore-first model) basis. Tooth mark frequency on the mid-shaft fragments was low (7-10%) and high (69-81%), respectively. At Kobeh Cave the frequency of mid-shaft tooth marks is 20%, which is much closer to the hominid-first model. Its slightly raised value is probably indicative of some opportunistic scavenging by the hominids, after carnivore action. This scenario is compatible with the ethnographic evidence put forward by O'Connell et al (1988; in Marean & Kim 1998).

4.2.2 - Recent Evidence from Neanderthal Sites:

Chase (1988) reassessed the faunal assemblage at Combe Grenal (where Binford drew his conclusions from) in the light of Blumenschine's empirical observations. "All this adds up to a complete lack of evidence for scavenging at Combe Grenal. In fact, because equid remains do not fit the expected skulls-plus-distal-limbs pattern, because large bovids and equids were butchered by cutting rather than hacking through desiccated tissue, because the cutmarks on these animals are concentrated on the meatiest parts of the body, and because these equids' ages indicate that they were hunted, there is considerable evidence that large animals were being killed regularly. Scavenging, if it occurred, was apparently too rare to leave a recognisable mark in the archaeological record....data from elsewhere in Europe are entirely in agreement with this conclusion. There are data that indicate that Middle Palaeolithic people were capable of killing very dangerous game" (Chase 1988; p 229-230). For example, the presence of only the skull, foot and tail bones of a leopard at Hortus (Southeast France) suggest that it was hunted for it~~'~~s hide (DeLumley 1972; in Chase 1988).

At some sites in the Middle Palaeolithic large-sized animals were killed in vast numbers. The most celebrated example is at Mauran in the French Pyrenees where Gerard & David (1982; in Chase 1988) recorded a minimum number of individuals of 108 *Bos* and *Bison*. This is not necessarily a single hunt episode, but the dominance of a single species is not representative of the carcass cross-section which would be expected to be available for scavenging. Bosinski (1988; in discussion with Chase; p

232) asks it to be acknowledged that "Although Chase mentioned exceptions, the general rule is for there to be mixed game and very low specialisation [in the Middle Palaeolithic]".

At Gabasa 1 Cave, in the Pyrenees, red deer exhibits the most long bones broken open by man (it also has the greatest number of diaphyses recovered!). Breakage of red deer and horse long bones was attained by striking the diaphysis closest to the epiphysis. The distal humerus received breaking blows to the lateral/medial face(s). On the distal femur they were near the distal epiphysis and on the proximal and lateral/medial faces of the diaphyses. (Fernanda Blasco 1997).

It is clear that the Neanderthals had primary access to adult red deer and horses from: the position and morphological characteristics of the cut and tooth marks on the bones; the detection of butchery marks associated with defleshing of 'high profitability' parts (e.g. humerus and femur) with subsequent breakage for marrow extraction; and the fact that these tasks were carried out on whole or the best parts of carcasses. The presence and position of tooth marks may indicate predators feeding on the Neanderthal's leftovers. (Fernanda Blasco 1997).

The subsistence pattern inferred from the faunal remains at Gabasa 1 is one of hunting, or primary access scavenging (primarily adult and very young red deer and horse), followed by exhaustive exploitation of the carcasses Fernanda Blasco (1997).

Stiner (1994) interprets zoo-archaeological evidence at Mousterian sites in Italy prior to 55,000ya as indicating episodes of pure scavenging. Accordingly this would place the subsistence shift between early and late Neanderthals, rather than Neanderthals and EAMH. Mellars (1996) observes that the representation of the primary species of the faunal assemblages at rock shelters is only 60-70% during the Middle Palaeolithic, compared to over 90% in the Upper Palaeolithic (but Mellars does not look for trends within the Middle Palaeolithic). This is interpreted as the outcome of the less specialised acquisition of game by the Neanderthals (i.e. their going for the most abundant prey rather than being more selective).

"We are therefore forced to conclude that the Middle Palaeolithic peoples of Europe were fully capable of systematically hunting large animals" (Chase 1988; p 231).

4.2.3 - Archaeological Methodology and Sampling Bias:

Very recently the 'selective' methodology of analysing and interpreting faunal assemblages has been called into question. This new research could cause the reinvestigation of body part representation at important sites leading to an alteration in the presently held views regarding the scavenging versus hunting debate. The analysis of faunal material excavated from Mousterian Levels at Kobeh Cave, in Iran's Zagros mountains (Marean & Kim 1998) and Die Kelders Cave, South Africa (Marean 1998) reveal a skeletal element profile that is dominated by the meatiest limb parts. These authors found that by finding the co-joining edges and refitting shaft fragments of long bones, the number of fragments identifiable to skeletal element increased. This has a profound impact on body part representation; since isolated small fragments are usually ignored.

At Kobeh Cave the meat bearing upper limb bones have high frequencies of cut marks on the near-epiphyses and mid-shafts (i.e. away from the joints). Marean and Kim (1998) take this as evidence for butchery aimed at flesh removal; which in turn implies that the hominids were getting primary (or at least very early) access to carcasses with significant amounts of fresh still attached. Carnivore access was subsequent to that of the hominids.

Marean & Kim (1998) criticise various workers for ignoring mid-shafts in their analyses of assemblages and thus obtaining artificially low cut mark frequencies (e.g. Binford 1985; Chase 1986; Stiner 1994); as the fragments most representative of flesh removal by hominids were excluded. Mid-shaft portions are important as they have taphonomically high survival rate; being resistant to weathering because of their high density and carnivores as they lack grease/spongy bone). Metacarpal and metatarsal ends are also dense and contain little or no grease/spongy bone; so are not susceptible to these destructive forces and will survive more readily than tibial or femoral ends. However, without long bone mid-shaft refitting, the majority of workers draw their conclusions regarding skeletal-element patterns from data based on the ends of these bones (e.g. Binford 1988 at Grotte Vaufrey; Chase 1986 at Combe Grenal; Evins 1982 at Shanidar; all in Marean & Kim 1998). Without the mid-shaft information the question of hominid/carnivore overlap is much harder to tackle; the epiphyseal portions studied by the aforementioned authors are not useful in resolving this question.

"Analysis of surface modification (cut marks, hammerstone percussion marks, and carnivore tooth marks) further substantiates a pattern of hunting by the Middle Palaeolithic hominids that inhabited Kobeh Cave" (Marean & Kim 1998; S79).

The Kobeh Cave pattern of a high abundance of flesh-yielding long bones is unique among the published Middle Palaeolithic/Stone Age Assemblages. If the mid shaft data are withdrawn from its analysis, a head-and-foot dominated pattern emerges as is characteristic of other sites. Marean & Kim (1998) conclude that the patterns seen elsewhere (head or head-and-foot dominated) are an artefact of methodology by researchers today; as opposed to the action of hominids and carnivores in the past.

"Clearly the Kobeh hominids regularly transported the highest-quality limb bones from the encounter site to the cave....considered in the light of the rarity of carnivore tooth marks on shafts, makes regular hunting the best explanation for the Kobeh pattern" (Marean & Kim 1998; S90).

"....we conclude that there was no evidence for regular scavenging, either opportunistic or obligate, during the Middle Stone Age or Middle Palaeolithic. Further more, our survey....has failed to find a single Eurasian cave or rock shelter site at which detailed refitting and identification of all the shaft fragments have been conducted....evidence for faunal exploitation by Middle Palaeolithic or Middle Stone Age hominids is seriously deficient" (Marean & Kim 1998; S92).

Klein (1998) and Cruz-Uribe (1998) point out that at Klasies River Mouth the head-and-foot bias is only apparent among larger animals and, even when only considering epiphysis presence, small-medium sized animals are represented by limb bones mostly. This has been interpreted by Binford (1984) as signifying that the hominids were scavenging larger animals and hunting smaller ones. Such a contrast is seen elsewhere too and is often more striking. An alternative explanation for the better representation of smaller animals by limb bones is that of differential transport of body parts by hominids determined by the size of the animal.

4.3 - Generalised Hunting:

"Certainly Middle Palaeolithic peoples appear to have been perfectly competent hunters of big game" and "...sharing was a regular feature of Middle Palaeolithic economic life" and Middle and Upper Palaeolithic subsistence patterns appear to be "remarkable similar" (Chase 1989; p 333).

The four principal animal species in the Mousterian faunal assemblages of Southwest France are: horse, reindeer, red deer, and bovids (aurochs & bison). Most sites also contain sporadic remains of other species, such as ibex, rhinoceros, and woolly mammoth, which implies an 'eclectic' exploitation methodology by hominids (Mellars 1996). At Combe Grenal the frequencies of the major herbivores present in assemblages alter corresponding to climatic and environmental fluctuations during the early last glacial; thus the species proportions are unlikely to be under strict hominid control (Mellars 1996). Elsewhere there could be a combination of human and climatic influences at work.

4.3.1 - Cliff-Fall/Driving and Ambushing:

Levine (1983; in Chase 1989) states that the age distribution of equids at Combe Grenal reflects a 'life assemblage' model, implying a 'catastrophic' death scenario. He sees the Dordogne, with its numerous cliff-lined valleys, as ideal for game drives. La Quina has the richest cliff-bottom assemblage of the area. Also at Mauran (riverside escarpment), Puycelsi (cliff face) animals are envisaged as being driven over such natural features to be subsequently retrieved by hominids (Jelinek et al 1988; in Mellars

1996). The best evidence comes from the later Rissian levels at Cotte de St Brelade, Jersey, where cut marks are clear and bones are piled up into heaps within the cavern (Scott 1980, 1986, 1989; in Mellars 1996). This is only in certain levels, and therefore is not due to a long-term gradual accumulation of random falls.

However, Frison (1978; in Stiner 1994) states that on the Great Plains of North America very few mass kill sites can be interpreted as 'jumps' resulting from herds being driven off cliffs by humans; this tactic being a late and limited development. Trapping methods using natural features (e.g. box canyons) are more usual. The Middle Palaeolithic sites of Breuil and Sant'Agostino are located near a natural bottleneck and small amphitheatre-like canyon, both of which are suitable for ambushing (Stiner 1994). Due to this proximity Breuil's assemblage has the full anatomical parts range; transport constraints being minimal over such short distances.

Kuhn (1998) also suggests that the size of hunting party would have been of substantial influence on success. Groups are able to chase, surround, and ambush making dispatch of the animal easier; whereas the lone hunter has to rely more heavily on technology. Many analyses concentrate on the faunal assemblages alone and do not consider the influence of group size, technology, or distance on their accumulation. Nor do they take the biomechanical or physiological factors operating to impose limits on hominid physical capabilities, which are to be the focus of this thesis.

Kuhn's (1998) point is demonstrated by the fact that all 'traditional' Eskimo groups today use tactical landscape methodology (encounter technique) combined with communal hunting (organisational technique) as the primary way of acquiring their main terrestrial prey, the caribou (Marean's terms 1997). The passive/active use of traps is common (natural features like gullies and cliffs, or cultural like snares and pitfalls) whereby the landscape becomes a weapon. Routed or interception hunts are also practised. Prey may be driven into a river or lake and subsequently dispatched from a boat; or intercepted and forced down box canyons or constructed traps (Boas 1888, Stoney 1900; Birket-Smith 1929; in Marean 1997). Unlike the Caribou Eskimos, the Nunamuit Eskimos have access to a greater species richness and are able to hunt dall sheep, moose, and smaller items (like the snowshoe hare) as well as caribou.

4.3.2 - Dietary Flexibility:

While it is unlikely that hominids introduced the rabbit and hare remains into the caves of Moscerini or Sant'Agostino; at the former they did collect quantities of marine shellfish bivalves and consume them in the cave, and in the latter tortoises and monk seal were eaten. In Italy the range of resource and land use tactics of the Mousterians overlaps and surpasses that of anatomically modern humans from the late Upper Palaeolithic (Epigravettian in Italy). Neanderthals appear to have been flexible in their foraging strategies both spatially and temporally, and variation in their behaviour is manifest in their responses to the changes in coastal habitats and foraging opportunities over time in Italy. (Stiner 1994; Ch. 6).

Red deer were the principal prey of Middle Palaeolithic hominids in Italy; but in total they consumed 24 species in 8 class sizes (in the late Upper Palaeolithic this diversity was narrowed to 15 species in 6 size classes). Part of the explanation may be in the longer time duration of the Middle Palaeolithic (120-35,000ya compared to the late upper Palaeolithic 20-10,000ya) or in the fact that the late Upper Palaeolithic populations were further from the coast and had less access to marine resources. The Neanderthals ate the species which were naturally abundant within their desired size range (Stiner 1994; Ch. 7). Climatic deterioration at 55,000ya would have caused sea levels to decline leaving the caves high and dry and expanding the diversity of open land floras/faunas, necessitating the observed behavioural shift.

The Mousterian open-air site of Salzgitter-Lebenstedt (northern Germany) was excavated by Tode et al (1952; in Butzer 1971) and is dated to 55,000ya. The faunal assemblage is dominated by reindeer (80 minimum number of individuals) and woolly mammoth (16); but individual animals, such as duck, vulture, perch and other fish, are also present. In South Africa, faunal assemblages of the MSA/LSA layers at Klasies River Mouth Cave (130-75,000ya) and Die Kelders Cave (from 75,000ya) contain the remains of shellfish and marine vertebrates (as would be expected due to their coastal locations). Seal and penguin are common throughout but it is only in the LSA levels that fish and flying sea birds become abundant (Klein 1987). This shift to vastly increased proficiency at fishing and fowling is also evident in the archaeological record as suitable implements become abundant (e.g. gorges and sinkers). Thus, Middle Palaeolithic hominids were capable of limited fishing and fowling. Although Middle Palaeolithic hominids were seemingly not as proficient as their Upper Palaeolithic successors, it should be remembered that the size of a faunal assemblage will affect species abundance, with larger sites having a greater the probability of including more species (Kuhn 1998).

4.4 - The Transition in Subsistence Strategies:

Most Mousterian assemblages, according to Hayden (1993) represent generalised hunter-gatherer adaptations (low population density, hunting and lithic procurement opportunistic, no evidence of food storage, and no evidence for economically based status competition - Butzer 1986; Geneste 1988). In contrast Upper Palaeolithic assemblages are more akin to complex hunter-gatherer adaptations (Higher population densities and reduced mobility, greater resource and extraction and storage capacities, surplus conversion into wealth and status competition - Hayden 1981; Testart 1982).

The late Mousterian sites in Italy show strong prime adult bias, implying that the shift to primarily hunting strategies took place before the transition at 55,000ya. The late Mousterian prime-dominated assemblages are further testimony that stone-tipped projectiles are not pre-requisites for hunting success (Stiner 1994). It is feasible that it was an increase in co-operation which enabled the shift to successful hunting, rather than advances in spear point technologies (Stiner & Kuhn 1994).

At the Italian Middle Palaeolithic sites studied by Stiner (1994) and Stiner & Kuhn (1994) a temporal shift in faunal assemblage composition is noted during the Middle Palaeolithic:

- The average amount of transported parts per red/fallow deer carcass encounter (based on the identification of a minimum number of individual animals) increases through time gradually, with a small 'jump' after 55,000ya.
- There is a reduction in the proportion of head to limb parts transports to caves over time. Prior to 55,000ya there is an abundance of head parts, whereas after this time head components are lower at the level expected for the acquisition of complete prey.
- A bias toward old-adult prey existed before 55,000ya, although late Mousterians 40-35,000ya showed a strong bias toward prime-adult prey. After 55,000ya assemblages indicate a non-selective procurement tactic.

Moscerini and Guitari sites (early Mousterian):

1. Spring/early summer ephemeral occupation; with frequent movement over expansive ranges to increase encounter probability.
2. Low returns from transported parts, an old-biased mortality profile, and head-dominated anatomical patterns indicate heavy reliance on scavenging of deer carcasses.
3. Correlation between animal bones and stone tools shows no relationship (i.e. they are independent). The amount of tools produced was not dependant on the acquisition of game. Scavenging may only have been ancillary relative to the wider foraging activities.

Sant'Agostino and Breuil sites (late Mousterian):

1. Fall/winter occupation; with more long-term settlement and restricted ranging.
2. Higher returns, prime-age bias, and a balanced limb:head composition indicate an emphasis on hunting.
3. There is positive correlation between tool production rate and game acquisition. Thus ungulate hunting was the central activity. Duration of occupation may have been determined by procurement.

Marean & Kim (1998) believe that this scavenging-hunting shift noted by Stiner (1994) and Stiner & Kuhn (1994) in Italy, as identified by a change in skeletal-element representation from head-and-foot to all parts, is false (section 4.2.3). They suggest that the pattern has arisen due to differential bias in assemblage analysis between the representative sites (the former excluding more mid-shaft fragments). Stiner (1998) replies that hominid sites, at which the carnivores are responsible for assemblage modification cannot be determined (including Kobeh Cave) are problematic to analyse as Marean & Kim have done. If the specific carnivore is unidentified then its behavioural tendencies cannot be characterised. Stiner (1998) is critical of their use of experimental data on carnivore activity (section 4.2.1), stating it is unrealistic.

The shift to prime adult-dominated faunas corresponds to increased cold of the last glacial. It would have provided a more reliable access to fat reserves, which would have been important as carbohydrate resources diminished seasonally (sections 2.3.3). This implies a shift to selective/controlled harvesting by the Mousterian hominids, rather than the random encounter scenario envisaged for them. A new balance within the ecological relationship between the hominids and their game species would have to have developed as the hunters began removing the reproductive section of the herd populations. It is likely that hominid omnivory meant that they did not hunt such animals all year round; switching to alternative more readily accessible resources as they became seasonally available. Variations in Mousterian faunal assemblages could just be due to seasonal shifts in foraging strategies displayed at the different sites (Stiner 1994).

Archaic humans were competently hunting large mammals long before the appearance of sophisticated stone or bone projectile points in the archaeological record. This runs contrary to the technologically driven interpretations of the evolutionary progress of hominids. However, the Middle Palaeolithic also lacks the advances in processing-related facilities, such as deep hearths and elaborate specialist tools (e.g. grinders and pounders), seen in the Upper Palaeolithic. These would have reduced processing time and effort, and also increased nutritional yield form resources acquired. Head collection during the Mousterian is greater than in any modern hunter-gatherer context, emphasising the perogative of these hominids to obtain fat reserves (section 8.3). Just because evidence seems to point to scavenging it does not mean that the group could not hunt, and vice versa. Every known extant predator, including humans, engages in both tactics.

4.4.1 - Specialised Hunting:

'Specialisation' is marked the predominance of a particular species in quantitative terms, and in cultural terms implies a preference or deliberate selection of that species as prey over the others available (Mellars 1996; Ch 7).

Evidence at European sites for specialised (single-species) hunting within the Middle Palaeolithic is now thought that there was probably just a natural dominance of the species in the vicinity. This scenario is referred to as 'locational fidelity' (Farizy & Joubert 1991) or 'niche geography' (Binford 1987; both in Soffer 1994).

Mellars (1973; in Chase 1989) proposed that the Dordogne, France showed evidence for specialised hunting of reindeer during the early Upper Palaeolithic. However, this could just be a reflection of a natural abundance of reindeer relative to other species at this time or they may represent groups going to the same location on a seasonal basis as the members know the particular species will be there. Such assemblages are unlikely to be due to random opportunistic scavenging. Examples of evidence for specialisation in game acquisition during the Middle Palaeolithic include: ibex at L'Hortus in France (Pillard 1972); horse at Starosel'e in the Crimea (Klein 1969); and ibex at Repolust Cave in Austria (Chase 1986; all in Clark & Lindly 1989). Full and consistent specialised hunting did not emerge until the late Upper Palaeolithic.

Sally Binford (1968; in Chase 1989) concluded that in the Levant the co-operative hunting of large herbivores on the move from the coastal plains to the highlands began near the end of the Middle Palaeolithic, and would have needed sizeable co-operating bands. There is also evidence at several Middle Palaeolithic sites in Europe for the hunting of large migratory ungulates (e.g. large bovines at Mauran in the French Pyrenees, and reindeer at Abri Pataud, France). If assemblages with large concentrations of a particular herd animal are indications of co-operative hunting then the practice was established within the Middle Palaeolithic, prior to the transition (Chase 1989; p326).

In the assemblages at La Borde, Coudoulos, and Mauran either aurochs or bison account for 93-98% of the fauna present, while reindeer specialisation reaches 99% in certain other Upper Palaeolithic sites (average proportion of the principal prey species in the Middle Palaeolithic is only 60-70%). All are open-air sites whose lithic assemblages are dominated by notched/denticulated tools with heavy duty choppers. Age mortality profiles are catastrophic, hence acquisition was unselective on the part of the hominids; but they were not relying on only the weakest young and old as an attritional profile would suggest. In such instances human specialisation is hard to deny without implying exceptional localised ecological conditions being at work (Mellars 1996).

Girard & David (1982; in Chase 1989) argue that at such specialised sites the large number of animals found in the assemblages indicates either repeated visits to the site to kill these specific animals or a few massive kills which would provide more meat than required to suffice immediate needs. Either way a degree of foresight and anticipation of future requirements is implied. The presence of highly varied excavated pit structures at La Quina, Combe Grenal, La Ferrassie, and Pech de l'Aze are suggestive of the Neanderthal capacity for storage and hence temporal and spatial planning (Jelinek 1994). It is unlikely that they would have been able to survive, within harsh environments with the tool industry assigned to them, without anticipatory capacity of where and when to find food and shelter. It was probably not random chance that brought them back to the same locations over successive years.

Clark & Lindly (1989) propose that the major subsistence threshold was only breached 20,000ya, implying that the above discussion concerns only a relatively minor alterations in hominid behaviour. It marks an acceleration of change in terms of resource base diversification and intensification. Where apparent it is related to stress on the balance with resources due to population expansion (which occurred 20,000y after the shift to an anatomically modern morphology). A qualitative and quantitative change in niche width/species diversity does not occur until the late Upper Palaeolithic when the intensification of food procurement is perceived; in Cantabrian Spain (Clark & Yi 1983), the Perigord of France (White 1985), and the Central Russian Plains (Soffer 1985; all in Clark & Lindly 1989).

"Our best evidence for significant changes in hunting, involving the regular, planned, efficient slaughter of large numbers of herd animals and the taking of elusive or dangerous game, appears around the time of the Last Glacial Maximum (20,000 years BP) , not necessarily at the beginning of the Upper Palaeolithic/Later Stone Age (35-40,000 years BP). There seems to have been a lag of twenty (or more) millennia between the evolution of anatomically modern *H sapiens* and the appearance of large scale, sophisticated hunting, although many of the technological innovations of the early Upper Palaeolithic/Later stone Age (e.g. bone projectile points, blades, standardised and hafted compound tools, etc.) may have been 'pre-adaptations'" (Straus 1987; 148).

4.4.2 - Intercept Versus Encounter Hunting in Southwest Asia:

Due to the length of the Neanderthal-EAMH co-existence in Southwest Asia, this region is very important in discussions attempting to discern behavioural contrasts between the two populations. Shea states that the Mediterranean woodland hominids would have practised 'encounter killing of a wide range of species' (1998; S49). The larger steppe dwelling animals tend to be gregarious and probably had seasonal migration cycles. With the ability to predict the location of substantial numbers of animals, Shea (1998) proposes that intercept hunting (outings limited in both time and space) would have been the norm in the steppe landscape. Animals such as dromedary, wild horse, and ibex are reported at many interior Levantine Mousterian sites (Bar Yosef 1995; In Shea 1998).

Shea's 'hunting technology hypothesis' (1998):

- In woodland environment wooden spears were used. These implements would have been more easily/quickly repaired or resharpened. They could also have functioned as digging sticks in the dense undergrowth.
- Under steppe conditions stone tips were used on spears. These would have increased their stopping power by lacerating muscles. This fact would have offset their high preparation and repair costs It is suggested that the hunters may have manufactured many and stashed them at ambush points ready for later use.

Shea (1998) claims the pattern that emerges from the study of the ratio of Levallois points (retouched or otherwise) to cores (LP/CR) follows the hypothesis' predictions:

- This ratio was found to be lower and less variable in the northern coastal region; and higher and more variable in the southern interior (the difference is statistically significant)
- The coast has fewer points than the interior (the distinction is not statistically significant; which is put down to the northern extension of steppe conditions during the warmer periods blurring the picture)
- North/south contrasts are more pronounced. Levallois points are four times more common in the south (highly statistically significant) This corresponds to the woodland/steppe distinction here during the Upper Pleistocene
- Variance reveals the differences in taxonomic richness between the four sub-regions to be statistically significant (Coastal areas averaging twice the number of species as found in the interior assemblages; but it is recognised that this may simply be a reflection of differential availability of species between the wooded and steppe environments)

Commenting on Shea's (1998) hypothesis Kuhn (1998) suggests quite the reverse link between hunting strategy and spear technology. Encounter hunters face unpredictably 'windows of opportunity' and would therefor benefit from having the most effective weapons at their disposal in order to minimise the likelihood of failure. In contrast for interceptors of gregarious animals at predictable sites who can predict multiple opportunities, spear effectiveness is less critical. (Kuhn doesn't state explicitly but presumably is referring to stone pointed and untipped spears, respectively)

"These data provide no support for a hypothesis of a single uniform chronological direction of change in the LP/CR ratio or of consistent trends in Levantine Mousterian hunting strategies....Rather, there appears to be a mosaic of patterns each possibly reflecting a combination of situational factors and unique histories of human occupation at particular sites" (Shea 1998; S57).

The LP/CR ratios are considerably higher in Neanderthal contexts, indicating a greater spear point production by them. Shea (1998) concludes that this identifies the Neanderthals as emphasising intercept hunting.

"....the Neanderthal and early modern human assemblages exhibit comparable degrees of variability...This suggests that while....strategies for adapting to the Levantine environment differed from each other, both human populations were capable of significant behavioural variability" (Shea 1998; S59).

4.4.3 - Pursuit Hunting by Hominids:

Despite numerous studies and experiments finding evidence for the inefficiency of human running (section 9.1), the ethnographic record details a number of instances where the hunting tactics involve long distance running. Schapera (1930) recorded instances of bushmen running down steenboks and gemsboks during the rainy season and wildebeest and zebra in the hot dry season. Bennett & Zingg (1935) bear witness to the chasing of deer through the mountains of northern Mexico until they collapse from exhaustion by the Tarahumara Indians, who then throttle their prey by hand. Lowrie (1924) and Sollas (1924) note the use of similar pursuit hunting techniques by the Navajo of the American Southwest (pronghorn antelope) and Aborigines in northwestern Australia (kangaroo), respectively. (all in Carrier 1984)

Carrier (1984) suggests that via the combined effects of the evolution of sweating, absence of body hair, independence of breathing cycle from the constraints of locomotor biomechanics, hyperplastic adrenal and thyriod glands, and significant carbohydrate input, man has overcome the high energetic costs of transport and become an endurance runner: "....the fact that humans have exceptional stamina suggests that at some point in the evolution of hominids there was a strong selective pressure for endurance running." Carrier (1984) also suggests that the fossil record reveals hominids to have had the biological equipment to practice endurance predation long before the appearance of complex culture and hunting weapons.

All this seems in direct opposition to the information regarding the inefficiency of human running, relative to walking. Commenting on Carrier (1984) Trinkaus notes an interesting conflict in the evidence with regards to the earlier members of *Homo*. All these early hominids display skeletal hypertrophy which indicates adaptation to high levels of fatigue stress, which could have been caused by protracted chases. However, their short legs would have accentuated the energetic costs. The reduction in skeletal robusticity (signifying a decrease in activity levels) in EAMH coincides with an increase in leg length, which would be more suited to pursuit hunting.

The hairless sweaty condition of man and its high capacity for enabling heat loss during exercise seems to be a key factor for human success at pursuit hunting (Carrier 1984). Such physiological adaptations may have offered a crucial advantage in the heat of the sun over prey with an insulating layer of body hair and a limited surface area for heat loss via panting and created a new predatory niche for *Australopithecus*. Although Carrier does concede that perhaps this ability was not properly realised until the emergence of early *Homo* with his longer, more fully bipedally committed hind limbs.

In comments on Carrier (1984) Scott notes that Old World anthropoids also sweat which suggests that the phenomenon evolved in the forests rather than on the savannah, where its use as a cooling mechanism would appear minimal. This suggests that its original function may have been for pheromone production and release to attract mates; the heat dissipation capacity being a subsequently realised plieotropic effect.

4.4.4 - Comparisons with Extant Predators:

Routine food transport over significant distances by humans distinguishes them from other primates, and links them with carnivore species (Stiner 1994; Ch. 8). Non-human predators gorge at kill sites as they cannot carry that much; unlike humans. Obtaining marrow may be a major incentive to transport certain bone portions, to allow processing at a more secluded location.

1. *Cursorial Predators:* long, usually social, chases of quarry across open habitats. predators, such as wolves, wild dogs, cheetahs, and hyenas, are adapted for endurance and select the weakest as prey (i.e. the young or old) meaning that prime-age adults are absent from the assemblages. (Ballard 1987; in Stiner 1994)
2. *Ambush/Short Chase Predators:* Tactics of the cats involving the use of game trails and natural features to limit escape options of their prey. Usually a solitary exercise, except for lions who use team work to cut off escape routes. Non-selective/living structure mortality profiles are produced as acquisition is based on encounter. (Fox 1984; in Stiner 1994)
3. *Human Social Ambush Predators:* From the late Upper Palaeolithic onwards humans have produced uniform ungulate mortality profiles regardless of varying hunting techniques. Profiles tend to lie in between living structure and prime dominated mortality. Humans are the only predator to regularly produce prime-based mortality profiles, and is a method which maximises fat acquisition. Nunamuits occasionally adopt juvenile-targeting strategies, but this is a response to the need for skins rather than meat *per se*. (Stiner 1994)

4.5 - Neanderthal Group Size and Settlement Patterns:

In the Negev Marks & Friedel (1977; in Clark & Lindly 1989) developed the idea that the Middle Palaeolithic was dominated by a 'radiating' settlement pattern (1 or 2 large residential camps being surrounded by many smaller specialised sites for different activities) with low residential mobility and high logistical mobility (definitions in section 9.3). In the Upper Palaeolithic there was a 'circulating' settlement pattern (composed of many similar sized sites with broader tool inventories) with the inverse mobilities. Henry (1984; in Clark & Lindly 1989) put forward the 'Transhumance model' based on the believed antiquity of modern Bedouin practices, but the archaeological data seems to directly contradict the theoretical movements of the groups.

"Mobility patterns and hunting strategies were essentially the same among all the populations mentioned above [Neanderthals and EAMH of Southwest Asia]. Differences of settlement patterns are of local origin (size of territory, availability of resources, competition)" (Bar-Yosef 1997).

The archaeology of the Russian Plain indicates that the regionally circumscribed opportunistic subsistence strategy of the Middle Palaeolithic gave way to foraging practices which mapped onto resources over expansive areas and involved seasonal group mobility during the Upper Palaeolithic (Soffer 1989; in Soffer 1994). Similar observations have been made in Europe (e.g. Binford 1985; Gamble 1986; in Soffer 1994).

In the 1980's Jelinek proposed that of the different Mousterian faces, the intensively reduced Quina, Ferrassie and Mousterian of Acheulean identified intense and prolonged habitation episodes, while the more expedient Typical and Denticulate forms were evidence of more ephemeral site use (in Clark & Lindly 1989). Hayden (1993) suggests that the relative rarity of Mousterian structural remains is a function of the Neanderthal's greater mobility (due to a less developed technology and resource extraction capacities, hence lower population densities and site frequencies) than Upper Palaeolithic groups.

At (western European) Middle Palaeolithic sites there is generally only evidence for occupation of restricted areas, which implies habitation by small groups (Mellars

1996). Evidence exists for higher population densities and more semi-permanent site occupation in the late Upper Palaeolithic of western Europe, as opposed to smaller frequently mobile preceding groups (Jochim 1983; Mellars 1985; Soffer 1985; all in Mellars 1989). These authors cite this as a strong incentive to define group territories more sharply and formalise reciprocal relations. This could be implicated in the expansion of the amount of material moving significant distances in the Upper relative to the Middle Palaeolithic.

4.6 - Environment, Technology, Subsistence and the Neanderthal - Early Anatomically Modern Human Divide:

So where does all of the above leave us as far as the 'transition' is concerned? It would appear that all of the factors discussed here have little relevance in the debate over the replacement of archaic forms (i.e. Neanderthals principally) by EAMH. Certain aspects, such as the shift from generalised opportunistic hunting/scavenging to competent specialised hunting, are noted as occurring distinctly prior to the transition. Both Neanderthals and EAMH crossed the threshold into the Upper Palaeolithic. Despite this capacity among both groups it is apparent that the rapid expansion of the technological repertoire (e.g. the proliferation of bone tools and ornaments) and the proliferation of artistic endeavours, did not occur until much later in the Upper Palaeolithic. The only change that is agreed to have happened actually at the time of the transition itself is the replacement of the distinctly Neanderthal skeletal and muscular morphology by that of EAMH.

There is substantial evidence for the synchronism of the two species in both Europe and Southwest Asia. Zubrow (1989) calculated that assuming that there were interactions between the two populations and that they can both be modelled demographically with stable populations; a demographic advantage of only a 2% difference in mortality rates results in the extinction of the Neanderthals within 30 generations (or 1,000y)!

But what was the mechanism which caused such a discrepancy between the two populations to arise? As has been shown above, the Neanderthals (or at least the late members of the group) and their EAMH counterparts appear to have had largely comparable technologies and subsistence capabilities. So why did the Neanderthals (or their distinctive morphology) disappear so quickly? It seems increasingly likely, via a process of elimination, that distinguishing factors relating to their relative morphology, physiology, or reproductive strategy should be sought in order to answer this question.

An improvement in one or more of these fields by these later hominids could have given them enough of an advantage. Alternatively, the highly derived Neanderthal system may have worked to their disadvantage as environmental and ecological conditions in western Europe shifted in response to the climatic deterioration (from 29,000ya) towards the cold maximum of the last glacial.

CHAPTER 5

Neanderthal Skeletons and Physiques:

"But although they were short, squat and powerfully built, even as children, the Neanderthals would have looked recognisably human as they carried out their daily activities" (Stringer and Gamble 1993; 95).

5.1 - Overall Body Dimensions of Neanderthals:

Modern high latitude (wider-bodied) populations are heavier for stature than more equatorial ones (sections 6.1 & 6.3). Neanderthals are near the modern upper limit of weight for height, and EAMH specimens are intermediate between higher latitude (but tending towards these) and tropical distributions (Holliday 1997a). Ruff (1994) estimated the difference in stature between Neanderthals and EAMH. The latter were found to be 10cm taller and 3.5kg lighter than Neanderthals:

Neanderthal mean stature = 167cm/5'6" and mean body weight = 73.5kg/162lbs
EAMH means are: 177cm/5'10" and 70kg/154lbs, respectively

Wolpoff (1980) found Neanderthals to be shorter than this; males averaging 5'4" and females only 5'. Trinkaus (1983) obtained values for his Skhul-Qafzeh EAMH sample 7cms taller than that of Ruff (1994); although Neanderthal stature was similar. These differences in estimated heights are probably due to the use of slightly different reference samples. Despite their short stature, European Neanderthals had a large body mass; up to 30% greater than modern high latitude peoples (Ruff et al 1997; in Holliday 1997a).

5.2 - Neanderthal Skeletal Robusticity and Biomechanical Loading:

The Neanderthals are well known for their high levels of skeletal robusticity and cortical thickening of long bones. Trinkaus 1975; Endo & Kimura 1970; and Musgrave 1970 (in Trinkaus 1980) all found Neanderthal postcranial robustness to be within the limits of variation observed in living populations; with the Neanderthals clustering at the upper extreme of the range.

Wolf (1892; in Ruff 1992) was the first to recognise that bone tissue would adapt itself during life to the kinds of mechanical 'loadings' (or forces) place~~s~~d upon the skeleton. x d Femoral and tibial shafts are under bending and torsion stress during locomotion; the force levels increasing as activity levels do (Saunders et al 1953; Schwartz et al 1964; in Trinkaus 1983). Long bones increase in cross-sectional area and density to resist such forces (Curry 1970; Tschantz & Rutishauser 1967; in Trinkaus 1983).

Large articulation surfaces reflect habitually high levels of joint reaction force. This increase in surface area would dissipate the pressure acting on the articular cartilage. Thus, the joint's wear and tear would be reduced and its life prolonged (Trias 1961; l Radin & Paul 1971; in Trinkaus 1980).

Cortical bone hypertrophy is produced by bone remodelling via endosteal and subperiosteal bone apposition and increased intracortical density. It occurs under conditions of normal fracture and repair (e.g. Chamay & Tschantz 1972; Goodship et al 1979; in Trinkaus 1987). The process is initiated by any stress on bone which creates a strain in excess of the bone's elastic limit which results in plastic deformation (Currey 1970; in Trinkaus 1987).

"Short term, peak loads can be responsible....but repetitive intermittent mechanical loading, especially given the low resistance of bone to fatigue, is much more likely to produce significant hypertrophy of diaphyseal cortical bone" (Trinkaus 1987; 133).

5.3 - Contrasts in Lower Limb Robusticity Between Neanderthals and Modern Humans:

The robusticity and dimensional expansion of Neanderthal femur and tibia shafts are at/exceed the limits of the modern range; which according to Trinkaus (1989) reflects the Neanderthals' strength and endurance. In contrast EAMH are less robust and their cortical expansion is limited to pilasters on the trailing edge of their leg long bones. This has been translated by Trinkaus (1989) as due to the Neanderthals experiencing stresses from all sides during locomotion, while the EAMH stresses are unidirectional (like modern Hunter Gatherers who walk long distances and have similar buttressing of their femurs).

Biomechanical analysis of Neanderthal tibial strength (bending and torsion) showed it to be twice as strong when scaled against its own length than that of modern humans. This is due to their amygdaloid (almond shaped) cross-section and the magnitude/distribution of cortical bone thickness (Lovejoy & Trinkaus 1980; in Aiello & Dean 1990).

The femoral morphology of the Neanderthals have several features which distinguish them from that of the modern version (Kennedy 1983; Trinkaus 1976; in Aiello & Dean 1990):

- Anteroposterior flattening of the shaft. This is reflected in the (virtual) absence of a pilaster; a feature which is pronounced in EAMH specimens.
- Medial convexity of the shaft. Modern femora display lateral convexity.
- A very low point of minimum shaft breadth (the 'waist')
- The cortex is thicker on the medial side at the mid shaft level. Such thickening is on lateral side in modern femora.

Neanderthals also show a distinct pattern of weight transfer through their femora compared to humans today (Aiello & Dean 1990). The load axis (vertical line from the femoral head to the bicondylar plane) intersects the anatomical axis (line running down the length of the shaft) at the distal end of the femur. This intersection is significantly higher up the shaft in modern humans. The load axis also falls between the lateral and medial condyles; whereas in modern humans it lies through or lateral to the lateral condyle. These patterns may reflect greater activity levels among the more archaic hominids or different biomechanical loadings due to their broader trunks.

"A result of strength adaptation combined with limb shortening in this [Neanderthal] sample can be seen in the femur shaft curvature in the anterior-posterior plane (of shaft bowing). Shaft bowing is a direct response to muscle force - in this case, a combination of marked muscularity and body weight relative to the shortened limbs" (Wolpoff 1980; 286).

Neanderthal femora also exhibit 'consistently large' gluteal ridges and a high frequency (8/12 European specimens) of hypotrochanteric fossa (Aiello & Dean 1990). This is said to be indicative of the large size, strength, and power of their muscles (sections 9.7 & 9.11.1). Among the Neanderthals these fossa take on a distinct configuration, occurring within the gluteal ridge. This is also found in Neanderthal juveniles, such as La Ferrassie 6. The proximal shaft of Neanderthal femora is less flattened than earlier forms and more rounded like the modern condition. Their ratios of both head size and midshaft circumference to femoral shaft length fall within modern ranges of variation; but lie at the upper end above modern means.

While during the early Last Glacial there are shifts in cranio-facial and dental morphology and size (implying a reduction in paramasticatory loading among later Neanderthals); a parallel trend in postcranial reduction of robusticity is not apparent. The latest Neanderthals (St Cesaire, Vindija, Upper levels at Shanidar) are postcranially indistinguishable from the earlier 'classic' Neanderthals. While variation is present there is no evidence of a temporal trend according to these authors (Wolpoff 1981; Smith 1982; in Trinkaus 1983).

European Neanderthals have very short femora relative to femoral head size, below the Aleut-Eskimo range of variation. Middle Eastern Neanderthals and EAMH samples from both regions have longer femora relative to femoral head size, but are closer to modern high latitude than tropical populations. The latter, particularly Nilotic peoples, tend to have the smaller femoral heads relative to their shaft length. The Skhul-Qafzeh femora are clearly longer relative to head size (within the range of modern tropical sample). As well as the ecogeographical patterning noted here, femoral head size/robusticity will also be responsive to biomechanical stresses.

Cross-sectional analyses of the shaft walls of the femora and tibia indicate that across the transition there was a marked reduction in the amount of bone present (Endo & Kimura 1970; Lovejoy and Trinkaus 1980; in Trinkaus 1983). Ruff et al (1993; in Trinkaus & Hilton 1996) recorded a continuing trend in decreasing robusticity in overall femoral and tibial diaphyseal robusticity from EAMH towards the condition seen today. The EAMH skeletons recovered from Combe Capelle and Grotte des Enfants show a substantial reduction in the features associated with muscularity and their shaft diameters and articular surfaces are smaller relative to limb length compared to those of the Neanderthals (Wolpoff 1980; 344).

5.3.1 - The Neanderthal Pelvis:

All the available measurements of the 95,000 year old Qafzeh 9 pelvis (most significantly those of the diagnostic obturator region) fall within the modern range. The modern pubic ramus is short, stout and has a rounded cross-section. The Skhul IV and IX pelves (100,000ya) are reported to also have a 'virtually modern appearance', being within the modern *H sapiens* cluster in every measurable aspect (Rak 1990).

The Neanderthal skeleton from Kebara (65-60,000ya) has certain features of the lowermost lumbar vertebra are only found among fully bipedal modern humans, as they relate to loading above the lumbo-sacral joint when fully erect (Arensburg 1989). The Kebara pelvis differs significantly from both Qafzeh 9 and human pelves today. Like other Neanderthal pelves it has a very long and slender superior ilio-pubic ramus which is positioned anteriorly, with a distinct outline to its cross-section. Other features imply a degree of lateral rotation of the hip joint when walking (Arensburg 1989). These are absent in the Skhul/Qafzeh sample. "They [the morphological differences between the pelves] apparently reflect differences in posture and locomotion" (Rak 1990; p 331).

"The length of the superior pubic ramus is found to stem from a more externally rotated innominate bone and not, as generally assumed, from the larger pelvic inlet. It is suggested that the uniqueness of the Neanderthal pelvis may be attributable to locomotion and posture related biomechanics rather than to obstetric requirements....the elongated superior pubic ramus....has no bearing upon the size of the Neanderthal pelvic inlet, as previously speculated" (Rak & Arensburg 1987; p 227).

In Neanderthals (relative to the modern human form) the inlet rim of the pubic ramus is situated more anteriorly relative to the acetabula, which is due to the innominate bones being more externally rotated. This puts the sacrum and symphysis pubis further forward in the pelvis, with the former being very close to the body of the ischium.

It has been proposed that there was a postural difference between Neanderthals and EAMH in terms of where the centre of gravity acted. Rak is quoted by Shreeve (1995) and Bilsborough (pers. comm.) as stating that, as a consequence of different pelvic dimensions, the centre of gravity came down between the hip joints in Neanderthals. This means that the hip joints of the Neanderthals bore the entire weight of their upper bodies directly, which would have been very jarring during any form of activity. In the modern configuration the centre of gravity lies slightly behind the hip joints, with the pronounced columns of muscles either side of the spine acting as shock absorbers. Rak suggests that this may have impaired Neanderthals' locomotor efficiency relative to the modern form; but in what way is omitted from the discussion.

Previous explanations for the long pubic ramus concentrated on obstetrics and tended to ignore the fact that the feature is also present in male Neanderthals. Rosenburg's (1986) estimations of lengths of the pubic ramus of males (La Ferrassie 1, Shanidar 1 & 3) are greater than those of females (Tabun C1, Krapina 208). In recent human skeletal samples from populations of different heights and weights; relative length of the pubic ramus was shorter in males but it was absolutely longer. The observed Neanderthal pattern would be predicted from these findings. The sexual dimorphism in this character fits Lande's model (1980; in Rosenburg 1986) regarding homologous characters, in which selection only acts on one sex. In this instance selection is on the female (obstetric demands) but males show a 'correlated response'. Hence the males' pubic ramus is longer than would be expected if selective pressures were based purely on locomotor efficiency.

5.3.2 - Neanderthal Foot Structure and Functional Morphology:

The most complete Neanderthal feet are: La Ferrassie1 & 2, Kiik Koba 1, Shanidar 1, and Tabun C1 (Trinkaus 1983). They are regarded as fully adapted to bipedalism, including having fully adducted big toes. The only differences between Neanderthal and living human pedal morphologies relate to greater robusticity in Neanderthals (i.e. large articular dimensions; enlarged regions for musculo-ligamentous attachments; elevated diaphyseal robusticity indices of the proximal phalanges) and their proximal phalangeal proportions (the first being short relative to other foot length dimensions among Neanderthals).

Many of the areas of attachment of the plantar surface's muscles and ligaments are more strongly developed in the Neanderthal foot relative to the modern one. The first metatarsals and all five proximal phalanges are more robust than modern ones. Neanderthal proximal phalanges are wider than they are high, which is the opposite of the modern dimensions, and is possible due to increased mediolateral bending stress experienced by the Neanderthal bones (Trinkaus 1983).

Neanderthals have moderately shorter proximal pedal phalanges with the phalanges of digits 2-4 having significantly wider (i.e. mediolaterally) diaphyses compared to recent humans. EAMH show intermediate values. According to Trinkaus & Hilton (1996) this suggests that:

- There was a higher level and frequency of mediolateral loading of the anterior foot during the Upper Pleistocene, related to higher activity levels.
- A higher level of robusticity of the anterior foot with elevated levels of dorsoplantar stress on the phalanges being resisted by extensor and flexor tendon tension, and the mediolateral and torsion stresses being resisted by the increased diaphyseal breadth.

Overall these findings comply with other studies, showing a reduction in locomotor anatomy robusticity, and by inference activity levels, through the later Upper Pleistocene and Holocene. There also exists the possibility that there as a change in lower limb loading patterns with the emergence of modern humans.

The large breadths of Neanderthal foot bones is thought to be a response to habitually great levels of biomechanical loading. The anterior foot of habitually unshod people today is more mediolaterally spread, often with a gap between the hallux and second toe (Barnicott & Hardy 1955; in Trinkaus & Hilton 1996). The middle three toes are found to be more important in traction generation and ground reaction force absorption in the push off phase. Contrasts in Neanderthal and recent humans feet may be a reflection on this.

Hilton (1994; in Trinkaus & Hilton 1996) showed that burden carrying increases ground reaction force. Today burdened foragers increase their speed by increasing step cadence. Since in running there is a decreased number of load intervals but ground reaction force is increased during mid-stance and push-off, Bramble (1990 &1991; in Trinkaus & Hilton 1996) was led to conclude that archaic humans utilised high levels of running in daily activities.

5.4 - Aspects of the Neanderthal Upper Body:

Schaafhausen (1858; in Trinkaus 1983) remarked that the thicker and heavier ribs of the Neanderthals were likely the consequence of the hypertrophy of their shoulder and back muscles which insert onto the ribs. Neanderthals also had exceptionally large pectoralis major tuberosities (well above the size range seen in European Upper Palaeolithic individuals and humans today), indicating that they had pronounced chest muscle development.

According to Trinkaus (1983 & 1989) the archaic-modern transition shows a marked decrease in the musculature of the upper limb (i.e. identifiable reductions in the size of muscular insertions). This phenomenon is most pronounced in the pectoralis major, latissimus dorsi, teres major on the proximal humerus, pronator quadratus on the distal ulna, opponens muscles on the metacarpals, and extrinsic flexors on the distal phalanges. There is not a marked change in forearm and hand shaft robusticity (in terms of external shaft dimensions or cortical thickness relative to length).

European Neanderthals exhibit robusticity in the tuberosities where muscles attach, in those features which are associated with supination and pronation. It is possible to increase the moment arms for the pronator/supinator muscles by increasing the inter osseous space; which is achieved by accentuating the curvature of the radial shaft. A comparison of the indices of curvature of the radius in Neanderthals and EAMH reveals that their ranges of variation do not overlap. This would indicate a reduction in the ability to powerfully pronate and supinate the forearm across the transition (Trinkaus 1983).

There is a reduction in scapula breadth (with associated smaller rotator cuff muscles and reduced rotary lever arms for the trapesius muscle - Doyle 1977 in Trinkaus 1983) and the height of the glenoid fossa/humeral head which implies that lower joint reaction forces were acting and that there was an increased use of the arm in an externally rotated position. Alterations in the articular orientation at the elbow (e.g. the ulna trochlear notch changed from a more directly anterior to an antero-proximal orientation, which modern humans have) indicate a shift in the average habitual peak-loaded position; from a more flexed to a more extended one. (Trinkaus 1989)

Neanderthals also show a much greater degree of bilateral asymmetry in their upper limb bones strength than modern samples, of which professional tennis players represent the upper extreme. This is evidence of a significant specialisation in use of a single arm (Trinkaus 1989).

This shift is perceived by Trinkaus (1989) to coincide with the early Upper Palaeolithic appearance of throwing projectiles of haftable bone and stone points, which contrast with the Middle Palaeolithic's wooden 'thrusting' spears with thick/wide stone points (section 3.7). Whether Neanderthal spears were of Trinkaus' (1989) thrusting type or the heavy wooden javelin variety described by Dennell (1987) the upper body activity involved would have had bearing on gluteal muscle development (section 9.7.1). If the gluteus maximus acts to maintain posture during upper body activity; it should follow that this marked asymmetry seen in the upper limb, and its inferred heavy one-handed bias, would have demanded substantial development of the gluteus maximus.

5.4.1 - The Neanderthal Hand:

Overall hand proportions are 'indistinguishable' from those of more recent humans (Musgrave 1971; in Trinkaus 1983). Certain minor differences muscularity and the sub-equal length of the Neanderthal thumb phalanges (Trinkaus 1989) indicate that the effectiveness of the precision grip is sacrificed in favour of increasing the mechanical advantage of short thenar muscles for a strong power grip (Trinkaus 1983). The tuberosities on the distal phalanges which support the nails are pronounced and semi-circular in Neanderthals. Such enlargement, most marked on middle digits, implies the considerable force was habitually exerted through the fingertips. Thus, there has been a shift in emphasis from muscular emphasis across the proximal phalanx (i.e. in a power grip) to across the distal phalanx (i.e. the precision grip). However, the total range of movement of the Neanderthal thumb appears to have been at least equal to, or possibly greater than, that of anatomically modern humans (Trinkaus 1983).

5.5 - Skeletal Trauma Among the Neanderthals:

Neanderthal remains show a high frequency of traumatic lesions and post-traumatic degenerative changes with a distinct anatomical distribution. At least one defect, whether major or minor, can be found on almost every reasonably complete Neanderthal partial skeleton aged past about 25 years. Neanderthals also suffered a very high incidence of degenerative joint disease. These findings are indicative of a very stressful lifestyle with high risks of attaining physical injury. (Stringer & Gamble 1993; Berger & Trinkaus 1995) eburnation and Schmorl's nodes of La Chapelle-aux-Saints skeleton. This pattern observed in La Chapelle-aux-Saints was compared to a sample of modern Euro-American male vertebral columns (from the Maxwell Museum collections at the University of New Mexico) and Inuits (Stewart 1979) and prehistoric southern Amerindians (Bridges 1994; both in Dawson & Trinkaus 1997); but was markedly different, particularly in its level of degeneration being so high in this vertebral region. Dawson & Trinkaus (1997) conclude that the osteoarthritis noted on this Neanderthal could be due to an atypical distribution of habitual vertebral loading (perhaps pronounced activity levels such as in burden carrying); but the experience of localised trauma with subsequent post-traumatic degeneration is more likely.

5.5.1 - Neanderthal Injury and Mobility:

The Neanderthals exhibit few pelvic/leg injuries; none that are evident would have impeded locomotion. Those that are present are not healed injuries, which implies individual mobility was vital and that it continued despite any injuries to the lower limb (Trinkaus 1985; in Trinkaus 1989). There is also a distinct lack of older Neanderthal individuals. Assuming these people were highly mobile foragers, these two facts suggest to Berger & Trinkaus (1995) that the aged and injured, no longer ably to keep pace with the group, were routinely left behind to die (in localities where they have not been preserved or found); thus group mobility was not sacrificed for the survival of one individual. There is also a reduction in the degree and frequency of trauma suffered by the available specimens indicating that the early moderns achieved lower levels of risk taking (Trinkaus 1989).

5.6 - Sexual Dimorphism Among Neanderthal Skeletons and its Implications:

Some studies have claimed that there was a pattern of progressive decrease in sexual dimorphism towards the modern state (e.g. Smith 1980; Brace 1973; Wolpoff 1976; and Frayer 1980; in Trinkaus 1980).

" Neanderthal sexual size dimorphism , both within single site samples and in the total sexable sample, is virtually the same as that of recent human samples. Furthermore, despite a tendency towards more robust limbs, the Neanderthals exhibit sexual dimorphism in limb bone shaft and articular robusticity similar to that of modern samples" (Trinkaus 1980; p 377).

Cranial and postcranial evidence from Atapuerca, Spain, on a sample of remains dated to 3-200,000ya also reveals a pattern comparable to that seen today (Arsuaga et al 1997). The remains are assigned to *H heidelbergensis* (considered ancestral to the 'classic' Neanderthals) and therefor show that the modern degree of sexual dimorphism in skeletal dimensions has been present for a considerable stretch of time.

However, the fact still remains that levels of robusticity in Neanderthals and other archaic humans were distinctly higher than today. A form of sexual division of labour can be assumed due to the constraints of child bearing, but analogies based on what is seen today are probably wrong. Archaic females are more robust than women today, which implies that they engaged in higher activity levels and suffered greater biomechanical stress (Trinkaus 1980).

5.7 - The Evolution of an Anatomically Modern Postcranial Morphology:

Proximal and distal parts of *H erectus* femora are poorly represented in the fossil record, but according to Kennedy (1984) their articular proportions do not differ significantly from those seen in recent humans.

Omo 1 from Member 1 of the Kibbish Formation, Omo River Valley, Ethiopia has been dated by Uranium Thorium ratios to 130,000ya (Butzer et al 1969; in Kennedy 1984). It is the oldest femoral specimen showing the full suite of anatomically modern characters. From Broken Hill (now Kabwe), Zambia five femoral fragments from at least two individuals have been recovered. Clark (1970; in Kennedy 1984) has identified the associated stone tools as being of the Sangoan Industry of the Middle Stone Age. Various datings have been made for the fossils placing them somewhere between 110,000ya (Bada et al 1974) and 125,000ya (Hendey 1974; both in Kennedy 1984).

Kennedy (1984) conducted a multivariate analysis including Kabwe, *H erectus* and male and female Romano-British controls (the Omo sample was left out due to its fragmentary nature). On the bivariate plot there was a clear discrimination between *H erectus* and the rest. A study of shaft breadth indices (i.e. as a % of length) showed the control femoral profile to have a maximum shaft roundness (highest index) to be at midshaft level, below which increasing lateral expansion produced successively lower indices down the shaft. Data from Kabwe and Omo I generally conform to this pattern. The pattern in *H erectus* is very different, with mediolateral shaft constriction occurring at a much lower level. *H erectus* indices increase with distance down the shaft. (section 5.3)

The E691 tibia from Kabwe, which is associated with the E689 femoral portions, is 409mm long. This value is long and above the control means (355.2mm). The Kabwe tibia is 5 standard deviations above the Neanderthal mean (of 325.5mm) and outside their documented range of variation (Kennedy 1984). The Kabwe femoral heads are large and above the male control mean. Head size is highly dimorphic in the control samples, so it is assumed that Kabwe remains represent males. The bicondylar breadth of E689 is wide and well above the male control mean. Both specimens have long femoral necks (above the male control mean).

The conclusion drawn by Kennedy (1984) was that essentially modern femoral morphology had developed in both east and south Africa prior to 100,000ya. Kabwe and Omo I have overall sapient shapes with their maximum mediolateral constriction, or 'waist', at mid shaft level. Currently available data on shaft articular proportions showed little change from *H erectus* to modern *H sapiens*. Europeans show a derived pattern. Despite their large articular surfaces (similar to that seen in Neanderthals) the Kabwe sample's lower limb proportions does not show distal limb shortening (unlike Neanderthals). Kabwe femoral and tibial shafts do show cortical thickening reminiscent of *H erectus*. The Omo and Kabwe specimens do not exhibit the characteristic marked antero-posterior shaft bowing and large articular sizes relative to shaft length of the Neanderthals.

5.8 - Comparing Lower Limb Proportions and Lengths Between Neanderthals, Early Anatomically Modern and Living Human Groups:

European Neanderthals have lower brachial (max radial length/max humeral length x 100) and crural (max tibial/bicondylar femoral length x 100) indices, lower limb/trunk ratios and deeper chests antero-posteriorly than are shown by their more modern-looking contemporaries/successors. Such features are widely recognised as the morphological manifestations of their adaptations to the cold climate during the Last Glacial (e.g. Holliday 1997a & 1997b; Ruff 1994; Holliday & Trinkaus 1994).

Modern equatorial populations have longer tibia relative to femora than higher latitude populations. WT 15000 and the Kabwe sample have very long tibia relative to femora, indicating relatively long lower limbs (ratio of radius to humeral length also very high for WT 15000). Both Middle Eastern and European Neanderthals have very short relative tibial lengths, thus shorter limbs. In Ruff's (1994) terms these are the 'hyper-tropical' and 'hyper-arctic' conditions respectively, with EAMH sample taking an intermediate stance. Holliday's (1997a) study (using trunk height and width, limb proportions and body mass data) found that the Early Upper Palaeolithic (i.e. EAMH) sample has closer affinities with recent Africans, while the Neanderthals, Late Upper Palaeolithic and Mesolithic populations ally with modern Europeans. (sections 6.1 & 6.3)

It can be seen in Table 1 that male Neanderthals have both tibial and femoral lengths above the mean values of cold-dwelling Lapps and Eskimos. The short tibia of Spy 2 is the only exception. All specimens therefor, including Spy 2, have longer legs than these living groups. Even male San Bushmen, mobile foragers of the Kalahari, have a shorter mean leg length than all Neanderthals, again except Spy 2. Their mean femoral length is shorter than all Neanderthals, and only Spy 2 and La Chapelle-aux-Saints 1 have tibia lengths shorter than the San mean. It should be noted that there is some doubt regarding the sex of Spy 2 and it may be female.

	Tibial Length	*Femoral Length*	*Leg length*
European Neanderthals			
M (n=4)	33.1-37.0	42.3-46.5	75.4-82.8
F (n=1)	30.1-31.1	40.1-41.1	70.9-71.8
Southeast Asian Neanderthals			
M (n=5)	35.5-38.6	42.2-48.3	81.3-86.8
F (n=2)	30.0-31.9	38.4-41.6	68.4-72.9
Early Anatomically Modern Humans			
M (n=5)	40.5-43.4	47.5-51.5	88.0-92.7
F (n=3)	34.5-35.7	43.47.6	78.0
Living Humans			
Lapps (Norway)			
M	32.5	41.0	73.5
F	30.0	38.1	68.1
Eskimos (Alaska)			
M	33.1	40.8	73.9
F	30.9	38.0	68.9
San Bushmen			
M	34.8	41.3	76.1
F	32.3	38.8	71.1
Pygmies (Africa)			
M	32.4	37.9	70.3
F	30.8	36.0	66.8
Bantus (S Africa)			
M	38.8	44.9	83.7
F	35.5	41.2	76.7
Egyptians			
M	38.7	45.3	84.0
F	35.4	42.1	77.5

Table 1: Lower Limb Proportions of fossil and living human groups (M = male; F = female). The living groups' values are means as reproduced in Trinkaus (1981; 202-203). The full range of variation is shown for the fossil groups to include all specimens recorded by Vandermeersch (1981; 253 & 261), Ruff (1994; 83), Kennedy (1984;104), Trinkaus (1981; 190-191 & 194-195).

The even smaller sample size of female Neanderthals makes assessment difficult, but in general overall leg lengths of these fossil specimens are around/above the Lapp and Eskimo means and around/just below the San means. An average Pygmy has shorter legs and leg segments than any Neanderthal of the same sex.

All measurements of EAMH specimens (including Skhul, Qafzeh and Cro Magnon) were above the means of all the living groups under consideration here, although they were closest to the Bantu and Egyptian values. The EAMH range of variation lies above those of the Neanderthals in both sexes, with no overlap. While male Southeast Asian Neanderthals have higher ranges of each value of leg length there is notable overlap with their European counterparts. The limited number of females from each region are comparable in limb proportions.

CHAPTER 6

Cold Adaptation:

Humans adapt to climatic stress via external morphology, physiological mechanisms (both genetic and ontogenetic), and behavioural/cultural changes. Indeed, these other factors may be more important thermoregulatory mechanisms than overall size or shape. Unlike these other factors, body form can be ascertained/reconstructed directly from the fossil record (Ruff 1994). However, this fact should not lead us into the trap of overemphasising its importance and the insights gleaned from it.

6.1 - Ecogeographic Patterning of Body Morphology - Allen's and Bergman's Rules:

These rules (in Ruff 1994) link body form to climate. Those living in colder/higher latitudes tend to be stockier with shorter limbs (especially distal segments) in order to conserve body heat; while tropical inhabitants are thinner, having long extremities to promote heat loss and aid cooling.

Allen's (1877) and Bergman's (1847) Rules are both special cases of a general relationship between surface area (SA) and body mass (BM); in which the surface area to body mass ratio (SA/BM) is maximised in warmer and minimised in colder climates. The SA/BM decreases as a body becomes larger (i.e. increases its linear dimensions). Heat production is taken to be directly proportional to body mass; and heat dissipation to exposed body surface area. Therefor a larger body will have a higher ratio of heat production to dissipation than a smaller body (of the same shape); which is the physiological basis for the clinal variation associated with Bergman's rule. Schmidt-Nielson (1984; in Ruff 1994) stated that any departure from sphericity will increase surface area relative to body mass. Thus, more linear bodies (or longer extremities) will cause an increase in SA/BM; which is the physiological basis for Allen's rule.

6.1.1 - Body Breadth and Thermoregulation:

Ruff (1991) modelled the human body form as a cylinder; with stature for its height, and bi-iliac breadth (maximum mediolateral breadth of the pelvis; measurable in both skeletal and living samples) as the diameter. Populations living in the same environmental conditions will have similar body breadths regardless of differences in their stature (SA/BM is maintained). Those in colder climates will have absolutely broader bodies, while those in warmer climates will be absolutely narrower (giving smaller and larger SA/BM ratios, respectively). Ruff (1991) stated that absolute body breadth may show the strongest relationship to climate of any whole body dimension.

Ruff's (1991) study of 71 living human populations was divided into four ecogeographic groups: sub-Saharan Africans (tropical), Southeast Asians (subtropical), western Europeans (cold-temperate), northern Asian-derived including Eskimos and Apaches (sub-arctic to arctic). In general, in each zone the tallest groups are the relatively thinnest, while the shortest are the relatively stockiest; and those in progressively colder zones are increasingly broad in absolute terms regardless of stature. In other studies absolute bi-iliac breadth correlates strongly with latitude (r = 0.866). Also SA/BM index decreases with latitude (r = -0.649). Ruff's (1991) conclusion is that variation in bi-iliac breadth is the principal driving force in latitudinal changes in overall body mass and SA/BM.

6.1.2 - Limb Length and Thermoregulation:

Increasing the lengths of limbs, but maintaining their diameters, will not increase the SA/BM of the limb itself. However, if the limbs constitute proportionally more of the body mass (i.e. are lengthened relative to trunk length) then SA/BM of the whole body will increase limbs (Robinson 1968). Modern tropical populations have both relatively longer and absolutely narrower limbs than higher latitude peoples, thus increasing SA/BM in two ways (Elveth & Tanner 1976; both in Ruff 1994).

[phrase missing?]

6.2 - Adaptation of a Population's Body Form to a Particular Climatic Regime:

18-15,000ya the first Asian populations crossed the Baring Strait to populate the Americas. Despite this significant length of time Amerindians today display less steep climes in body mass and proportion than is seen in the Old World, even though environmental diversity is as broad in each land mass (Newman 1953; Roberts 1978; in Holliday 1997a). So it is concluded by Holliday (1997a; 426) that "body proportions tend not to be very plastic under natural conditions".

Ecogeographic variations in body shape closely follow expectations when looking at living, recent and fossil hominids. Ruff (1994) concludes that environmental adaptation is 'chiefly responsible' for this convergence in patterning. Evidence indicates that (skeletal) body breadth is more evolutionary conservative than stature, limb length, and distal-proximal limb proportions. Native Americans show much less ecogeographical variation in body breadth than Old World populations do; possibly due to the fact that they have not lived in the more equatorial regions of the New World long enough to demonstrate such adaptations (e.g. Pecos Pueblos Amerindian skeletal sample from New Mexico has a bi-iliac breadth average only fractionally less than the Aleut-Eskimo sample. Body breadth proportions here seem more adapted to the environmental conditions experienced prior to and during migration to the New World (i.e. arctic/sub-arctic).

6.2.1 - Eskimo Body Form:

Man moved into the Arctic only 2-3,000ya. Eskimos are the classic example of a cold adapted population complying with the ecogeographical rules of body form, being short and stocky with low crural and brachial indices. Johnston et al (1982) studied 57 male and 56 female St Lawrence Island Eskimos. US Health Examination Survey data for both black and white Americans was used as reference points. The Eskimos were shorter with lower leg length values, but no difference in sitting height relative to the reference samples was noted. Thus Eskimos have a high ratio of sitting height to overall height.

Lapps (Norway), another cold dwelling population, actually have slightly lower mean brachial and crural indices than Eskimos. Together these populations lie at the lower limit of variation in these indices among living peoples (Trinkaus 1981)

Eskimos also displayed a greater upper arm circumference; but there was no difference in body weight or triceps skinfold thickness. Deviations from the reference data were more pronounced in males rather than females (Johnston et al 1982). Eskimo children and youths have higher proportions of lean body mass than either reference group (section 6.6).

Mann et al (1962) and Beaton (1975 both in Johnston et al 1982) stated that mild nutritional deficiencies may occur among Eskimo populations (section 7.5).

6.2.2 - Pygmy Body Proportions:

The African pygmies represent a major anomaly to the rules of ecogeographic patterning among modern humans since they live in tropical Africa but are short. Addersen (1969; in Shephard 1991) pointed to the morphological contrasts between the Bantu Negroes (Ntomba) and the pygmies (Twa) who live alongside one another under the same jungle environment. Many experimental studies (e.g. Pagezy 1978; Ghesquiere & Karuonen 1981; Strydom & Wyndham 1963; in Shea & Bailey 1996) have failed to find any physiological advantage pygmoid peoples may hold over taller ones under conditions of heat and/or humidity stress. Indeed in certain instances the pygmies became more stressed under the experimental conditions.

"....the proported distinctiveness in body shape in African pygmies compared to other, taller populations arises primarily through allometric changes due to ontogenetic scaling....adult pygmies are proportioned in comparison to other groups just as we would expect, based on their smaller overall size and a general pattern of ontogenetic scaling" (Shea & Bailey 1996; 324-325). sp?

"....the most parsimonious explanation of the changes in body dimensions and specific proportions of the African pygmies examined....is that they are non-adaptive allometric correlates of overall size reduction, and they are not indicative of independent adaptive novelties individually selected for in response to the demands of their rainforest environment" (Shea & Bailey 1996; 331).

The idea that their small size has been selected for under conditions of limited food supply, hence reduced calorie intake, has not been tested directly (section 7.5.3). Bailey & Headland (1991; in Shea & Bailey 1996) state that the tropical rainforest offers only a minimal supply of calories in the form of fats and carbohydrates. In general resources there are poor, dispersed and variable. They believe that people were only able to inhabit the rainforest on a more permanent basis once ways of enhancing its productive capacity had been developed (e.g. plant domestication).

6.3 - General Implications for Regional Variation in Body Form Among Hominids:

Badoux (1969; translation by Holliday 1997) stated that "since modern humans obey ecological rules, there is absolutely no reason to presume this would not have been the same for fossil humans."

Neanderthal remains are sufficiently complete to allow proper measurement and analysis: "....the Neanderthals....exhibit both a cold climate pattern and regional differences in limb and body proportions that may be attributed to long-term climatic selection" (Holliday 1997a; p 426).

The high brachial and crural indices (indicative of heat adaptation) of EAMH in Europe have led many authors (e.g. Holliday 1997a and Ruff 1994) to conclude that significant gene flow out of Africa was present during the archaic-to-modern morphological transition. Morphological evidence (e.g. low brachial and crural indices and leg length:hieght ratio) is consistent with models of Neanderthal evolution under periglacial conditions of Europe and central Asia, with repeated expansions or possible continuity of populations into Southwest Asia (Jacobs 1985; Valladas et al 1988; Trinkaus 1991; in Ruff 1994).

Body breadth (and weight for height) of Neanderthals did not differ (remaining large) between Europe and the Middle East as this body dimension is slow to change, while the less evolutionary conservative limbs show more expected ecogeographical patterning. Moderate body breadth of all EAMH groups (including those in periglacial Europe) may reflect recent expansion northwards; but some other measures of limb proportioning indicate incipient adaptation to the new colder environment. (Ruff 1994)

For a geographically wide-ranging taxon, such as *H erectus* or *H sapiens*, no 'typical' body morphology for the whole taxon should be assumed. Body breadth evaluation for Asian *H erectus* is currently not possible, but northern representatives are unlikely to be proportionally similar to their African counterparts. Available evidence from Zhoukoudian indicates an *H erectus* stature much shorter than WT 15000 (Weidenreich 1941); while those from Trinil in Java do appear more comparable in stature (Dubois 1926; Day & Molleson 1973). It seems reasonable to assume that ecogeographic trends in body breadth among modern humans also characterised earlier *Homo* populations (all in Ruff 1994).

6.4 - Reassessment of Neanderthal Lower Limb Proportions and Thermoregulation:

In assessing the role of limb proportions in heat dissipation or conservation, which is more important: the absolute length of the limb or the relative proportions of its segments? Considerable emphasis has been placed on the crural and brachial indices (indicators of the degree of distal segment shortening) and their ecogeographic patterning. For the purposes of heat conservation such segment proportioning should not matter.

For example, the crural index is neither a measure of leg length nor one of the leg-to-total height ratio, both of which would have more bearing on a discussion of cold adaptation. Longer legs in general and in relation to overall stature will have greater heat dissipating qualities (section 6.1.2). This should occur regardless of relative tibial/femoral proportions.

With the questionable exception of Spy 2, it can be seen that male Neanderthals had longer legs than the average Lapp, Eskimo, Pygmy and San bushman (section 5.8). This statement begs certain questions relating to the ecogeographic rules of body form. Given that today's traditionally living Lapp and Eskimo populations have highly sophisticated means of artificial insulation at their disposal, and the Neanderthals did not (section 6.10.1); should the Neanderthals not be more cold stressed and therefor lc have shorter legs? Given the fact that the San Bushmen live in the Kalahari Desert, exposed to much higher temperatures than those the Neanderthals experienced; should they not have much longer legs? Pygmies live in tropical Africa but have shorter legs than cold adapted populations (fossil and living). It is apparent that there are factors other than the cold that are influencing leg length in these populations. Significant contrasts in leg segment proportions and/or lengths, as well as stature/physique in general also have an impact on the biomechanical efficiency of locomotion (chapter 9).

The measurement of long bone lengths, so long as they are reasonably complete, is straight foreword and thus gives solid data (although a slight inter-observational sp. (forward) difference is only to be expected). Theory, on the other hand, is more open to debate. It would appear that there is an anomaly within the Neanderthal data which cannot be explained in terms of ecogeographic patterning alone. In other words there must be confounding variables in operation to determine Neanderthal body form.

6.5 - Human Physiology and Metabolism in a Cold Environment:

The heat production of a 65kg man at rest is 78 kcal/h (or 1872 kcal/day). Contrary to the assumption that heat production is directly proportional to body mass by proponents of the ecogeographical rules (section 6.1), it is in fact the main internal organs (including the brain), together only weighing 5 kg, which account for 72% of the body's heat production (Ashcroft 1971; in Schmidt-Neilson 1997). While at rest skeletal muscle only contributes less than 16% of the body's heat generation; during strenuous exercise a much higher value is reached (section 6.7.5)

	Heat Production (kcal/h)	*Percentage of Total Heat Production*	*Percentage of Body Mass*
Splanchnic Organs (abdominal organs excluding kidneys)	26.2	33.6	3.8
Brain	12.5	16.0	2.1
Heart	8.4	10.7	0.45
Kidneys	6.0	7.7	0.45
Lungs	3.4	4.4	0.9
Skeletal Muscle	12.2	15.7	41.5

Table2: Metabolic Heat Generation within the Human Body (Adapted from Ashcroft 1971; as reproduced in Schmidt-Neilson (1997; p242)

Roberts (1978) first noted the strong negative correlation between BMR and mean annual temperature; and suggested that there was either a genetic and/or a developmental component to BMR variation in humans. Further metabolic studies on indigenous high latitude populations from Europe and the New World (Itoh 1980; Rode & Shephard 1995) and high altitude populations in the Andes (Picon-Reategui 1961; Mazess 1969) have recorded elevated BMR levels relative to those predicted by the WHO's equations (FAO/WHO/UNU 1985; all in Katzmarzyk et al 1996).

Prolonged cold stress has been shown to increase the rate of turnover of the thyroid hormone thyroxin, which leads to a sustained elevation in resting metabolism (McArdle et at 1996). Eskimos display higher metabolic rates than whites under warm (13% higher) and cold (45%) conditions (Frisancho 1993). (section 6.7.2)

“The thyroid hormones are the single most important determinant of BMR for any given size, age, and sex....increases the oxygen consumption and heat production of most body tissues, a notable exception being the brain. This ability to increase BMR is termed a **calorigenic effect**. The mechanism of the thyroid hormones’ calorigenic effect is the major factor that ‘sets’ the body’s BMR” (Vander et al 1994; 632; highlighting in original).

6.5.1 - Metabolisms of Human Populations Living in Cold Climates Today:

Rode & Shephard (1995) sampled Iglook Eskimos and, as a control, villagers who Lli ? were of European descent but had lived there for at least one winter. The Iglook BMR averaged 184+/−18 in men and 170+/−25 in women; 15.8% and 18% higher than the control sample, respectively. If values are calculated per unit lean body mass, then the Iglook values are 11.8% and 9.6% higher.

Among the European ancestry controls a linear/accelerating age-related decrease of BMR was noted. In contrast the Iglook data tends to a ‘nadir’ at 40-50 years of age; higher readings being recorded among the older generations relative to the control sample. The proposed explanation is due to their maintaining a more traditional lifestyle, thus exposing themselves to the cold more frequently (Rode & Shephard 1995).

“The magnitude of the BMR has a major influence upon the daily energy needs of a population....The energy cost of traditional living is also high (Godin & Shephard 1973), further augmenting the total daily energy needs of the traditional Inuit population” (Rode & Shephard 1995; p 728). The recorded BMR substantially exceeded those expected, even in the acculturated younger generation of Iglooks. Rode & Shephard (1995) ask whether it could be that this ‘hypermetabolism’ is genetically determined in this population?

The central Siberian *taiga* (boreal forest) is a high latitude environment characterised by cold stress, a changing photoperiod, and restricted energy flow. The Evenki are reindeer herders, and today they live in collectivised villages that have organised brigades (work parties); the members of which look after the herds. The Keto were formerly nomads but have settled in villages along rivers and lakes, and now subsist mainly by fishing.

These RMR are higher than expected for small bodied people (Katzmarzyk et al 1994). The sex differences in RMR in this study are virtually eliminated if calculated per unit lean body mass. Thus, metabolic rate has a high dependence on the lean tissue mass of the body.

The significantly higher RMR of the Evenki brigade dwellers relative to the villagers is due to their exposure to a greater range of temperature variation and environmental stress. Since the brigade members return to the villages during winter, Katzmarzyk et al (1994) suggest that the noted hypermetabolism is a short-term environmental acclimatisation of ambient *taiga* conditions; as opposed to genetic adaptation to the northern latitude. This study did not have the temporal scope to test whether there was a seasonal fluctuation in RMR among the brigade members coinciding with their residence within or away from the villages. Disparities in activity levels between summers with the herds and winters in the villages should also be taken into account when assessing RMR. However, a longitudinal study by Suzuky (1959; in Ulijaszek & Strickland 1991) of Japanese subjects noted a significant fluctuation in BMR according to season, which is closely related to temperature.

In a later study Katzmarzyk et al (1996) compared agricultural farmers from highland and coastal Ecuador with these central Siberian herding/fishing peoples. Energy costs at rest (lying, sitting, and standing) and while performing a standard stepping exercise did not differ significantly between these groups. Katzmarzyk et al (1996) found resting energy costs were elevated relative to predicted values using the James & Schofield (1990) standards (averaging +16% in men and +11% in women). This appears to reflect a response to thermal stress. Throughout the course of a normal day these traditionally living populations experience "temperatures that are outside their thermoneutral range".

6.6 - Natural Insulation and Subcutaneous Fat:

At first it may seem logical that if living in a cold environment, maintaining protective fat layers would be a good thing. For example, the cross-section of a frozen seal reveals a thick layer of blubber, comprising 58% of the cross-sectional area (Scholander n.d.; in Schmidt-Neilson 1997). The blubber provides both insulation and buoyancy, both of which are beneficial to the seal in terms of heat and energy conservation. However, the implications of having such substantial sub-cutaneous layers in a terrestrial species are very different, and possibly even detrimental.

"An insulative rather than a metabolic type of response to a cold habitat is energy efficient, and *could* have an adaptive value in an environment where food supplies are limited." (Shephard 1991; p 202; emphasis added) But it seems that this is not the case in practice.

Eskimos today have been shown by Shephard (1991) to have low subcutaneous fat levels/skinfold thickness, relative to co-resident populations of European descent. This phenomenon seems to be a result of the combined effects of the caloric demands of metabolic heat generation and the non-adaptive nature of body fat in their energetic lifestyle.

Surface body fat layers do indeed have insulative properties which may be beneficial under the conditions of relatively inactive lifestyle, but offer little flexibility if the individual has to adapt to a substantial increase in heat flux. Daily activity levels are high among traditional-living Eskimos which can lead to a tenfold increase in metabolism during a day's exertions (Godin & Shephard 1973; in Shephard 1991). This could lead to hyperthermia with associated excessive sweat generation which could have potentially fatal consequences once exertions stop and rapid body cooling ensues. The carrying of the excess weight of body fat increases effort and hence heat generation during exercise, which also has negative effects on energy consumption (section 9.9.1).

Rode & Shephard (1971) noted that the traditional Canadian Inuit hunter has a very low skinfold thickness; and Shephard et al (1973) showed that traditionally-living Eskimos stored fat for energy in deep reserves rather than in subcutaneous deposits. O'Hara et al's (1979; all Shephard 1991) experiments on Canadian soldiers and civilians recorded a cumulative fat loss of 2-4kg over a period of 1-2 weeks when exercising in Arctic conditions (even though only their faces were unprotected from the cold).

The amount of body fat has an important effect on body heat conservation during cold stressing under water immersion testing techniques (Toner & McArdle 1988; in Cachel 1997). However, Yokoyama & Iwasaki (1975; in Shephard 1991) have showed that Japanese Ama experienced a cumulative decrease of body mass (4.6kg) over the course of the pearl diving season.

Eskimos, and these other active populations in cold environments, therefor have a higher proportion of lean body mass, and appear not to maintain insulative layers of body fat. So metabolic heat generation, rather than its conservation via insulative sub-cutaneous fat layers, is in practice the human body's preferred way of maintaining core temperature.

6.7 - Physiological Responses to Cold Stress:

The potential for any metabolic response is constrained by the availability of calories; whether in the form of food sources or body fat reserves (Shephard 1991). Obviously such metabolic solutions to the problem of combating the cold have high energy demands.

Changes in body metabolism (internal heat generation) and external climatic conditions act to disturb body temperature balance. Peripheral thermoreceptors in the skin and central thermoreceptors in deeper structures (e.g. spinal cord, abdominal organs and hypothalamus). The central thermoreceptors are the most important in negative feedback mechanisms. Primary integration of all reflex information occurs in the hypothalamus. (Vander et al 1994)

6.7.1 - Shivering:

"From shivering alone, the total metabolic rate can increase threefold to fivefold" (McArdle 1996; 501).

However, this increases heat loss and is energetically costly even where food supplies are plentiful. Shivering may be an effective short term response but over longer periods has severe drawbacks (Shephard 1991). For instance the intense isometric contractions induced utilise and are dependant on intramuscular glycogen reserves, which are rapidly depleted and can take up to 2 days to be replenished providing food intake is sufficient.

So whilst having short-term heat generating benefits, shivering has numerous more serious and survival-threatening consequences. So it is not adaptive in the long term.

6.7.2 - Non-Shivering Thermogenesis and Polar T3 Syndrome:

Heldmaier (1974) showed that mammals could maintain their core temperature via non-shivering thermogenesis. There is evidence for this capacity among children; and well-nourished adults experiencing prolonged cold exposure whether in arctic air (Schloander et al 1958) or when sea diving (Hong et al 1986) develop a similar metabolic rise (all in Shephard 1991).

Frisancho (1993) summarises the hormonal induction of two stages of non-shivering thermogenesis: Continued exposure to the cold acts to raise the activity level of the Sympathetic Nervous System, which in turn stimulates the release of noradrenalin. An increased sensitivity to noradrenalin induces non-shivering thermogenesis, and thus increases body resistance to the cold via a change in calorigenic effect of noradrenalin.

Under prolonged cold stress thyroxin output may increase by up to 100%; and as it stimulates calorigenesis the resultant rise in body temperature can be 20-30%.

It was Itoh (1974) who first proposed an increase in thyroid hormone production as a homeothermic cold adaptation. The 'polar T3 syndrome' of Reed et al (1990) hypothesises increased serum levels of Thyroid Stimulating Hormone (TSH), Thyroid Binding Globulin (TBG), and a modified extravascular pool of thyroid hormones (T3 and T4) in response to high latitude (cold) residence. The 'free fraction' of thyroid hormones was shown to decline with residence in Antarctica implying a greater rate of their uptake by tissues (consistent with increased concentration/affinity of TBG). Shephard & Goode (1988) stated thyroxin may stimulate hypertrophy of brown adipose tissue to effect non-shivering thermogenesis. This is seen as an adaptive advantage over shivering which reduces dexterity and hastens fatigue and mental confusion due to glycogen depletion. Thus, subcutaneous layers are utilised rather than retained for insulation. (all in Lazenby 1997)

The creation of low 'free fraction' T3 levels by this process could be analogous to levels of circulating thyroid hormones in hypothyroidism. A link between these two conditions has not been recognised, or tested experimentally yet, but logic would dictate that they would have similar consequences. Hypothyroidism is known to cause growth retardation (sections 7.2 & 11.1). Therefor, if non-shivering thermogenesis diverts the available circulating thyroid hormones from their actions in stimulating proper growth, it follows that phenotypic plasticity rather than pure genetic coding could have a role in the development of short limbs in cold-living peoples, both past and present (section 6.1.2).

6.7.3 - Liver Metabolism:

Itoh (1974 &1975; in Shephard 1991) proposed that thyroxin can stimulate the liver to generate increased internal heat. The liver is a highly metabolic organ which is able to uncouple the oxidative phosphorylation reaction to release heat rather than producing ATP (i.e. converting ADP to ATP by the addition of a 'high energy' phosphate bond) for energy storage. Its large size, central location within the body, and the substantial blood flow through it enables the effective distribution of the metabolic heat it produces throughout the body.

6.7.4 - Peripheral Blood Flow:

If cold exposure is intermittent an adaptive response is to reduce circulation (via vaso-constriction) to the extremities. By lowering peripheral (and skin) temperatures heat loss can be limited (Skreslet & Aarefjord 1968; Shephard 1985; in Shephard 1991). However, the reduction of peripheral blood flow hinders manual dexterity which will be counter-productive in the long-term for a cold-dwelling population.

Higher peripheral temperatures (due to greater red blood cell concentrations, plasma volume, and globulins) and fluctuations in blood flow (via intermittent vaso-dilation) in these regions have been noted among circumpolar populations relative to white controls (Frisancho 1993). Eskimos and fishermen have less vaso-constriction in their fingertip blood vessels when exposed to the cold, relative to control subjects. This permits them to maintain dexterity despite intense cold (Vander 1994).

6.7.5 - Raised Voluntary Activity Levels:

The theory is simple. During exercise skeletal muscles are worked (heat produced as a by-product) and heart rate and blood flow are increased (improved circulation of heat). Measurements of increases in metabolic heat production with exercise vary dramatically from tenfold (Schmidt-Neilson 1997) to fifteenfold (Vander et al 1994), or even as much as twenty five times resting rate (McArdle et al 1996). However, just as in the case for shivering this is energetically costly to sustain.

The raised metabolism found in cold-dwelling populations directly increases energy expenditures and hence is important in determining their caloric requirements. It can be seen from table 3 that, as well as RMR, the caloric costs of exercise are greater under colder conditions. At very high day time temperatures higher than expected values are recorded. This cold be due to high diurnal temperature oscillations (temperatures plummeting over night) as experienced by Australian Aborigines (Frisancho 1993).

Temperature (Degrees C)	*Resting Metabolic Rate*	*Activity (Increment in Caloric Cost as %)*
-5	12	10
5	8	6
15	4	2
25	0	2
35	4	6

Table 3: Estimates of the Effect of mean Environmental Temperature on Resting Metabolic Rate and the Energetic Cost of Exercise (Adapted from Leslie et al 1984; p 150).

"This kind of biological response [to cold stress] implies significantly more physical activity to retain viable core temperature levels through the intake of food calories and oxygen in relatively prodigious quantities to manufacture heat in a veritable metabolic furnace of muscle mass" (Jelinek 1994; 88).

This idea is fine so long as the individual is moving, but what happens when exercise stops (due to fatigue or completion of a task), and rapid body cooling occurs? (section 6.6). It also demands a vast carbohydrate (and fat) intake to fuel such exertions which may not have been available to Neanderthals (sections 2.3.3 & 2.4). So the value of such a mechanism is questionable on two important counts.

6.8 - Extracellular Calcium Concentration and Bone Mineralisation:

Bone is constantly being remodelled according to the stresses it is subjected to, which requires calcium and energy. Fraser (1988) states that a unifying characteristic among all vertebrates is their possession of sensitive control mechanisms for the maintenance of a constant concentration of extracellular calcium ions (Ca++). Serum concentrations are kept close to 1.25mM. A rise from this is met with an excretory response; while a fall is countered by either enhanced absorption from the environment (i.e. ingested food) or the mobilisation of internal stores (i.e. bone).

"Approximately 99% of total-body calcium is contained in bone. Therefore, deposition of calcium in bone or its removal very importantly influence plasma calcium concentration....It is important to recognise that its role in maintaining proper plasma calcium concentration takes precedence over the mechanical supportive role, sometimes to the detriment of the latter" (Vander et al 1995; 547).

Homeostasis of extracellular calcium ions is vital since muscle, nerve, and endocrine cells are all so sensitive to fluctuations in its level (sections 8.3 & 9.5.1).

"A low calcium concentration increases the excitability of nerve- and muscle-cell membranes, so that individuals with low plasma calcium suffer from hypocalcemic tetany, characterised by skeletal muscle spasms. Hypercalcemia [excessive plasma calcium] is life threatening too, in that it causes cardiac arrhythmias as well as depressed neuromuscular excitability" (Vander et al 1994; 546).

Secretion of parathyriod hormone (distinct from thyroid hormone) is stimulated by a decrease in plasma calcium concentration. It acts to stimulate (Vander 1994):

- bone resorption (moves calcium from bone into the extracellular fluid)
- activation of vitamin D (increasing intestinal absorption of dietary calcium). Ultra Violet radiation on the skin turns 7-dehydrocholesterol into inactive vitamin D3 (or this can be ingested). This is then metabolised into the active 1,25-dihydroxyvitamin D3, under control of the parathyriod gland.
- increases renal tubular re-absorption of calcium (decreasing urinary calcium output).

(an increase prevents its release and these actions are stopped/reversed)

A dietary deficiency of calcium during growth creates competition for calcium between bone growth demands and the need to maintain the concentration of the extracellular pool. The importance of the latter to the functioning of all body cells gives it precedence over bone mineralisation. Thus, bone is either undermineralised or its growth stops. Chondrocyte and osteoblast function in bone is also dependant on the extracellular concentration of calcium, so a drop would not only starve bone of its main growth substrate, but could lead to its improper functioning of its cells. (Fraser 1988)

In principle calcium deficiency could provoke two responses (Fraser 1988):

- A continuation of growth at a rate compatible with the supply of other nutrients (energy and protein), but the bone is left undermineralised with a defective structure
- Bone growth is retarded to a rate which calcium supply allows normally structured and mineralised (but smaller) bone to develop.

Thompson et al (1981; in Shephard 1991) identified the poor calcification of bone in Eskimos. The bones of recent populations of Eskimos show that this has been a common feature of these people for centuries. Eskimo bone also shows a high level of secondary osteons indicating a more rapid turnover of bone relative to other populations in warmer climates. But why does this rapid turnover occur; is it a specific response to the cold or are activity levels influential?(sections 5.2 & 9.8.1)

<u>6.8.1 - Bone Loss in High Latitudes and Seasonal Environments:</u>

"Temperature and humidity are basic climatic factors that directly affect a level of thermoregulation and, indirectly, affect activity of the circulatory system, including the basal metabolism rate and the various metabolic processes....the inhabitants of diverse climato-geographical regions differ substantially in parameters of water-salt exchange, in their basal metabolism rate, and in their circulatory and endocrine functions....the parameters of bone ageing need not be considered merely as estimates of selective damage to the skeletal system, but should rather be regarded as a much broader reflection of the status of regulatory mechanisms monitoring the complex ageing changes in the organism" (Belkin et al 1988; 355).

Lazenby (1997) found that when adjusted for Lean Body Mass (LBM) Eskimos (Inuit and Inupiat) show a distinct pattern and magnitude of ageing bone loss relative to Caucasians (i.e. there are real inter-population differences).

Lazenby's study (1997) demonstrated that reductions in bone mass (density) occurs a decade earlier (in the 30's) and is more pronounced among Eskimo samples relative to Wisconsin (US) and Belgium samples. It is the 'post 40' patterns of precipitous loss which most distinguish the Eskimo and Caucasian samples. Thus, age seems to be an important variable. Previously it had been proposed that inter-population variation in LBM could account for differences in ageing bone loss. However, Lazenby (1997) has shown that such differences remain even after adjusting for estimates of LBM.

Belkin et al (1988) took hand radiograms from 7,500 individuals of 20 different ethnic groups, then used multiple regression analysis to evaluate the association between bone ageing parameters and various climatic factors (e.g. hours of daylight and average humidity in January and July). It is the acuteness of seasonality rather than the particular climatic conditions themselves which seems to be most influential. The greater the seasonal differences the narrower the time lag between the first individual and the involvement of the entire population. The earliest age at which signs of bone ageing appear correlates significantly with latitude. Mean January temperature and average July humidity also independently affect the timing of this event.

Belkin et al (1988) conclude that the greater the difference in 'meteo-regime' between seasons, then the less favourable are the conditions for bone metabolism, and hence the higher the chance of an early onset of bone destruction. Humidity and temperature appear to be significant factors in triggering individual initial bone changes. The combination of these and other climatic factors which combine to create seasonal contrasts, predispose populations to corresponding onset of bone changes.

6.8.2 - Hormonal Explanations for Bone Loss:

Traditional explanations for the accelerated bone loss among coastal Arctic groups involve physiological buffering of their high animal protein diet; occurring due to endogenous acid production (sulphate and hydrogen ions) associated with protein (methionine and cysteine) catabolism (Einhorn 1990; Watkins et al 1985; in Lazenby 1997). The current ambiguity surrounding the 'protein-calcium buffering' model has led to the formulation of an alternative hypothesis: that accelerated bone loss among Inuit and Inupiat (both North American peoples) reflects higher production and utilisation of thyroid hormones (T4 & T3) as a mechanism of cold adaptation via enhanced non-shivering thermogenesis. Itoh (1974; in Lazenby 1997) was the first to propose such an increase in thyroid hormone production as a homeothermic cold adaptation. (section 6.7.2)

Clinical studies show that bone loss is associated with hyperthyroidism or thyrotoxicosis consequent to treatment for thyroid dysfunction with L-thyroxin. The reductions in cortical and trebacular bone mass were observed to be 'dose-dependant' (Schneider et al 1994; McDermott et al 1995; in Lazenby 1997). So as thyroid hormone levels fall under treatment a reduction in bone mass ensues. The exact mechanisms involved are currently unknown, but increased osteoclastic activity is suggested by the fact that bone mass is lost. Regardless, the distinctive pattern of ageing bone loss among Eskimos could be due to either chronic cold causing the low 'free fraction' thyroid hormones or seasonal fluctuations in temperature and hence accordingly fluctuating thyroid hormone levels.

6.8.3 - Bone Loss and Diet:

Diet may still be a factor in this hormonal explanation. The traditional Arctic diet is low in carbohydrates which suppresses T3 concentration under conditions of reduced caloric intake. Danforth & Burger (1989; in Lazenby 1997) showed energy balance correlates with free T3 concentration in non-Inuit populations. Thus, Inuits having high

BMR and activity levels could result in their having lowered T3 levels (if expenditure exceeds intake).

Eskimos and other circum-polar populations also have had the physiological problem of needing to counteract high protein intake so as to limit calcium loss (section 8.3). In modern humans a diet very high in protein causes calciuria; probably related to a relatively high phosphorous intake, whereby the balance of the two is upset (Draper 1977; in Cachel 1997). If urinary calcium output increases then the rate of bone resorption accelerates (in order to maintain the extracellular pool of calcium ions) and a decline in bone mass ensues, as shown via animal experimentation. Osteoporosis has been a problem among Inuit groups since before Western contact (Klepinger 1992; in Cachel 1997) and it appears to be a direct result of the very high protein component of their traditional diet.

6.9 - Metabolism and Bone Remodelling in Neanderthals:

Jelinek (1994) asks if the very active lifestyle and resultant raised metabolism are responsible for premature ageing and death among Neanderthals, due to excessively straining their biological systems? Evidence here shows that it is possible that a combination of different physiological stresses, via the action of thyroid hormones, may have played such a role.

The Neanderthals inhabited Europe at a time of low temperatures and significant seasonality. It is likely that they maintained body temperature via the process of non-shivering thermogenesis rather than by insulative layers of sub-cutaneous fat (sections 6.6 & 6.7.2) and thus had low circulating thyroid hormone levels. This effect on thyroid hormone turnover may also have influenced the linear growth of Neanderthals (sections 7.8 & 11.3).

The thick cortical bones of Neanderthals are based on their ability to mobilise sufficient amounts of serum calcium and transfer it to living bone tissue, which is continually being remodelled. Serum levels of calcium are not simply a reserve to supply the demands of bone mineralisation (section 6.8). If levels drop below a critical threshold then nervous and muscular function is impaired, causing tetany and seizures, along with memory loss and anxiety. "These processes of bone biology and normal muscle and nervous system function are universal in living mammals" (Cachel 1997).

It is a reasonable assumption that Neanderthals suffered physiological stress due to their high protein/low carbohydrate intake (sections 2.3.3 & 2.4) and the resultant excretion of calcium and suppressed thyroid secretion (sections 7.7, 8.3 & 9.6.1).

The need to maintain a substantial bone mass to permit high activity levels appears to have been met by the Neanderthals (chapter 5). Under the stresses of high activity levels bone resorption would not have been permitted, and calcium (and energy) would have been a vital commodity for both its repair and remodelling as well as proper muscular functioning (section 9.5.1). The consequences of a high protein diet would have been at odds with these demands, causing the excretion of calcium ions.

Perhaps among the Neanderthals a compromise was met whereby the length of long bones (legs/distal portions particularly) was sacrificed in preference to developing skeletal robusticity and strength. This would have enabled proper bone mineralisation (to cope with the high impact stresses to which they were subjected) while still allowing the maintenance of a sufficient extracellular pool of calcium ions (for muscle activity) in the face of physiological stress stemming from dietary imbalance.

Neanderthals probably had an elevated BMR and suffered ageing bone loss in a similar fashion to present day Arctic populations. Due to the combined factors of metabolism to combat the cold and demands for bone remodelling from high activity levels, the onset of the condition may have been more sharp or at a younger age. Such a process of bone loss may have some bearing on the high degree and frequency of skeletal trauma observed within the Neanderthal group (section 5.5), and their apparent short lifespans. The 'old man' of La Chapelle-aux-Saints is estimated to have been less than 40 years old at the time of his death, and 90% of the Neanderthal sample being younger than 35 (Stringer & Gamble 1993).

6.10 - Colonising cold Environments and Cultural Buffering Against the Cold:

Morphological cold adaptations, such as short distal limb segments with low brachial and crural indices and high body breadth, are evident in the Neanderthals (e.g. Ruff 1994, Holliday 1997a; Trinkaus 1981). Steegman (1972; in Ruff 1994) claimed that inefficient cultural adaptation to the cold, dry environment selected for maximum biological adaptation among Neanderthals. It is argued in this thesis that developmental adjustments to the cold climate may have played a significant role in this (section 6.9). The maintenance of such Neanderthal morphology in Southwest Asia is slightly anomalous due to its supposedly warmer climate. However, Neanderthal expansion southwards probably coincided with glacial expansions in Europe, with temperatures in Southwest Asia falling to a level closer to that which Neanderthal body form was adapted (section 2.2).

The high brachial and crural indices of EAMH is thought to be evidence of their equatorial African ancestry and increased capacity to guard against the cold via cultural mechanisms (Holliday 1997a). The persistence of equatorial limb segment proportions in the early European Upper Palaeolithic means that thermal stress was less intense for these later populations. At this time the first modern humans moved into arctic Eurasia where they would have needed significant thermal protection in order to survive (Ruff 1994).

Early human cultural adaptations to climate may actually have promoted the ecogeographical clines in body form (rather than buffering against their effects, especially of cold) by allowing habitation of regions otherwise impossible to survive in. Ultimately the cold would still have placed strong selective pressures on morphology (Ruff 1991). Increased cultural buffering today may explain why ecogeographical variation now is much less marked than was apparent in past hominids (i.e. between WT 15000 or the Skhul-Qafzeh EAMH sample and the Neanderthals).

6.10.1 - Artificial Insulation at the Time of the Transition:

Evidence for artificial shelter or hearth construction by Neanderthals is scarce and rudimentary. There are only a few examples of supplementary structures in caves, such as the low wall at Pech de l'Aze (Bordes 1972; in Jelinek 1994). Open hearths, such as at Grotte Vaufrey and Grotte du Lazaret, generally did not produce much heat as underlying layers are unaffected (Mellars 1996). At Pech de L'Aze II it has been suggested that fires were lit on paving stones, ashes cleared, and food cooked on the hot stones (Bordes 1971; in Mellars 1996). At a small number of other sites stones were placed around the fire presumably to protect them from wind, such as Terra Amata (de Lumley 1969, 1976) and Grotte du Bison (Farizy 1990; both in Mellars 1996).

A shift in hearth structure is observed after the transition (Bordes 1971; Perles 1973; Singer & Wymer 1982; in Mellars 1996). The open thermally inefficient fires of the Middle Palaeolithic become replaced with stone-lined pits which conserve heat for longer. There is also evidence for a degree of spatial organisation or structuring in the Middle Palaeolithic, although Rigaud (1989) notes that recognised evidence for true spatial organisation of living sites/differentiated activity areas only becomes common after 28,000ya in later Aurignacian and Gravettian levels.

Evidence for clothing in Neanderthal times is limited to interpretations of the use-wear patterns on lithics. There is some evidence for the practice of hide scraping but woodworking is the most common activity. *Rangifer* and *Alopex* would have had the best fur-bearing hides; and these species are present in Neanderthal associated faunal assemblages in significant numbers (Scholander et al 1950; in Jelinek 1994). But without evidence of tools designed specifically for hide working, it is difficult to imagine the production of effective garments by Neanderthals.

Natural hides are very effective insulators. According to Shephard (1991) a double layer of caribou skin offers 11 CLO units of thermal protection, while current arctic military clothing gives only 4 CLO units. Studies of Eskimos and Antarctic explorers have shown that decent clothing can sustain a warm and comfortable micro-climate even at ambient temperatures of 40 degrees below freezing. However, although the Neanderthals probably did use hides, if untaylored their insulative properties would have been questionable.

Improvements in clothing manufacture and the construction of more sophisticated shelters and hearths is evident from certain technological innovations present in Upper Palaeolithic archaeological record (Ruff 1994; Jelinek 1994). This would have been a vital development for the tropically proportioned EAMH expanding into Europe and persisting there as the last glacial maximum approached. Artificial insulation could have been potentially very effective in terms of clothing (Shephard 1991).

Jelinek (1994) argues that the EAMH, with their less massive and longer physiques, were only able to survive in glacial Europe with the aid of effective artificial heat conservation. Such artificial insulation would have relieved the selective pressures of climate which drove the evolution of the Neanderthal physique and reduced metabolic demands. The time spent in calorie acquisition would have been reduced, leaving more time for social and technological elaboration, as is seen in the (later) Upper Palaeolithic. Since caloric demands per individual were lowered the effective carrying capacity of the landscape would have increased and a larger population of hominids could have been supported. Thus, the greater organisation and intensity of occupation of sites is proposed to have ensued (Jelinek 1994).

CHAPTER 7

Human Growth and Development:

"Growth is a complex process influenced by genetics, endocrine function, and a variety of environmental factors, including nutrition and the presence of infection" (Vander et al 1994; 624).

7.1 - Caloric Demands of Growth:

Waterlow (in Tanner 1989) states that a 1 year old child on average needs 330 kiloJoules per kilogramme of body weight per day (kJ/kg/day) for bodily maintenance; a further 20 kJ/kg/day for normal growth; and uses 80 kJ/kg/day more in regular physical activity. When calorie intake falls below the 330 kJ threshold growth ceases, which is a regular occurrence in the developing world. The energy margin for physical activity is eroded first which leads to a restriction in the child's exploration, play, and social interaction. This delays its intellectual and emotional development more so than direct nutritional effects on the nervous system.

In infancy, particularly the second year of life, nutritional requirements per kilogramme of body weight per day are highest. Children who are stunted are more likely to be susceptible to infection and greater degree of suffering, and more likely to die than those growing 'normally' (section 7.5.2) Immunocompetence is impaired under nutritional stress (Kielmann et al 1976; in Martorell 1989) which accounts for these factors.

"Protein intake seems less important [for growth] than once thought." (Tanner 1989; p131)

7.2 - The Hormones Associated with Growth:

Thyroid hormone or thyroxin is an iodated tyrosine, whose release is regulated by the pituitary gland. In the foetus thyroid hormones are important in neuronal development and osseous maturation but not overall tissue development (Milner 1988). Thyroid hormones are necessary for normal growth during childhood and physiological functioning throughout life. Thyroid hormones control BMR, ATP consumption rates, and blood glucose levels (Vander 1994; Robbins 1991). In the very young it is essential in the mechanisms promoting protein synthesis in the brain and nerve cell development. Deficiency at birth causes mental handicapping (called cretinism).

These hormones also influence skeletal development and physical growth indirectly. "The thyroid hormones....are required for both the synthesis of growth hormone and the growth promoting effects of that hormone" (Vander et al 1994; 627).

Growth hormone is in fact a protein, which is released from the anterior pituitary gland. In the young it stimulates growth and mitosis and in adults protein synthesis. Retention of Na, K, P by the kidneys is increased and uptake of Ca, Mg in the gut is increased by this hormone.

Thyroxin (T4) and/or Triiodothyronine (T3) have a permissive role on and influence the secretion of growth hormone by the pituitary gland, as well as the cellular response to somatomedin. Growth hormone does not stimulate growth in hypothyriod children. Thyroid hormones are necessary for growth at all ages and has a major effect on bone maturation. After birth congenital hypothyroidism immediately causes retarded growth, a major characteristic of which is retardation of osseous development.

7.3 - Bone Growth and the Development of Body Proportions in Humans Today:

Long bone growth occurs within the 'growth plate' (a zone of dividing cartilage separating primary from secondary ossification centres) which deposits substances that form the bone matrix. As growth rate slows this growth plate narrows until its elimination when the bone of the main shaft meets the epiphysis and growth stops. During the growth period bone remodelling and moulding takes place continually in response to changes and demands of the skeleton; and in order to fuel this process the right balance of sufficient nutrients needs to be provided (Davies 1988).

The first and most rapid period of leg length growth is from birth to 2 years. Later at puberty the development of secondary sexual characteristics is accompanied by a rapid increase in the somatic growth (in other words the adolescent or second growth spurt). Growth rate accelerates to attain the Peak Height Velocity (PHV) and subsequently falls (Marshall 1978). Normally the increase in leg length contributes more to PHV than that of sitting height (Tanner 1978; both in Gonzales et al 1982).

Sitting height represents 70% of a new-born's length; 57% at 3 years; and 52% at the time of menarche in girls and at a slightly later comparative age in boys. Growth rate of leg length is greater than that of the trunk (Yun et al 1995). Leg length reaches its peak 6-9 months ahead of that of the trunk. The short legs of the Asiatics is due to an earlier onset of puberty; the period of rapid leg lengthening just prior to puberty being curtailed. Europeans have a relatively later puberty (1 year) which allows a longer period of this increased rate of leg growth (Elveth & Tanner 1990). So this would imply that post-natal leg growth should be more susceptible to the effects of environmental stresses, relative to that of the trunk.

Adult body proportions develop early in childhood and are enhanced at adolescence. For example, Eskimo and Aleut body proportions comprise short distal limb segments. These proportional contrasts with whites (and other lower latitude populations) appear at a young age. Heller (1967; in Y'edynak 1976) noted that weight/height ratios are consistently higher among Eskimo than white children. Hrdlicka (1941; in Y'edynak 1976) reported that Eskimo children are shorter than whites with the difference increasing at adolescence. Both genetic and nutritional stress factors are considered by these authors as possible and plausible agents of these differences.

7.4 - The Secular Trend in Height:

"A rapid secular change has been observed in many of the classically small populations, such as the Eskimos (Jamison 1976), the Japanese (Nukada 1975), the Lapps (Skrobak-Kaczynski & Lewin 1976) and the sub-Arctic Icelanders (Palsson 1981).

Among the Eskimos (Jamison 1976) a gradient of stature, with an associated accentuation of the 'shortness for body mass' characteristic, has been observed; the tallest people are found among the most acculturated groups on the Alaskan north shore, while the smallest are seen in Eastern Canada (where there has been more pressure to preserve a traditional lifestyle)." (Shephard 1991; p 171)

7.4.1 - The Proportional Increase in Leg Length:

As might be expected from the differential rates and timings of leg versus trunk growth, there is "....evidence that the secular trend towards a larger size involves a change towards relatively longer legs in relation to trunk." (Tanner 1989; p130)

Hamill et al (1973; in Yun et al 1995) found that Japanese children are 1.2cm shorter at 12 years and 5.3cm shorter as adults than Caucasoids and Negroids; but there were no differences in sitting height. The ratio of sitting height:overall height is greater in the Japanese, meaning that they have relatively shorter legs than either Negroids or Caucasoids. Later Hayashi et al (1982; in Tanner 1989) sampled the Japanese population and recorded inter-generational height changes in fully grown adults:

- 1957-67: 2.8cm in men, 1.5cm in women.
- 1967-77: 1.5cm in men, 1.2cm in women.

Overall change for the 20 year period of 4.3cm in men and 2.7cm in women was accounted for entirely by increases in leg length, while sitting height remained constant throughout. Note the dramatic increase seen in men during the earlier decade. Zhang & Huang (1988; in Elveth & Tanner 1990) noted the same phenomenon among the Chinese over the course of the 1970's and 80's. The short lower limbs thought of as innate Asian characteristics has been shown to be environmentally liable and responsive labile ? to better nutritional and living standards (Tanner et al 1982; in Ruff 1994).

A 1956-7 study reported that American-born Japanese were significantly taller, heavier, longer-legged, and more advanced in skeletal development than those born in Japan. Greulich's re-examination of them as young adults (1968-74) found the American-born Japanese to be taller, heavier, but shorter-legged than those born in corresponding years in Japan. Differences seen in adulthood were less marked than those during younger years. This is due to an acceleration of growth rate in the native Japanese and a decline in that of the American-born group in the intermediate period. (Greulich 1976)

There have been similar findings in other parts of the world, such as in Peru. In the secular trend noted among the native children and adolescents of Puno, a high altitude community, "....only leg length contributes to the body height differences between 1945 and 1980" (Gonzales et al 1982; p 192). Among native children and adolescents in Huancayo it was found that: "The observed changes in stature [between 1937 and 1978-82] are related to a proportionally greater increment in leg length relative to trunk length" (Gonzales et al 1984; p 47).

"....it would appear that the factors that account for the increase in stature also modified body proportions" (Gonzales et al 1984; p 50).

7.4.2 - A Secular Trend in Body Mass:

Although notable increases in leg length have been identified, measures of body mass have altered more markedly than those of body proportions over the last 40 years. Katzmarzyk & Leonard (1998) found that, compared with past studies, the slopes of the best fit regression lines between measures of body mass and temperature are more modest/less steep.

Katzmarzyk & Leonard (1998) invoke a secular trend in body mass, particularly among tropical peoples, to explain this phenomenon. Increases in body mass and BMI are greater among populations of warmer (mean annual temperature 15 degrees or more) climates; while surface area/body mass ratios show sharper declines at warmer temperatures.

"Thus, although there has been a general, world-wide increase in body mass over the last 40 years, the increases appear to be disproportionately larger in tropical regions" (Katzmarzyk & Leonard 1998; 488).

The decline in the strength of the association between body size and climate in Katzmarzyk & Leonard's (1998) study suggests that the very strong, inverse relationship between mass and temperature initially reported by Roberts (1953; in Katzmarzyk & Leonard 1998) was at least partly attributable to differences in nutritional status during development, as well as those in genetic adaptation to thermal stress.

7.4.3 - The Primary Cause:

The causes of the trend are multiple, including various environmental and socio-economic improvements. Better nutrition is 'certainly' a major factor, in particular in terms of increased calorie (and protein) intake during infancy (Tanner 1989).

"Substantial socio-economic and/or nutritional gradients of overall body size have been described within ethnic groups in India (Malhotra 1966), Tunisia (Parizkova et al 1972), Samoa (Greksa & Baker 1982) and Kinshasa (Ghesquiere & Eekles 1984)....In general, the malnourished person is small, but the body form (weight for height) remains relatively normal (Ghesquiere & D'Hulst 1988)." (Shephard 1991; p 169)

"....there are major differences of adult height in homogeneous populations, attributable to the impact of unfavourable economic circumstances in the early part of life (Ferro-Luzzi 1988)" (Shephard 1991; p 215). Once again evidence points to the difference in height between rich and poor being more due to leg length than to length of the trunk, at least in some societies (Billewicz et al 1983; in Tanner 1989).

Koreans, like the Japanese, were thought to be genetically shorter than Caucasoids and Negroids. However, over the last 20 years the height of children has increased as nutritional and environmental status has improved (Korean Paediatric Association 1967 and 1985; in Yun et al 1995).

7.4.4 - Non-Dietary Explanations:

Ruff (1994) dismisses variation in environmental factors other than climate (section 6.1) as being unlikely to explain the observed ecogeographic clines in modern human body form. However, Katzmarzyk & Leonard (1998; 483) claim that "....although climatic factors continue to be significant correlates of world-wide variation in human body size and morphology, differential changes in nutrition among tropical developing world populations have moderated their influence."

There is a possibility that the noted secular trend is linked to migration and subsequent interbreeding. The genetic hypothesis (Damon 1965; Van Wieringen 1978; in Martorell 1988) states that the breakdown of small isolated breeding populations due to increasing social and geographical mobility leads to the phenomenon of 'hybrid vigour' or 'heterosis'. One manifestation of this is increased stature. The theory has been rejected by Martorell (1988) since evidence from Hawaii's rapidly evolving multi-cultural society does not show any such change to be taking place. It appears to be generally agreed according to Shephard (1991) that environmental factors, such as improved nutrition and sanitation, play a more causal role than genetic ones.

Findings by numerous authors (e.g. Katzmarzyk & Leonard 1998; Shephard 1991; Tanner 1989) suggest that both relative sitting height/leg length and body mass measures have significant developmental components, shaped by nutritional and other environmental parameters.

7.5 - Malnutrition and Stunting:

"That the rate of linear growth is related to the type and amount of diet is incontrovertible, even though a concise, integrated, biological account of the nature of the deficits responsible for stunting is not yet available. It may be that the same nutritional inadequacy that limits the achievement of genetic potential for linear growth is also responsible for dysfunction of host immunity and tissue repair....stunted children often come from homes with social, economic, and environmental deprivation. Those factors that may well explain why the dietary intake was not adequate to achieve the potential for linear growth in the first place may also influence the outcome of an infection in the stunted child" (Tomkins 1988).

It should be noted that studies on linear growth among malnourished children largely do not assess body proportions. Stunting as a term and its measurement generally refers to overall height relative to international reference standards; differential growth in legs and trunk are not usually investigated. However, knowledge about growth patterns and evidence recorded in the secular trend is suggestive that stunting may well be more akin to shortening of the legs (limbs) as opposed to the trunk.

7.5.1 - The Question of Adaptation:

Biological and physiological adaptations are determined by a combination of the genetic make-up and phenotypic characteristics of the individual present at the time in question (Scrimshaw & Young 1989). Adaptation is change which keeps functioning within the preferred range. It is supposedly an adjustment whereby equilibrium is maintained without impairment. Accommodation, on the other hand, is where a new homeostatic level is reached via an impairment of function somewhere. It is a form of compromising which allows survival, but at a cost. Bennett (1976; in Pelto & Pelto 1989) stated that much of what is termed adaptation does in fact disturb the existing state in order to arrive at a new one which is more in balance with the environmental circumstances. As such, this 'coping' is neither good nor bad. The issue of stunting and the small-but-healthy debate is very much concerned with the concept and implications of such adaptation.

7.5.2 - The Small-But-Healthy Hypothesis:

"To judge the adequacy or otherwise of energy intake by anthropometry alone is to neglect entirely the possible relationships between intake and physical activity and the consequences of different levels of activity" (Beaton 1989).

In 1980 the economist David Seckler (in Pelto & Pelto 1989) proposed that the short stature resulting from Mild to Moderate Malnutrition (MMM) is an adaptation that is 'small but healthy'. Under circumstances of nutritional deprivation growth rate is reduced so that the limited resources can be diverted elsewhere in order to maintain proper physiological functioning. Short stature is claimed to be the only impairment. Later in life a short adult stature better prepares the individual for periodic food scarcity as less nutrients are required for physiological maintenance and exercise.

Further assertions to back up the small-but-healthy hypothesis (as quoted by Messer 1989 and Pelto & Pelto 1989) have also been made. For example: certain abstemious food habits of some groups resulting in smaller adult size may provide successful bio-cultural adaptations at the population level to scarce resources; and many populations in developing countries are capable of survival on food intakes well below those recommended by the FAO/WHO/UNU.

It should be noted that even backers of the small-but-healthy hypothesis recognise that wasting (low weight for height) is not healthy, being synonymous with maurasmus. The weaning period (typically between 3 months and 3 years in traditional societies) is the danger zone in which stunting will occur. Children develop maurasmus when limited/no breast milk or an inadequate substitute is ingested. Fat reserves are used up as energy stores, then lean body tissue is broken down to provide the amino acids for gluconeogenesis and protein synthesis. This latter process wards off the development of kwashiorkor. (Scrimshaw & Young 1989)

Martorell (1989) and Pelto & Pelto (1989) voice several problems with the small-but-healthy hypothesis, including:

- If stunting is healthy then its causes must also be considered so. Malnutrition and infection are not desirable.
- The conditions that cause stunting have other negative consequences. Stunted individuals are susceptible to infection, have reduced work capacity, and have impaired cognitive function.

- Stunted women often have birthing complications and a high likelihood of producing underweight babies.

"With the possible exception of certain Papua New Guinean and neighbouring island peoples, individuals and cultural populations that consume less and grow less than nutritionists recommend may be functioning at low or slow levels. They are by no means healthy...." (Messer 1989; p 44).

But do these phenomena only kick in once stunting can no longer successfully buffer against shortfalls in dietary calories? In other words: beyond the threshold whereby the next level, in a progressively more detrimental sequence, of energy/nutrient conservation is instigated. Unless nutritional deprivation becomes worse or is prolonged, stunting may be the first and sufficient mechanism whereby no other changes are required.

Under conditions of more severe or chronic undernutrition, as has been correctly stated by the hypothesis's critics, various more immediately/obviously detrimental changes occur in the attempt to cope. By ceasing growth an individual is taking evasive action with respect to suffering other physiological problems. It is only when it fails that resorting to the next level of action is instigated, with infection (due to suppressed immune response), wasting (muscle protein used as an energy source), and so on ensuing.

As is noted by Martorell (1989) stunting acts as a warning signal for morbidity and mortality. As such it could be seen as the first link in the chain of physiological responses, associated with ongoing and degenerating conditions of undernutrition, in the human body's successive attempts to cope with such stresses. In less demanding circumstances (such as MMM) compromising height would be 'healthy' if by doing so conditions such as reductions in physical work capacity and morbidity were staved off.

"....both stunting and mortality are different outcomes - often successive but without direct causal relationship - of a succession of stresses on the children's health....Stunting may not be a 'disease' *per se* or a 'cause of death'; it probably only results from the adaptation of the body to an incomplete recuperation after exposure to various stresses in an unfavourable environment" (Van Lerberghe 1988).

Most of the clinical, epidemiological, and experimental reports on the risk of childhood infection and morbidity have emphasised the importance of protein-energy malnutrition, being underweight and thin (i.e. wasting), rather than having short stature and slow rates of height gain. Studies in Nigeria (Tomkins 1981) and Bangladesh (Black et al 1984) have shown that episodes of infection (particularly diarrhoea) are indeed longer in stunted children. However the greatest association was between wasting and the subsequent duration of the infection. Children are not susceptible to disease and death simply because they are small, but because of the increasingly unfavourable environmental conditions in which they are growing up. The greater association between wasting and infection arises because, as a more desperate coping mechanism, it occurs subsequent to the failure of stunting to enable adaptation to the stresses experienced.

7.5.3 - Explaining Pygmy Body Proportions:

Explanations for the pygmy stature, being anomalous to the ecogeographic rules of body form, have tended to focus on their ecology (section 6.2.1). It could be that their body size has reduced in accordance with the low energy availability of the tropical forests. Forester's (1964; in Shea & Bailey 1996) 'island rule of body form' states that such a phenomenon will occur in an isolated area (the island) with limited resources. However, with competition for scarce resources an increase in body size is expected.

Rather than experiencing the pattern of proportional stunting seen in other populations more recently becoming nutritionally stressed, their population has had sufficient time to scale down the entire body to be more in tune with the energy availability of their ecosystem. In this hot and humid environment maintaining a large trunk and set of internal organs is not important in terms of thermogenesis, but in the Arctic it would be. This is perhaps why they have different body proportions to Eskimos who have longer trunks relative to their legs/overall stature and are wide-bodied. In other words, the stocky cold adapted physique may be proportioned in relation to the capacity to generate metabolic heat as much as conserve it. The contrasting body proportioning between pygmies (or indeed any lower latitude populations) and Neanderthals may also be partly explicable in these terms.

7.6 - Basal Metabolic Rate and Growth Under Conditions of Restricted Calorie Intake:

In individuals experiencing a chronic deficiency energy intake, BMR is lower than expected and the cellular level metabolic efficiency is greater than expected. Waterlow (1986; in Ulijaszek 1995) proposed three mechanisms of reduction to achieve this in:

- protein turnover
- ion-pumping (sodium-potassium ATPase and calcium)
- futile cycling in energetically important metabolic pathways

The latter two points are under the control of thyroid hormone levels. Waterlow (1986; in Ulijaszek 1995) showed that the production of T3 (Triiodothyronine) was low when the activity level of the T4-5-monodeiodinase enzyme was also low. This enzyme stimulates the conversion of the less active thyroid hormone T4 into active T3, and is hindered in its action by a low carbohydrate intake and the associated insulin response. This is consistent with Danforth's (1983 & 1985; in Ulijaszek 1995) demonstrations that circulating concentrations of T3 vary directly with the amount of dietary energy needed to maintain energy balance, and that within 48-72 hours of the onset of fasting conditions T3 levels drop by 40%.

Therefor/, lower than predicted BMR may be an indirect outcome of developmental /e plasticity. In other words, a small body size due to growth faltering during childhood would require a lower food intake to maintain energy balance, causing a reduction in T4-5-monodeiodinase activity, thus lowering levels of T3 and consequentially BMR (Ulijaszek 1995). If the level of carbohydrate is the primary factor involved, then individuals with higher levels of physical activity who maintain energy balance with higher carbohydrate intakes would have higher rate of thyroid hormone turnover and raised BMR levels (section 9.9).

A corollary to this is that individuals with low carbohydrate intakes (i.e. those subsisting largely on fat/protein), who were still physically active, would have lower T3 and BMR levels. Jackson (1990; in Ulijaszek 1995) notes that a low BMR conserves energy but the associated decrease in calcium ion pumping may cause an acceleration of free calcium ions at intra-cellular sites, and hence cell damage.

These effects on thyroid hormone status and BMR noted in instances of long-term energy deficiency are likely to be the mechanism underlying the observed stunting. Since a low carbohydrate diet suppresses T3 production and thyroid hormones are instrumental in the realisation of full growth potential, thyroid hormone status would appear to be the mediator acting to balance energy availability and demands of growth.

7.7 - Stunted Stature and Physical Work Capacity:

Spurr (1983) stated that stunted adults had reduced muscle masses and hence diminished Physical Work Capacity (PWC). However, Martorell & Aroyave (1988) claim that other measures of nutritional status (e.g. weight-for-height, energy intake, and iron levels) are better indicators of work capacity than height in most cases. (both in Martorell 1989)

Theories of body form relating to PWC and aerobic capacity have been proposed. Viteri (1975; in Spurr 1988) found PWC among groups of Guatemalan adults experiencing differential levels of malnourishment to have significantly lower VO2 max and maximal aerobic capacity than army cadets who had never suffered nutritional deprivation. These differences were shown to be associated with body composition (they disappeared when compared on the basis of cell residue - body weight less fat, water, and bone mineral).

Spur (1988) showed VO2 max and maximum aerobic power to be markedly depressed in those suffering chronic malnutrition; the degree of this reduction was relative to the severity of the lowering of nutritional status. Most of the inter group differences were accounted for by variation in muscle cell mass (measured from daily creatinine excretion). The rest is accounted for by reduced oxygen carrying capacity in the blood due to low haemoglobin levels and/or reduced maximum cardiac output.

Bergstrom et al (1967; in Spurr 1988) stated that diets in which the proportion of energy value obtained from carbohydrates has been replaced by fat and/or protein lead to reduced stores of muscle glycogen. Maximum endurance time in humans is directly related to initial glycogen content of skeletal muscle (section 9.5.2). Undernourished subjects have reduced PWC due to a decreased muscle mass. Larger men have more lean body mass and higher values for maximum PWC; but also expend more energy on body movement. However, this is at a lower relative effort and % VO2 max than smaller men (nutritionally normal or deprived status). (Spurr 1988)

Rather than stature *per se* lowering levels of PWC, the evidence suggests PWC varies under different conditions of nutritional deprivation. It is the severe/chronic energy deficiency (and the consequential metabolic adjustments made under the direction of thyroid hormones) which is the primary limiting factor to PWC, as opposed to the boimechanical limitations of shortness. A small frame may confer some biomechanical disadvantage during heavy lifting or carrying for example (or possibly even an advantage in terms of lowered centre of gravity), but if nutritional status is favourable then there is no reason why with training a high level of PWC cannot be achieved and maintained. This would appear to be the scenario experienced by the Neanderthals (sections 9.11.3 & 12.2).

7.8 - Diet, Growth, and Neanderthal Stature:

Dietary inadequacies, such as chronic or acute energy deficiency, can lead to stunting and small adult stature (section7.5), and have also been linked to low thyroid hormone production. The secular trend in certain countries is wholly accounted for by a substantial increase in leg length, as opposed to trunk elongation (section 7.4.1). Could the dietary inadequacies for which there is evidence among Neanderthals (section 2.4) be responsible for their shortened limbs, or at least play a significant part in a multi-factorial causation?

Diet is only really one part (the intake side) of the energy balance. Other factors (on the output side) include metabolic processes and physical activity levels. If energy is to be available for growth, then a positive balance of all the other factors is necessary (i.e. intake>output). Among Neanderthals living in a cold climate basic metabolism was probably very high (section 6.9). Skeletal indicators also suggest that Neanderthals were highly active and very muscular (chapter 5). Therefor, Neanderthal energy e expenditure would have been substantial. Combined with nutritional inadequacies, this would suggest that a negative imbalance in the Neanderthal energy budget was likely. Something would have had to have given way, and it seems highly probable from the lines of inquiry noted here, that that something may have been leg length.

Thyroid hormones are both influential on the secretion of growth hormone and its functioning. They also act to set the body's level of BMR (sections 7.2 & 9.6.1). So the thyroid gland can be regarded as the regulator of metabolic and physiological activity, including growth, with its action being dependant on overall energy balance. Chronic energy deficiency causes stunting, reduced work/activity capacity and BMR, and low thyroid hormone secretion. A direct causal link between the latter and former has not been made, but seems logical. Non-shivering thermogenesis stimulates increased thyroid hormone uptake by tissues, and cold dwelling populations have higher than expected BMR and rate of bone remodelling (sections 6.7.2 & 6.8.1). Both scenarios act to reduce circulating 'free fraction' thyroid hormone levels.

It could be that rather than a strict genetic adaptation to the cold, the short limbs and stocky physiques of Neanderthals were a phenotypic adjustment to two environmental stresses, namely the cold and a limited energy availability, under the direction of thyroid hormones. It appears logical that the human body's first defensive tactic to accommodate a negative energy imbalance is leg length stunting (and presumably arm length also). Maintaining proper trunk growth would be vital for development and correct physiological functioning of the internal organs (especially if metabolic heat generation is a major concern as it was for the Neanderthals), and as such appears to be more protected than limb length.

CHAPTER 8

Dietary Balance of Protein, Fats, and Carbohydrates:

High protein intakes may be detrimental to modern hunter-gatherers during seasonally (the cold or dry varieties) recurrent periods of weight loss and inadequate total calorie intake. In the Arctic having to subsist on lean meat is known as 'rabbit starvation' (Gamble 1993; p 121). It causes dietary stress due to the inefficient metabolism of protein as a (poor) energy source. Evidence suggests that the Neanderthals had a highly animal derived diet which is likely to have been deficient in fat (and carbohydrate) content, and so would have suffered the same physiological consequences as those living peoples with such dietary inadequacies (section 2.4).

8.1 - Specific Dynamic Action:

Specific Dynamic Action (SDA) is the rise in metabolism accompanying food ingestion (Speth 1987). This rise with fat or carbohydrate is only 4-6%, whereas with protein it reaches 15-20% and maybe more. This has been observed in 'traditional' Eskimo diets and Stefansson's (1944) experiment on himself (in Speth 1989). In other words, for every 100 calories of protein ingested, a further 15-20 calories are required to fuel the increase in metabolism incurred (by the liver mainly as it works to process the absorbed nutrients). During times of reduced total energy intake, the metabolic costs of satisfying energy needs with pure protein/lean meat become greater as the total meat component of the diet does.

8.2 - Protein Turnover in the Human Body:

Scrimshaw & Young (1989) state that there is extensive and continuous breakdown and re-synthesis of body proteins at a rapid rate. In general, rates of turnover exceed those of required dietary intake. Turnover rates vary between tissues and are sensitive to fluctuations in dietary intake.

The average adult male has a daily protein turnover of 230g (Tanner 1989). Most of this is from recycling proteins already present in the body, as is shown in table 4. On a high protein diet ingested protein accounts for up to 50% of this turnover; under a low protein diet this figure drops to below 33%. Turnover maintenance requires a high energy intake and accounts for much of basal energy expenditure (i.e. the heat produced when at rest). If energy intake is insufficient then the organism will begin to break up.

	Protein Synthesis (g/kg body weight/day)	*Protein Allowance (g/kg body weight/day)*
Infant (15 months)	6.3	1.3
Child (2-8 Years)	3.9	1.1
Adolescent (13 years)	5.0	1.0
Adult (20 Years)	4.6	0.75

Table 4: Protein Turnover at Different Stages of Human Development (Adapted from Scrimshaw & Young 1989)

8.2.1 - Liver Functions Relating to Amino Acid Processing:

- *Deamination* of excess amino acids: AA → keto acid + [NH3]. Keto acids are then converted into glucose or fats for storage or broken down to provide Acetyl CoA for use in the Krebbs Cycle. The NH3 is immediately combined with CO2 via the Ornithine Cycle to produce urea and water (within the hepatocyte mitochondria): $CO_2 + [NH_3] \rightarrow CO(NH_2)_2 + H_2O$. Urea is either used in the biosynthesis of creatinine, purine, or pyramidine or removed by the kidneys. A [NH3] concentration greater than 1:40,000 is fatal in mammals.
- *Transamination* of differentially present amino acids: when the amino group (NH2) of an amino acid in excess is transferred to the keto acid of one that is in short supply (only non-essentials can be manufactured). Vitamin B6 (as a cofactor) and the (appropriate) transaminase enzyme are required for this process.

There is a physiological limit to the liver's ability to maintain these functions under conditions of excessive protein consumption.

8.3 - Protein Proportions in the Diet:

There is a ceiling to the amount of protein that can be safely consumed and assimilated for caloric use on a sustained basis. This upper limit is placed at 300g or 50% of total caloric requirements under normal/non-stressful conditions. The other half (but preferably more) of a person's energy needs should come from fat or carbohydrate. Prolonged intakes above this threshold exceed the rate at which the liver can metabolise amino acids and synthesise urea, and the kidneys can filter it for subsequent excretion (Buchanan 1988; in Speth 1989). This ultimately leads to hypertrophy and functional overload of the kidneys and liver, elevated/toxic levels of ammonia in the blood, dehydration and electrolyte imbalance [making site location close to permanent water sources vital in the dry season], severe calcium loss, and lean tissue loss. So simply increasing intake of lean meat to make up the increased SDA metabolic demands is not a viable option.

McGilverie (1983) noted that most contemporary human populations obtain only 10-15% of their total caloric requirements from protein. A global study of 118 societies including a number from northern latitudes by Whiting (1958) arrived at the higher figure of 19.9%. Lemon et al (1984) concluded that a diet in which protein provides 12-15 % of calories is adequate for most athletes. (all in Speth 1989)

Turkana pastoralists in northern Kenya obtain 80% of their daily energy requirements from animal sources (milk, blood, meat), with 21% of the calories provided by protein. During periods of stress in the dry season protein's contribution to caloric requirements rises to nearly 30% (Galvin 1985; in Speth 1989). Eskimos and other circumpolar hunting groups record the highest daily per capita protein intakes (section 2.5). These peoples can thrive on a diet consisting of purely meat and fat, with protein intakes accounting for up to 45-50% of their calories, but this does not appear to be a unique genetic capacity since Euro-American explorers have survived on similar diets for extended periods. Stefansson (1944; in Speth 1989) notes the benefits of 'pemmican' (a mixture of fat and powdered jerked bison or caribou meat in the ratio of 1:6 or 1:7) on which many different peoples (from natives to immigrant explorers and trappers) throughout the North American Plains and Arctic rely on for months at a time with no ill effects. The proportion of protein provided calories in pemmican is 30-35%.

Some modern hunter-gatherers have been observed to systematically avoid lean game (Plains bison hunters seek out animals with specific hair patterns known to be indicative of high fat levels; Wilson 1924) or abandon lean meat (Australian Aborigines leave kangaroos found to be fat depleted after butchering; Hayden 1981) even under conditions of food shortage. (Both in Speth 1987)

The safe upper limit to protein ingestion is probably lowered when intakes seasonally oscillate giving limited time for the body to adjust; and in more arid ecosystems where water is scarce and enhanced dehydration must be offset (Harper; in Speth 1989). This latter factor could actually lower protein tolerance to a level of only providing 1/3 of caloric requirements.

8.3.1 - Protein Sparing Effect of Non-Protein Dietary Energy:

'Protein sparing' is the ability of ingested fat and carbohydrate to reduce the loss of body protein when ingested protein is being utilised for energy provision. Energy demands of the body, and especially the brain (nervous tissue can only utilise glucose for energy production), take priority over protein needs. When caloric intake is limited the amino acids of ingested protein are degraded, and the non-nitrogenous residues are converted into glucose (gluconeogenesis), fat, or are oxidised directly to meet energy demands. Protein is thus unavailable for its normal uses in the body (e.g. antibody production by the immune system) and is not replenished (section 7.5).

If calorie shortage becomes severe, skeletal muscle is catabolised to meet energy demands. Amino acids (alanine in particular) are converted into glucose in the liver.

'Glucose sparing' then also occurs as non-nervous tissues reduce their glucose catabolism and increase their fatty acid utilisation, so that the brain has sufficient glucose for normal functioning (Vander 1994).

Human metabolic processes preferentially use fat and carbohydrates as energy sources (Blaxter 1989; in Cachel 1997). Substrate cycles may explain the differential thermal response to food types (Newsholme 1978; in Cachel 1997). Thus, when fat or carbohydrate are ingested they offer a more readily desirable energy source, and a reduction in body protein loss ensues since protein is no longer the body's primary energy source (Munroe 1964; Richardson et al 1979; in Speth 1987). The clinical treatment of severe protein malnutrition requires administration of protein accompanied by sugar and fat; protein alone has insufficient dietary energy and such supplementation is necessary even though it is the lack of protein from which the body is dying (Whitehead 1992; in Cachel 1997).

Studies show the protein sparing capacity of carbohydrate exceeds that of fat. So carbohydrates should preferentially be selected over fat. However, their relative availabilities in a seasonal environment plays the major role in this decision, often meaning that it is actually fat which is sought during periods of stress. As Cachel (1997) states "....a fatless diet is effectively a starvation one".

8.3.2 - Fat/Marrow Acquisition:

In the brain, tongue, lips, nose, and spinal cord fat is 'structural' in the form of myelin sheathes for nerve cells and is not 'metabolisable' like the stored fat tissues elsewhere in the body which are utilised in times of nutritional stress. The brain also contains 18% more cholesterol than any other body parts; but the role of this nutrient in the traditional diet is unknown. Binford (1978; in Stiner 1994) noted that in fall/winter the Nunamuit concentrate on the metabolisable fat reserves and muscle of their prey, but come spring their primary target becomes the head parts (especially the tongue) preferentially of the young and female. Past hominids seem generally preoccupied with the head and axial parts, or at least incorporated such parts into their diet on a very regular basis (sections 4.1 & 4.2). A similar tactic is observed among tropical hunters where fat is chronically unavailable.

Yellen (1977; in Speth 1989) observed modern San of the Kalahari Desert going to the lengths of removing marrow and boiling the smashed up bones in order to obtain the last remaining lipid reserves in their prey. Significant weight loss occurs annually, despite such efforts to compensate for diminishing overall caloric returns, during the late dry and early wet season (Wilmsen 1978; in Speth 1987). Konner & Worthman (1980; in Speth 1987) noted increased frequency of San infant suckling during the late dry/early wet season, which may be due to inadequate nutrient content or insufficient total production of breast milk. Enforced lean meat (and protein) consumption also increases to up to 2 kg/4.5 lb daily per person. All of which points to a significant level of food stress during this period, with non-protein energy sources having become scarce and thus a critical issue.

Some Middle Palaeolithic groups concentrate on the very young of medium-large sized species (Klein & Cruz-Uribe 1984; in Fernanda Blasco 1997); others on exploitation during the breeding season (Stiner 1994). These scenarios would correlate with Cachel's (1997) claims for the need to maximise fat acquisition, since the young tend to have greater fat reserves than the old and breeding season is one marked by a fattening process. However, the very young and mothers approaching or having recently given birth are weaker members of the group and would also be attractive to hunters in this respect. Their body fat status could just be coincidental.

At Italian Middle Palaeolithic sites, there is widespread evidence of marrow extraction which is often extended to the third phalanges of ungulates (i.e. deer and aurochs). Stiner (1994) suggests such processing was carried out in early autumn/winter when animals were in a fattened state and the marrow worth extracting. But if fat was abundant why did these hominids bother to tap such extreme reserves? It seems more likely to have been done during the lean period when fat acquisition became most vital. (section 2.3.3 & 4.1)

8.4 - Diet and Fecundity:

Fecundity in females today is highly sensitive to seasonal deficiencies in dietary energy intake and also exercise/physical work levels (Frish 1988). Both have a negative effect on the energy balance and act to block the possibility of conception.

Frish and McArthur (1974) postulated that the age of menarche and maintenance of menstruation is dependant on attaining a minimum weight-for-height ratio threshold (i.e. having a critical body fat buffer), with undernourishment causing delayed menarche, irregular/anovulatory cycles, amenorrhoea, and early menopause.

Ellison (1990) claimed that energy balance is the critical factor and that sudden drops/oscillation in weight cause infecundity. The *'Hypothalamus Tracking Process'* states that fat levels in the blood are monitored and accordingly pituitary gland stimulation is controlled (it releases various hormones associated with ovulation and the menstrual cycle).

Either way, females are only able to conceive when energetically capable of completing the pregnancy. This seems to have become a crucial factor among humans in particular as brain size and complexity increased and a greater impetus was placed on the mother to fuel its growth during gestation and lactation (section 10.1).

"....low birth rate due to undernutrition during pregnancy is associated with higher infant morbidity and mortality and poorer growth" (Scrimshaw & Young 1989; p 28).

"Low maternal height is widely recognised as a risk indicator of low birth weight and infant mortality" (Martorell 1989; 19).

Acclimatisation to low fat reserves can allow ovulation under chronic nutritional stress, but usually with detrimental effects on the foetus/new-born. Shutdown of the reproductive system is rapid if sudden weight loss is experienced with acute nutritional stress.

8.5 - Physiological Stresses in Neanderthals Stemming From The Composition of Their Diet:

Generally speaking the Neanderthals were heavily reliant on meat, at least on a seasonal basis. It is also apparent that such nutritional stress began early in the life of Neanderthals, with the very prompt introduction of a meat-based diet during infancy (sections 2.4.1, 2.4.2 & 2.4.3). The carcasses they were obtaining were probably largely devoid of fat and grease reserves, at least on a seasonal basis in synchrony with the Neanderthal's peak demand for them (section 2.3.3). Evidence identifies a substantial degree of some form of nutritional stress within Neanderthal populations (section 2.4.6). It is these factors, relating to the (seasonal) reliance on (lean) meat and lack of carbohydrates, that are most likely to have been responsible for generating this stress.

So, it is feasible that the Neanderthals suffered the knock-on effects of dietary inadequacies which are noted as affecting certain populations today. (section 8.3) Thus the need for calorie acquisition and the excessive ingestion of protein would have detrimentally affected the Neanderthals in several ways.

In the individual disproportionate protein consumption would have created several barriers to functioning at full capacity on a daily basis:

- The instigation of a low (possibly negative) energy balance in the face of the energetic demands of high activity levels (chapter 5) and the hypermetabolism associated with living in cold climates (section 6.5.1).
- The onset stunting if experienced during childhood and other associated conditions (section 7.5), including being detrimental to the maintenance of muscle mass since lean tissue is broken down to provide energy.
- The functional overloading of internal organs, with subsequent muscular and nervous impairment (section 8.3).

On the population level such nutritional stress would have reduced fecundity/fertility hence the regenerative capacity of the population (section 8.4). Could this factor have had a fundamental influence on the Neanderthals demise, particularly in the face of competition from a less stressed more effectively reproducing population: Zubrow's (1989) 2% advantage perhaps (section 1.1)? Cachel (1997) sees the European Middle-Upper Palaeolithic transition as being backed by increased fat availability due to its fundamental role in initiating population growth, as is theorised to have accompanied the change.

It is obvious that in order to have successfully survived for so long the Neanderthals must have developed a substantial capacity for energy conservation (chapter 11). Fuelling their robust muscular physiques and associated activity levels, high rates of bone remodelling/mineralisation and metabolic heat generation, reproduction (highly expensive considering the large size of the Neanderthal brain) in the context of their low energy ecosystem and the physiological stresses experienced because of their reliance on lean meat was a remarkable feat.

CHAPTER 9

Neanderthal Locomotion, Mobility and Activity Patterns:

"....despite significant differences in postcranial morphology between the Neanderthals and their modern appearing successors, there is nothing in their skeletal anatomy to indicate that they had basic patterns of movement different from those of modern humans. The configurations and orientations of their lower limb articulations are all within the ranges of variation of modern humans" (Trinkaus 1983; p 167). (section 5.3)

9.1 - The Energetic Cost of Hominid Locomotion:

Numerous authors (e.g. Napier 1963; Cambell 1966; in Rodman & McHenry 1980) state that human bipedalism is efficient for walking long distances. The efficiency of human walking is partly due to "a finely tuned system of storage and recovery of the energy used for motion within each stride....The bipedal posture of man is ideally suited for this pendular motion" (Carrier 1984).

However, compared to most quadrupedal mammals, humans are energetically inefficient when running. Empirical studies have shown that at maximum speeds human bipedalism costs twice as much energy per kilogram body weight per kilometre travelled, as predicted for a mammalian quadruped of equal size (Taylor et al 1970). Fedak et al (1974) claim that human running is 75% less efficient than walking. (all in Rodman & McHenry 1980)

At a middle distance running speed the cost of overcoming wind resistance is about 7.5% of the total energy consumption (at sprint speeds this cost rises to 13%). Deformation of and friction against the ground is negligible, unless running on unstable surfaces such as sand or loose gravel. Therefor, work done on the environment is only a tiny fraction of the total. The work required to increase breathing movements and heart pumping rate is significant but still small compared to that needed for mechanical body movements, which consumes the majority of energy used in running by humans. (Schmidt-Neilson 1997)

9.1.1 - The Adaptive Importance of Improved Locomotor Efficiency:

Leonard & Robertson (1997a) hypothesised that the adaptive importance of reducing maintenance energy expenditure (the locomotor component, in particular) was in allowing a greater proportion of the total energy budget to be channelled into reproduction and offspring rearing. The ability to conceive is related to the individual female's energy balance and energy conservation in other spheres will be beneficial in terms of reproductive rates (section 8.4).

Increases in locomotor efficiency should be more adaptively beneficial for animals with larger ranges since this would produce a larger (proportional) reduction in the maintenance energy budget. All other factors being equal, energetic benefits of more efficient locomotion will increase as the daily range of the animals considered does (Leonard & Robertson 1997a). Increased locomotor efficiency would also be important in low energy ecosystems and/or cold climates whereby energy balance will be driven in a negative direction. Both were conditions of Neanderthal existence.

9.2 - Neanderthal Lower Limbs and Locomotion:

Bone tissue adapts itself during growth and life to the kinds of mechanical forces that act upon the skeleton. The robusticity and dimensional expansion of femur and tibia shafts (and articular surfaces) of the Neanderthals are at/exceed the limits of the modern range. (sections 5.2 & 5.3).

According to Trinkaus (1989) this lower limb hypertrophy among Neanderthals offers increased strength against peak biomechanical loads and repetitive stress, suggestive of long continuous/vigorous movement across the landscape (in contrast to the EAMH pattern of reduced skeletal robusticity). Wide pedal phalanges and femoral/tibial shaft cross-sectional shapes indicate considerable irregular, poorly directed movement (contrasting with the straight line, uni-directional striding of the early moderns). Trinkaus (1989) sees this as evidence that the Neanderthals' subsistence related locomotion was less organised and therefor less efficient than that of the EAMH. e

Many studies note the morphological shift across the transition as being a consequence of ecogeographic variables, namely those relating to climate (sections 6.1, 6.2 & 6.3). Caspari's (1994) study supports the 'mobility hypothesis' whereby limbs lengthened under selective pressures for increased individual and group mobility in the Upper Palaeolithic. This is claimed to be independently supported by archaeological data and other aspects of early Upper Palaeolithic skeletal morphology (e.g. the rugosity of markings for muscle attachments on long bones). Ecogeographic variation is an important explanation of clines in body form, but it is not the only factor affecting limb proportions. "Alternative, non-climatic explanations of Upper Palaeolithic limb proportions may be more appropriate" (Caspari 1994; p 58).

9.3 - The Mobility Hypothesis:

Wolpoff (1989) and Caspari (1992) proposed that an increase in mobility was the driving force behind the longer limbs of the earliest modern Europeans. Selective pressure for improved locomotor efficiency produced long limbs, rather than their being a consequence of a tropical origin. (in Holliday & Falsetti 1995)

Differential mobility affects limb proportions, with such proportional differences overlying climatic patterning. The extreme view was voiced by Frayer (1992; in Holliday & Falsetti 1995), who claimed that climatic adaptation had little if any influence on distal limb segment lengths in Late Pleistocene Europe. However, the majority of supporters would limit the mobility hypothesis' ability to explaining the observed deviations from climatic expectations. The retention of high crural indices through the European Upper Palaeolithic and Mesolithic, in the face of considerable climatic change, is interpreted as evidence for the lack of a positive relationship between climate and lower limb length. The basic premise is that the early modern humans were more mobile than their Neanderthal predecessors/contemporaries. The selective pressures for efficient locomotion explain why they evolved and retained longer legs. The shift also involves other associated morphological features, such as reduced muscularity of the lower limb.

Lower limb length has important implications for hominid locomotor energetics. Longer legs increase stride length and thus reduce the number of strides necessary to cover a set distance (Yamazaki et al 1979; Jungers 1982; in Holliday & Falsetti 1995). Heglund et al (1982; in Holliday & Falsetti 1995) stated that the primary energetic cost of bipedal locomotion at any given speed is the number of strides taken. So the proportionally longer limbs of all hominids, to some degree or another, have acted to reduce the energetic costs of bipedal locomotion; and have almost certainly arisen due to direct selective pressures for this saving.

Despite their longer legs relative to much earlier hominids, there is considerable variation in length within the genus *Homo*. The retention of a longer lower limb in European EAMH, compared to the short legs of the Neanderthals, is proposed to have resulted from a shift in subsistence strategy whereby the EAMH were more mobile than the Neanderthals. The subsistence shift and mobility increase is backed up by archaeological evidence for the increase in the quantities of 'exotic' materials at early Upper Palaeolithic sites (Klein 1969; Mellars 1972; in Holliday & Falsetti 1995; section 3.5)

Contrary to this idea, Steudel's (1994) study of 21 mammalian species and compared the variation in limb length to that in energetic costs of locomotion; and even having removed the influence of body mass disparities no correlations were significant. Steudel (1994) concluded that " limb length does not importantly influence an animal's locomotor efficiency". But presumably by locomotion Steudel is referring to walking rather than running.

grammar

9.3.1 - Types of Mobility:

Binford (in Holliday & Falsetti 1995) differentiated between two types of mobility among non-sedentary subsistence-level groups, such as hunter gatherers.

1. Logistic Mobility - describes short-term forays away from the base camp, for purposes such as food getting or trading with other groups.
2. Residential Mobility - this is a shift in the location of the base camp.

9.3.2 - Mobility Versus Cold Adaptation Hypotheses:

Holliday & Falsetti (1995) assembled anthropometric, residential mobility, and climatic data for 19 recent hunter-gatherer peoples. No relationship was found between lower limb length (in terms of relative sitting height) and residential mobility. Thus the authors reject high mobility as providing the selective pressure behind longer limbs. A significant relationship between climate and relative lower limb length "could not be rejected".

It should be noted that the data used here did not take logistic mobility into account, only residential mobility. But Holliday & Falsetti (1995) claim that each type of mobility is correlated and that the home range variable they used is reflective of logistic mobility; so their results are reliable. Besides which, they say that the collection of logistic mobility data is very difficult.

However, it seems more likely that selective pressures on body/limb form relating to mobility should operate on the basis of logistical mobility activity. The ability to efficiently secure subsistence on a daily basis would be more important than seasonal migrations. The former involves a range of activities carried out at different intensities over limited durations which may be quite specialised but always vital in securing game, while the latter is a steady prolonged trek to which hominid bipedalism is generally highly adapted. Physical adaptations among hominids that could substantially improve short-term hunting success would probably not have significantly hindered the efficiency of walking long distances (sections 12.2 & 12.3).

So, Holliday & Falsetti's (1995) argument could be considered flawed on this account and their conclusion weak as their study only "fails to reject" the correlation of climate with body form rather than proving it outright. This distinction between types of mobility and their implications also seems to be a problem with the mobility hypothesis. Its central proposition of reduced mobility for the Neanderthals due to their short legs does not sit well with the picture painted by their substantial physical presence which seems to be one of a highly active population (section 9.11.3).

9.4 - Muscular Development and Activity Patterns:

As well as lower limb length and other biomechanical aspects of the skeleton affecting locomotor efficiency, physique also plays an significant role. Factors including body weight and muscle fibre type are important determinants of hominid mobility and activities relating to hunting. Critical assessment of the large Neanderthal physique in discussions of their behaviour has been generally lacking beyond the recognition that it must have been both costly and vital.

"The pervasiveness of this robusticity among the Neanderthals implies that it was an important part of their biological adaptation. It would have enabled them to generate and sustain more strength and higher levels of activity on a habitual basis than can most anatomically modern humans. However, the development, maintenance, and operation of such a hypertrophied body would have been energetically costly, an important consideration for hunting and gathering populations that....were frequently close to the limits of their energy reserves. This suggests that their massiveness was necessary for survival; otherwise selection would have acted quickly to reduce the level of hypertrophy in their populations" (Trinkaus 1983; p 177-178).

9.5 - Muscle Structure:

On average approximately 40% of the mammalian body mass is comprised of voluntary skeletal muscle.

Schmidt-Neilson (1997) summarises the basic protein components of a muscle fibre:

1. Thick filaments - myosin protein molecules
2. Thin filaments - actin protein (globular) molecules
   - tropomyosin protein (strand) molecule
   - troponin protein (calcium-binding) molecule

A membrane, the sarcolemma, surrounds and penetrates deep into the muscle forming transverse tubules that run across the muscle fibre's cells. This set up is known as the T system. Waves of depolarisation reach the muscle interior via this system (Aiello & Dean (1990).

The sarcoplasmic reticulum is an extensive intracellular network of flattened vesicles, that surrounds the muscle fibrils. It sequesters calcium ions, pumping them from the sarcoplasm into the lumen of the sarcoplasmic reticulum. The sarcoplasmic reticulum acts (Schmidt-Neilson 1997):

- to maintain the low concentration of calcium ions in the sarcoplasm of the muscle when at rest
- as a source of calcium ions during stimulation of the muscle fibre, allowing contraction to occur
- to remove calcium ions when the waves of depolarisation over the T-tubule membrane cease, thus halting the contraction

The ionic calcium concentration necessary to initiate a contraction is 10 to the power -5 mol/litre. This is only one one thousandth of its concentration in blood plasma.

9.5.1 - Muscular Contraction:

A twitch (or single contractile action) is initiated at a neuromuscular junction. At the synapse, when an impulse arrives the synaptic knob becomes permeable to calcium ions at the pre-synaptic membrane. This causes microfilament contraction so that the synaptic vesicles migrate and release the transmitter substance via exocitosis. The transmitter substance binds to receptor sites on the post synaptic membrane. At a neuromuscular junction the post synaptic membrane then becomes permeable to calcium ions. If summation of transmitter substance reaches the required threshold then a post synaptic potential is generated.

The action potential, or wave of depolarisation, moves along the sarcolemma and down the T-tubules. Successive waves act to increase the sarcoplasmic reticulum's permeability to calcium ions. The resultant influx of calcium ions is necessary as a cofactor of contraction, and its initiation occurs if the calcium ion threshold exceeds 10 to the power -6 M.

Calcium ions bind to the troponin molecules which undergo a conformational change. This in turn causes the tropomyosin molecules to swivel out of their resting positions which plug the actin binding sites. Once the tropomyosin molecules have moved the actin molecules are free to interact with the myosin molecules of the thick filament, and a twitch occurs. A single contraction from a single stimulus is a twitch. The summation of additional stimuli gives a smooth sustained contraction, called a tetanus.

So having calcium ions available in the extracellular pool enables the proper initiation of muscular contraction. Competition for calcium is present between muscle and bone tissue, however the former seems to take priority (section 6.8). The sarcoplasmic reticulum subsequently acts to remove excess calcium ions and thus stop the contraction.

9.5.2 - Energy Storage and Muscle Weight:

The energy source for muscular contraction is Adenosine Triphosphate (ATP). When the terminal phosphate group is split off the energy from the 'high energy' phosphate bond is released. ATP only makes up 2-4% of the wet weight of muscle and is thus used up very quickly. An additional source of energy comes from Creatine Phosphate (CP), whereby its phosphate group is transferred to ADP (Adenosine Diphosphate) to form ATP. CP is present in significant quantities in muscle, but as it is used for short periods of high intensity exercise it is depleted rapidly. For extended heavy muscular activity glycogen (1-2% of the wet weight of muscle) is oxidised to release energy. If activity is prolonged (i.e. of lower intensity but over a longer time frame) carbohydrates and fatty acids are mobilised in the liver and adipose tissue. (all in Schmidt-Neilson 1997)

The storage of glycogen as an energy reserve requires the carrying of more weight than fat because (Schmidt-Neilson 1997):

- Its lower energy content per unit weight
- For every gram stored in the liver or muscles, 3 grams of water must be stored as accompaniment
- Thus for a given energy value, glycogen storage may necessitate the carriage of up to ten times the weight relative to the storage of fat.

Despite being effectively a heavy component of muscle, glycogen is a very important source of energy in power athletes. Under such exercise conditions the cost of carrying the additional weight of glycogen is offset by two important capacities. Schmidt-Neilson (1997) describes the beneficial aspects of glycogen storage as follows:

- Rapid provision of energy for carbohydrate metabolism
- Can provide energy under anoxic conditions, most common during heavy muscular exercise when the cardio-vascular system cannot keep up with the demand for oxygen by the tissues.

The depletion of muscle glycogen is also involved in the onset of muscular fatigue during exercise. Its depletion rate depends on the level of blood glucose and rate of fat oxidation (Holloszy & Booth 1976). The human body's glycogen and fatty acid reservoirs vary greatly with diet and physical conditioning. A diet rich in carbohydrates can double the muscle glycogen stores in 2-3 days, and thus an individual's endurance capacity (Bergstrom 1967) - the 'carbo-loading' practice by athletes. In contrast a diet rich in protein and fat causes a decrease in stored muscle glycogen and prematurely depletes glycogen during exercise (Gollnick et al 1972). During exercise the mobilisation and utilisation rates of glycogen and fatty acids are controlled by a number of hormones; one of which is thyroxin (Stryer 1975). (all in Carrier 1984)

9.6 - Muscle Type and Mechanical Efficiency:

Kuffler & Williams (1953; in Schmidt-Neilson 1997) distinguished between two fundamentally different types of muscle fibre:

Type I - Slow or 'tonic' muscle fibres -

- contain many mitochondria have higher myoglobin content and are red in colour
- operate on an aerobic principle (oxidative metabolism)
- are connected with small nerve fibres
- produce prolonged low force contractions and are fatigue resistant (e.g. maintaining body posture and jogging)

Type II - Fast or 'twitch' muscle fibres -

- have a lower myoglobin content and are pale or white
- operate on an anaerobic system (glycolytic metabolism)
- are associated with large nerve fibres with high conduction velocities
- produce rapid body movements (e.g. sprinting and jumping)

There are two varieties of fast twitch fibres (McArdle et al 1996) -

- Type IIa are the true fast-glycolytic fibres with maximal anaerobic potential
- Type IIb are intermediate fast-oxidative-glycolytic fibres. These fibres have a fast shortening speed combined with the capacity for both types of energy transfer.

So effectively, there are three different fibre set-ups which give rise to different classifications of muscular contraction, as shown in table 5. Wendt & Gibbs (1973; in Strickland & Ulijaszek 1990) found that maximum mechanical efficiencies (work/total enthalpy) varied from 16% in fast contracting/fatiguing fibres to 23% in slow twitch ones.

Muscle Description	*Twitch Contraction Time (ms)*	*Tetanic Force (gram force)*
Fast Contracting & Fast Fatiguing	34	60
Fast Contracting & Fatigue Resistant	40	20
Slow Contracting & Non-Fatiguing	73	5

Table 5: The Three Muscle Fibre Configurations and their Contractile Properties (Adapted from Burke et al 1971; as reproduced in Schmidt-Neilson 1997)

9.6.1 - Nutritional Status, Thyroid Hormone Levels, and Muscle Type:

Robbins (1991) identifies three aspects of thyroid hormone activity which will affect the ability of the individual to perform physical work:

1. increased relaxation rate of skeletal muscle subsequent to contraction
2. increased heart rate and contractile force in cardiac muscle
3. increased oxygen consumption (except brain, spleen and testis), and metabolic processes such as the oxidation of body fuels

Mixed evidence exists regarding the ability to convert fibre types through training. Proportions of each fibre type appear to be largely under genetic control but some limited transformations may be possible. Ianuzzo et al (1977; in Kulkarni & Shetty 1992) first postulated that thyroid hormone may affect muscle fibre types, favouring the slow twitch variety. Further studies have also concluded that muscle phenotype characteristics may be modified by thyroid hormone status (Nicol & Bruce 1981; Jolesz & Sreter 1981; in Strickland & Ulijaszek 1990).

Clinically hypothyroid patients show significant improvement in energy economy during quadriceps muscle function tests compared to euthyroid controls (Wiles 1979; in Strickland & Ulijaszek 1990). Experimental studies show thyroid hormones to influence the sequestration and release of calcium ions by the sarcoplasmic reticulum and ATP consumption in calcium pumping during the contraction cycle, and therefor overall mechanical efficiency (Suko 1973: Limas 1982; in Strickland & Ulijaszek 1990). Millward (1986; in Ulijaszek & Strickland 1991) showed that severe dietary energy deficiency and the resultant reduced thyroid hormone levels are associated with reduced RMR.

Kulkarni & Shetty (1992) found a Chronically Energy Deficient (CED) group to have significantly higher net mechanical efficiencies than a well nourished control sample. They also had 15% lower energy costs, when expressed as a percentage of predicted data. The inheritance of higher proportions of slow twitch muscle fibres and greater ergonometric efficiency were thought to be contributing factors to the overall mechanical efficiency and energy conservation in such CED subjects. Nwoye et al (1982; in Strickland & Ulijaszek 1990) propose that the low thyroid hormones in populations on low food intakes actually mediate adaptive changes in resting energy expenditure by determining the inter-conversions of contractile and metabolic properties of fast and slow twitch muscle fibres Henriksson (1990; in Kulkarni & Shetty 1992) also found that in humans there is a selective reduction in the size of fast twitch fibres during undernutrition.

Strickland & Ulijaszek (1990) found that at lower levels of step exercise well nourished Gurkha soldiers showed significantly lower gross and net energy expenditure (therefor greater net mechanical efficiencies). The ratio of gross energy expenditure to BMR was lower in Gurkhas at lower rates of stepping, but differences in energy expenditure were not significant at higher levels of exercise. Thus, it is possible that the Gurkhas also have a higher proportion of the slow twitch muscle fibre type.

There is endemic goitre in the Himalayas (Ward et al 1989; in Strickland & Ulijaszek 1990); the prevalence of which reached 57% in 1985 in some regions (Acharya 1987; in Ulijaszek & Strickland 1991). Goitre is a condition which arises due to a deficiency of iodine, which is a component of thyroxin hormone. An increase in dietary iodine availability results in a rapid response in terms of the production of thyroid hormones (Hetzel 1987; in Ulijaszek & Strickland 1991). Any change in BMR due to this among the Gurkhas would have occurred prior to stationing in Britain during build-up programmes in British army camps over there, so a phenotypic adjustment during development being maintained after the environmental stress had been relieved is envisaged. Similarly, the Tamang (in Nepal) have net mechanical efficiencies of 22-27%. Their high level has been proposed as being a reflection of their adaptation to nutritional stress (Strickland & Ulijazsek 1990) and/or anaemia (Panter-Brick et al 1992; both in Katzmarzyk et al 1996).

It is speculated that differential thyroid hormone status during growth and development could influence greater muscular efficiency via its effect on skeletal muscle phenotype. This could result from suffering chronic iodine and/or energy deficiency during childhood, since both seem to affect thyroid hormone levels.

9.7 - Lower Limb Muscle Activity During Walking and Other Tasks:

"....work strongly suggests that the importance of bipedal locomotion in evolutionary terms lies with walking rather than running." (Aiello & Dean 1990; p 272)

In human bipedalism the leg operates like a compound pendulum which maximises the use of kinetic energy. Electromyographic studies by Suzuki (1985) demonstrated that muscle activity in walking is not intense. Previously Tuttle et al (1979) had found surprisingly little activity in the hip and thigh muscles during walking. (both in Aiello & Dean 199)

9.7.1 - The Gluteus Maximus Muscles:

These muscles are inactive during walking but contract significantly during running. Indeed, Duchenne (1959; in Luttigens & Hamilton 1997) has claimed that paralysis of the gluteus maximus did not have any effect on normal walking among human subjects. They function as an abductor to maintain the lateral flexibility of the hip joint in running (Stern et al 1980), and stair climbing (Lyons et al 1983; both in Marzke et al 1988).

Karlsson & Jonnson (1965; in Marzke et al 1988) determined that the cranial portion of the gluteus maximus functions in the extension, lateral rotation, and abduction of the femur on the trunk and in controlling the flexion of the trunk on the femur. Cranial portions of the left and right gluteus maximus muscles were studied by Marzke et al (1988) with electromyography while subjects performed different tasks. These muscles was used significantly in throwing and clubbing as they initiate rotation of the pelvis and stopping it as trunk rotation ceases and the forelimb accelerates. They also act to stabilise the pelvis when digging. The muscles also show marked and prolonged activity when the trunk is held in partial flexion in the course of lifting/carrying heavy objects.

The gluteus maximus inserts onto the gluteal ridge (also known as the hypertrochanteric line) and the ilio-tibial tract. The gluteal ridge is a highly variable feature:

- it may include a linear depression along the ridge's lateral border (the hypertrochanteric fossa)
- this depression can be present and the ridge absent
- a distinct knob of bone may develop (the third trochanter or gluteal tuberosity) in combination with either of the other two features or on its own
- The Neanderthal form is distinctive. The hypertrochanteric fossa occurs within the gluteal ridge which is pronounced (section 5.3).

9.8 - Muscle Development and Physiology in Modern Athletes:

Developing, fuelling, and maintaining a substantial muscle mass is dependant on several factors:

- A protein intake sufficient to allow the high protein turnover rate in muscle.
- A calorie intake such that the breakdown of lean tissue for energy is not necessary.
- Specific types of physical activity undertaken.
- Rest also seems to be important.

The underlying theme running through these points is the individual's energy balance which must be kept positive in order that a large muscle mass is viable.

The male somatotyping system was devised by Sheldon (1954; in Tanner 1964). Three extreme body forms are categorised:

1. Endomorphy - "approaches the spherical as nearly as is humanly possible". Internal organs are large and sub-cutaneous fat deposition is all over the body (except distal limb segments).
2. Mesomorphy - "muscle and bone predominate". The classic male Herculean physique where even distal limb segments are well muscled.
3. Ectomorphy - "linear". Both muscle and sub-cutaneous fat are lacking. Skin surface area and nervous system are extensive.

Physical education students (mostly body contact players e.g. rugby and boxing) group near the mesomorph extreme but with significant elements of both endomorphy and ectomorphy. Olympic track athletes tend to fall somewhere the continuum between mesomorphy and ectomorphy, with virtually no endomorphy quotient. By contrast, Olympic weight lifters, throwers and wrestlers lie on the endomorphic side of mesomorphy. Tanner (1964; 45) describes "....a gradient of decreasing mesomorphy and increasing ectomorphy as we pass from the sprints through the 400m to the 800m and the longer races....The sprinters and the 110m hurdlers together stand out as being considerably more mesomorphic than all other track athletes".

"Sprinters are relatively short and very muscular men, compared with middle distance runners. Their shortness is chiefly due to short legs, not a short trunk. All their limb muscles are larger in relation to their bones than are those of other runners....a clear gradient of build is seen running from the 400m to the marathon....The 400m men are large, long-legged, broad-shouldered in relation to their hips, and fairly heavily muscled. Long distance runners are small, short-legged, narrow shouldered, and relatively lacking in muscle" (Tanner 1964; 104).

Tanner (1964) does miss the importance underlying the distinction between sprinters and distance runners in terms of their upper bodies development. Tanner claims that sprinters have large arm and shoulder muscles due to favourable environmental conditions during growth as sprinters do not train "by running on their hands" (p 112). Upper body strength, and hence size, is significantly more important in sprinters. The biomechanical counterbalance of arm action during locomotion becomes more important as speed increases. Arm swing is accentuated when sprinting and especially starting. Sprinters will therefore naturally develop their arm and shoulder muscles, and in order to improve arm speed (and hence leg speed) will weight train to further enhance these muscles.

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9.8.1 - Skeletal Development in Modern Athletes:

Tanner (1964) proposes that the short legs of sprinters are beneficial in terms of rapidity of movement and the length of the lever from hip to ankle. Thus a mechanical advantage in terms of natural frequency of leg oscillation is achieved (Shephard 1991).

Short legs could be due to their large musculature indirectly. Heavy/stressful exercise levels and large muscular development during growth acts to cause premature skeletal maturation; with premature epiphyseal closure resulting in shorter legs (Tanner 1964 & Shephard 1991). Leg growth rate just prior to puberty is faster than that of the trunk (section 7.3). Therefore, early onset of puberty deprives the individual of more leg (limb) than trunk length increment. Prime examples are modern gymnasts and weight lifters.

Extracellular calcium levels may also play a role. The high demand for calcium ions (and energy) in powerful muscle contractions will prevent resorption by bone and length may be sacrificed for proper mineralisation and strength (sections 6.8 & 6.9).

9.9 - The Effects of Exercise on Metabolism and Daily Energy Consumption:

"Exercise-training can substantially increase daily energy expenditure, because of the energy cost of exercise and the increase in post-exercise energy expenditure" (Almeras et al 1995).

Poehlman et al (1989; in Ulijaszek & Strickland 1991) stated that highly trained men have higher RMR than less- or un-trained men, even when adjusted for metabolic size. This is probably linked to the increased turnover of thyroid hormones noted to occur with athletic training (McArdle et al 1996).

9.9.1 - The Effects of Body Weight:

Carrier (1984) defines the energetic cost of transport as oxygen consumption per unit body mass per unit distance travelled. The cost of any exercise, especially a weight-bearing one, is generally higher for heavier people. Table 6 shows the energy cost of locomotion at different speeds to increase directly with body mass. While walking people of the same body mass record such a minor variation in oxygen uptake that the energy expended can be accurately predicted from body mass alone (McArdle et at 1996). It is clear from these lines of inquiry that 'weight economy' is an important aspect of limiting energy expenditure (Schmidt-Neilson's term 1997;172).

"The total number of calories expended by the heavier person....is still considerably larger than that by a lighter counterpart, simply because the body mass must be transported during the activity, requiring proportionately more total energy." (McArdle et at 1996; p 161)

	Energy Expenditure (kcal/min) for different locomotor activities		
Body Weight (kg)	*Marching*	*X-Country Running*	*Field/Hillside Walking*
47	6.7	7.8	3.9
50	7.1	8.2	4.1
53	7.5	8.6	4.3
56	8.0	9.1	4.6
59	8.4	9.6	4.8
62	8.8	10.1	5.1
65	9.2	10.6	5.3
68	9.7	11.1	5.6
71	10.1	11.6	5.8
74	10.5	12.1	6.1
77	10.9	12.6	6.3
80	11.4	13.0	6.6
83	11.8	13.5	6.8
86	12.2	14.0	7.1
89	12.6	14.5	7.3
92	13.1	15.0	7.5
95	13.5	15.5	7.8
98	13.9	16.0	8.0

Table 6: The Effect of Body Weight on Energy Expenditure at Varying Speeds (Adapted from McArdle et al 1996; Appendix D; p 770-781). To obtain Total Energy Expenditure for a given activity simply multiply the value corresponding to the appropriate weight by the duration of that activity.

Given sufficient time, the weight and composition of the human body will adapt to any sustained exercise/dietary regime within its physiological limits. In terms of its fat free mass, a balance will be struck between muscle development and the muscular effort to carry that muscle bulk within the particular exercise regime. Under certain exercise conditions the benefits of having a large muscle mass will be eliminated/inverted as carrying the extra weight raises the energetic costs beyond this optimal point. (section 9.5.2)

9.9.2 - The Balance Between Muscle Bulk and Activity Levels:

Maughan et al (1983; in Shephard 1991) used CT scans to show that marathon runners had the same thigh dimensions and muscle strength as untrained control subjects. Sprinters showed a 10% greater muscle cross-section and an 18% advantage in muscle strength. Slender muscles obviously confer an advantage in distance running. In such endurance events there is a need to maintain a high rate of oxidation in muscles in order to avoid lactic acid production and oxygen debt. Slender muscles with fully dilated capillaries need less blood to profuse them than larger muscles (if capillary density is equal). The least requirement for blood, and hence cardiac output, will be by "....the slenderest muscle capable of producing the necessary power to maintain the required speed of limb movement" (Tanner 1964; 110). A large muscle would require a greater cardiac output and is therefore more costly, but ultimately beneficial in terms of speed and strength. (section 9.8)

"....endurance athletes exhibit slow twitch fibres of relatively normal size. Weight lifters and other power athletes....show a definite enlargement, especially in the fast-twitch muscle fibres. These fibres may be 45% larger than those of endurance athletes or sedentary people of the same age. This is because power and strength training induces a definite enlargement of the fibres' contractile elements - specifically the actin and myosin filaments and the total glycogen content" (McArdle et al; 333)

In essence it is apparent that sprinters and power athletes tend to have larger muscle cross-sections compared to endurance/stamina athletes and control subjects, and a greater proportion of enlarged fast-twitch fibres. In other words, those athletes involved in limited explosive bursts of vigorous activity interspersed with long periods of rest develop greater overall muscle masses than those undergoing long periods of sub-maximal monotonous exertion.

The latter also tends to involve a greater degree of weight bearing, the faster an individual runs the lower the contact time with the ground. So, it appears that a fine balance is struck between the muscle bulk needed for the activity and its resultant weight which must be carried. Presumably in endurance athletes having a lower body weight compensates sufficiently for the limited muscle mass more than large muscles would for having to shift a greater weight - muscular efficiency is important. The reverse must be true for power athletes. As their activities do not involve prolonged weight bearing/carrying (as they are either static or moving at high speeds for minimal duration) having a large muscle bulk is beneficial to their requirements and offsets its own handicap of creating a greater weight to carry - muscular power is important. Thus, substantial muscle bulk develops and is sustained.

Muscular activity raises thyroid production. Energy balance is lowered by prolonged stamina exercise, which in turn would lower thyroid hormone production/activation. As a consequence, the low circulating thyroid hormone level acts to increase the mechanical efficiency of muscles and creates preference for slow twitch fibres (section 9.6.1). Thus, muscle mass is kept lean and energy efficient. Thyroid hormones increase the contractile force of muscle (Robbins 1991) and stimulate a preference for fast twitch fibres. Powerful bursts of activity, interspersed with significant rest periods, will cause greater fluctuations in energy expenditure but also possibly reduce the overall energy deficit. In this instance the circulating thyroid hormone level would be maintained and muscular power (hence size and proportion of fast twitch muscles) is facilitated, rather than efficiency.

9.10 - Plantarflexion and Calf Muscle Activity in Sprinting:

Plantarflexion is the act of raising the body weight up onto the toes. This is done by the calf muscle (triceps surae), which is particularly well developed in humans. This consists of two muscles (the gastronemius which originates on the lateral and medial condyles of the femur; and the soleus which originates on the top of the fibula and the lateral side of the tibia) which unite at their bases to form the Achilles' tendon (tendo calcaneus). This tendon comprises 65% of the total calf length in humans. (all in Aiello & Dean 1990)

In sportsmen today different activities employ different use of the foot. In jogging or distance running, as in normal walking, there is a definite heel-strike as the foot first comes into contact with the ground which can be quite jarring on the lower limb and lower back. During the stance phase body weight rolls forward onto the anterior foot, culminating in toe-off.

In power athletes (sprinters, rugby players, etc.) there is a very different loading pattern on the foot. The heel contacts the ground less, if at all, with most of the weight bearing being concentrated on the ball of the foot and toes. Thus the calf muscle is placed under greater stress as it needs to maintain the body's weight raised up on the toes; and the foot will experience different stresses to those of slower locomotion. Toe-off has a much more distinct propulsive element as the lower leg is driven back and up at a rapid rate by contraction of the hamstrings and gluteus maximus.

9.11 - The Lean and Muscular Neanderthals:

Adult Neanderthals of both sexes as well as juvenile specimens had robust skeletons and substantial muscle masses (Stringer & Gamble 1993). The energetic cost of both maintaining and transporting such a body mass implies that the Neanderthals would have needed a significant intake of calorie dense food and oxygen (Jelinek 1994).

Jelinek (1994) also argues that Neanderthals also carried a substantial weight of body fat, at least on a seasonal basis, to act as insulation or an energy reserve. This would have further raised transport costs (section 9.9.1). However, it is apparent that cold-dwelling populations do not have layers of natural insulation; instead maintaining body temperature via metabolic processes to generate heat (sections 6.5 & 6.7.2). The hindrance of a layer of sub-cutaneous fat in terms of transport costs and its inflexibility as a mechanism of thermoregulation, means that it is highly unlikely that Neanderthals carried a significant amount body fat.

9.11.1 - Neanderthal Lower Limb Muscle Mass and its Implications:

The image of Neanderthals having particularly muscular physiques is based on the observation that sites for tendon insertions on bones tend to be extensive and/or pronounced. In particular, the gluteal tuberosity and hypertrochanteric fossa on Neanderthal femora are both highly developed and in a unique configuration (chapter 5) which indicates substantial gluteus maximus muscles. Inactive during normal walking, the developed nature of these muscles would have been highly beneficial in sprinting and in activities requiring them for maintaining lateral stability, including throwing (section 9.7). The gluteus maximus is most pronounced in sprinters and other power athletes.

Most of the muscular activity during locomotion is by the quadriceps femoris, which inserts, via the patellar ligament, into the tibial tuberosity. Calculations of the mechanical advantage of this muscle (using limb length proportions and positioning of insertion markings along the bones) shows it to have been more highly developed in Neanderthals than EAMH and living humans. The thick nature of their patellae causes the anterior displacement of the ligament, which in turn would increase the load arm of the quadriceps femoris and increases its strength relative to that in modern humans (Rhoads & Trinkaus 1977; in Trinkaus 1983).

Several aspects of the Neanderthal foot attest to it having to withstand serious punishment during locomotion, such as medio-laterally robust metatarsals and phalanges and pronounced areas of attachment for plantar surface muscles. Could these distinctive and hypertrophied conditions be due to excessive activities with body weight raised onto the ball of the foot and toes, not simply a consequence of greater weight bearing stresses (sections 5.3.2 & 9.10)⊙ /⊙

9.11.2 - Neanderthal Chest Musculature and its Implications:

Trinkaus (1981) pointed out the very high claviculo-humeral index of Neanderthals which could indicate either large chests or short humeri. These scenarios could be considered concordant with Bergman's or Allen's Rules, respectively (section 6.1). He concedes, however, that this index is not correlated with climate in modern humans.

Neanderthals also had exceptionally large pectoralis major tuberosities (well above the size range seen in European Upper Palaeolithic individuals and humans today), indicating that they had pronounced chest muscle development (section 5.4). The relatively expanded ribs of the Neanderthals reflect the development of significant muscle masses which inserted onto them (i.e. those of the pectorals, shoulder, and back).

It is certainly possible that the large chest could be related to cardio-vascular capacity or some other measure of the form of 'exercise' the Neanderthals were participating in. A large chest (hence lung volume) would be beneficial in terms of rapidly re-oxygenating the body's tissues and organs during and after a high intensity burst of activity to ward off lactic acid build up. This would be particularly useful if available recovery time was limited.

The human upper body is also used considerably more in sprinting and other explosive stop-start activities than slower monotonous ones. Due to the nature of our bipedal gait the movements of arms and legs are biomechanically 'tied' together (section 9.8). The faster the running speed the more active the upper body becomes, and the more important it is in aiding the generation and maintenance of rapid leg oscillations. This is one principal reason why sprinters tend to be more heavily muscled in the upper body (and work harder on its development and maintenance) than their distance running counterparts. This could provide an explanation for the importance of maintaining a large upper body mass (and chest size) among the Neanderthals in the face of its energetic costs.

9.11.3 - Reappraisal of Neanderthal Activity Patterns:

If the Neanderthals had large muscle masses, they were probably engaging in high intensity activities of limited duration in their daily subsistence rounds. Because of this they probably also had a high proportion of fast-twitch muscle fibres. An associated large store of glycogen logically should have been maintained by Neanderthals. However, this would also have been dependant on a sufficient fat and carbohydrate intake, or at lease an energy sparing mechanism operating elsewhere to facilitate glycogen production (section 9.5.2).

"Activation of the fast-twitch fibres is also important in the stop-and-go or change-of-pace sports such as basketball, soccer....These activities at times require rapid energy that is only supplied by the anaerobic metabolic pathways" (McArdle et al 1996; 330).

The different muscle masses and compositions that are seen today in highly active people do reflect different activity patterns, but not in the way that has previously been proposed, and generally accepted, to distinguish Neanderthals from EAMH. If one believes the popular myth of the Neanderthals being the muscle men of the hominid lineage, then they are not likely to have been doing much in the way of sustained/prolonged activity (sections 9.9.1 & 9.9.2). The Neanderthals, if made in the sprinter/gymnast mould, would have been engaging in activities of similar exertion levels, duration, and stresses. The nature of this form of active lifestyle, involving explosive bursts of exertion (accompanied by a high rate of metabolic heat production) followed by periods of rest and relative inactivity, would have placed an additional thermal stress on the Neanderthals operating in cold ambient temperatures (section 10.5).

Previous interpretations of the Neanderthal physique all involve instilling a capacity for feats of endurance. For instance: the haphazard charging about the countryside in search of game due to poor planning capacity as Trinkaus (1989) envisages; or without artificial insulation having to undergo prolonged physical activity in order to employ their massive muscles in heat generation (Shephard 1978; in Jelinek 1994). It is clear from the various lines of evidence presented in this thesis that neither of these scenarios was a reality for the Neanderthals, as both are very energetically expensive and simply not feasible given their body morphology.

A form of ambush hunting would be more compatible with the available evidence. Rushing part-enclosed or unaware game from a hiding place, would be feasible considering their physiques and the activity patterns proposed here. At the same time it would account for the high degree of trauma evident in their skeletal remains. In accordance with this, substantial residential mobility would be implied. Being close to available game would have been important in reducing logistic mobility (hence daily transport costs and energy expenditure), leaving more time to track prey and conserving energy for the explosive 'final chase'. So due to their highly specialised physical morphologies and despite their shorter legs, Neanderthals may actually have been more mobile in residential terms. (sections 9.3 & 12.2)

In contrast, EAMH were more physically adapted to more endurance related logistic mobility, being longer legged and more lightly muscled. Prolonged and more extensive daily ranging would have been energetically viable. As such frequent residential upheavals may not have been necessary. Considering their physiques still retained a degree of robusticity (sections 5.3 & 5.7), their 'final chase' was probably over what would now be termed a 'middle' distance (i.e. one or two miles at the most).

Such a distinction could have an environmental basis. Factors relating to the landscapes in which these different populations existed may have been decisive (chapter 12). Lieberman & Shea (1994) cite subtle differences in behaviour as distinguishing archaic and modern humans both associated with the Mousterian in the Levant (section 4.5), claiming that the former had greater residential mobility and hunted more frequently, with sites demonstrating multi-seasonal occupation rather than circulating mobility (based on zoo-archaeological mortality profiles, butchery techniques, and taphonomic analysis).

CHAPTER 10

Brain Development and Cranial Morphology:

No specific correlations between increases in brain size and technological, cultural, or social innovations among humans have been identified. Neanderthals had larger brains than living humans as did EAMH, although not to the same extent as the Neanderthals. The most impressive behavioural innovations have occurred after a decrease in brain size over the last 30,000 years or so. This paradox is avoided if a direct link between behavioural capacity and brain size is rejected. Martin (1996) proposes that explanations for changes in human brain size could come from investigations into changes in maternal BMR and resource allocation (relating to foetal and infant feeding). Alternatively, according to Beals et al (1983 & 1984) climatic adaptation plays an important role.

10.1 - Fuelling Brain Growth and Functioning:

The brain makes up 2% of total body mass but consumes 20% of ingested calories (Sokoloff 1981; in Armstrong 1984). The brain's energy consumption rate remains roughly constant under varying levels of activity, from sleeping to intense mental concentration. The brain only uses glucose as an energy source. Protein turnover in the brain is as high as that in the liver, and higher than that in other body tissues (Tanner 1989). Protein is continuously being synthesised and degraded (e.g. made into transmitter substance, and used in generation/degradation of organelles to/from the spinal cord axons) associated with structural changes in the brain itself.

Dodge et al (1975) noted a pre/post-natal malnutrition produces lower brain weights in both humans and laboratory animals. Miller & Corsellis (1977) recorded an increase in mean adult brain weight of people dying in London Hospital between 1907 and 1977 (52g in men and 23g in women). This was put down principally to nutritional improvements in the country over this time. (all in Armstrong 1984)

The "Maternal Energy Hypothesis" of Martin (1996; 154-156) states that there is a positive correlation between the BMR of a gestating female and the brain growth of the foetus. The principal stage of brain growth during life is during gestation and prior to weaning, hence solely dependant on the mother's capacity to provide sufficient nutrients and calories. There is not a tight relationship between an adult's brain size and own BMR, due to environmental and lifestyle influences on the latter (sections 6.5.1 & 7.6). Several factors are implemented in having a modifying influence on ultimate human brain size: duration of gestation and breast feeding; efficiency of nutrient transport across the placenta; and the quality and quantity of breast milk.

Overall brain growth is protected somewhat from malnutrition compared to that of other tissues, such as muscles and bones (Armstrong 1984). There is no observed direct correlation between deficits in physical growth (i.e. stunting) and deficits in intellectual capacity. Due to the brain's characteristic timing of peak growth and nutritional requirements, mental development is preserved in children under conditions of malnutrition up to a point (Pelto & Pelto 1989). The brain also has diminished recuperation capacities (Dobbing & Sands 1973; in Armstrong 1984). Starving the brain of nutrients must be the final, and futile, stage in the succession of adjustments to cope with nutritional stress (section 7.5).

Where children suffer early severe malnutrition; mental development may be affected in the long term (Colombo et al 1988). Chavez & Martinez (1982; in Pelto & Pelto 1989) found malnourished rural Mexican children to have retarded emotional maturity, low confidence, and reduced exploratory and inquisitive activity levels.

"Mammalian brain sizes have been linked to specific behavioural or physiological features because of simple scaling correlations. Examination of the correlation network for body size, brain size, basal metabolic rate, and gestation period indicates that the primary link is between maternal metabolic capacity and the developing brain of the offspring" (Martin 1996; 149).

Nutritional status ante- or post-natally has been shown to have a strong influence on brain growth and development. Indeed, the energy balance of females determines their ability to conceive thus protecting any potential offspring from such nutritional stress (section 8.4). Thus the ethnic differences in cranial size observed today could be influenced, at least partly, by variation in nutritional standards.

10.2 - Hominid Encephalisation and Climate:

Weidenreich (1945) first noted the trend towards brachycephalisation among recent hominids. It was Coon (1955) who suggested that it would be an advantageous development in cold climates. Beals (1972) took a world-wide sample of 339 different ethnic populations and found climatic associations with brachycephalisation to be highly significant. (all in Beals et al 1983)

Surveys of living populations identify a clinal variation in braincase size of 100-150cc and an increase in mean cephalic index of 4.3 units moving between the Equator and the Arctic. Beals et al (1984) claim that the initial evolutionary expansion of the hominid braincase correlates with temperature. In essence the theory states that smaller heads are easier to cool in the hot climates.

10.2.1 - Cold Adaptation and Brain Size:

"....extreme cold is typified by moderate stature, moderate nasal index, round cranium, large cranial volume, small brain size relative to weight, large brain size relative to stature, and lateral body build" (Beals et al 1983; p 436).

Beals et al's (1983) study showed that in living groups winter conditions were more influential than summer ones in the determination of a group's cephalic index. Temperature was also found to be more important than humidity. During the Pleistocene, the mean hominid cranial index increased 9 units. The rate of increase was slow initially while they remained confined to the tropics; but it accelerated dramatically when hominids expanded northwards into harsher, colder, and more seasonal latitudes.

The hypothesis proposed by Beals et al (1984) is that it was the hominid expansion into cold climatic regions produced a change in head shape, which contributed to the increase in cranial volume. There is the alternative explanation whereby increases in brain size (and hence intelligence) actually permitted the colonisation of such challenging environments. This begs the question as to whether this feature was the cause or an effect?/ However, Gamble (1993) notes that despite only reaching the 9 ⊙ Americas within the last 35,000 years Native Americans show a similar latitudinal variation in cranial size; which is strong evidence that this feature reflects climate as opposed to intelligence or race.

10.2.2 - Evolutionary Trends:

Beals et al (1983) state that there is variation in mean cranial index between the 'glacial' and 'temperate' dwelling Neanderthals (presumably synonymous terms with European and Middle Eastern, respectively). The 'glacial' Neanderthals fit the round headed model of cold adaptation. In contrast Trinkaus (1984) argues that the differences in cranial capacities/indices among 'glacial' and 'temperate' samples from archaic and early modern *H sapiens* are minimal showing a lack of climatic patterning; although does concede a slightly greater value in the 'glacial' samples. Trinkaus (1984) also warns that the small fossil sample sizes and sex bias can influence the results of such a study.

The evolutionary trends of brachycephalisation and encephalisation are considered functionally connected in the analysis by Beals et al (1984). The study found that variation in endocranial volume between modern ethnic populations is "significantly associated with every climatic variable examined" (e.g. latitude, climatic zone, winter temperature, solar radiation, etc.).

Structurally, it is breadth which contributes most to brain volume. Groups with rounded heads tend to have the greatest volumes. Arctic peoples have large cranial capacities due to their more globular head shape. Beals et al (1984) claim that thermoregulation (in particular cold stress) has greater effect on the cranium, than on body form as a whole. The highest correlations occur with the coefficient of cranial morphology, absolute volume, and capacity relative to stature. The differences in cranial capacities between winter-frost and dry/wet-heat ethnic groups is statistically significant but, as noted by Armstrong (1984), only small in terms of absolute volume (98 cubic cm).

However, it should be noted that the evolutionary trend for more capacious and rounder crania is seen among earlier hominid species not exposed to winter frosts (i.e. prior to the adaptation to the cold in the last half a million years). According to Beals et al (1984) climatic adaptation is merely superimposed upon other causal mechanisms. While it is accepted that initially encephalisation would have been selected for on an intellectual/linguistic basis; latterly (in the last 200,000 years) climatic factors are seen to have become the principal force of variation. The hominid data generally suggest that the conclusions drawn from the ethnic study (i.e. the pattern of larger, more globular braincases in colder climates) is observable in the fossil record. This is particularly evident in the case of the Neanderthals, but less so among EAMH.

10.3 - Regulation of Brain Temperature:

The human brain, although only comprising 2.1% of the body's mass, produces 16% of its heat at rest and unstressed (Ashcroft 1971; in Schmidt-Neilson 1997). Despite this high capacity for heat generation, in all species of mammal, bird and reptile brain temperature is kept below core temperature (Baker 1982). Brain function appears to be especially susceptible to heat stress (Bowler & Tirri 1974; Burger & Fuhrman 1964; in Baker 1982). Carithers & Seagrave (1976; in Baker 1982) showed that so long as the brain is kept cool, the tolerance to elevated deep body temperature is extended. Thermo-sensitive structures within the brain are therefor thought to dominate those e located elsewhere in the body (Cabanac & Caputa 1979a).

Brain temperature is determined by (Baker 1982):

- Heat production rate by the brain cells
- Rate of blood flow through the brain. The temperature of cerebral arterial blood is most variable and influential
- Temperature of the blood supplying the brain
- The temperature of surface regions is influenced by direct heat exchange through the scalp or base of the skull

10.3.1 - Meninges and Sinuses of the Brain:

Venous sinuses are enclosed within the dura mater (outermost cranial membrane) and transport blood from the brain, its meninges (membranes that surround the brain and spinal cord), and the skull to the internal jugular veins. The cavernous sinuses lie on either side of the body of the sphenoid bone (figures 1 & 2). The anterior and posterior intercavernous sinuses act to connect the cavernous sinuses, in front and behind the stalk of the pituitary gland. The configuration is simply referred to as the cavernous or circular sinus (Bruni 1991).

The channels of the cavernous sinus extend from the superior orbital fissure to the apex of the petrous temporal bones. The internal carotid artery runs forward through it. Each cavernous sinus receives its sphenoparietal sinus anteriorly. Posteriorly they drain via the superior and inferior petrosal sinuses into the internal jugular vein. The cavernous sinus receives blood from the frontal and temporal lobes of the brain and also 'communicates' with veins outside the skull (Bruni 1991).

The cavernous sinus receives venous blood draining from the nasal mucosa and skin of the face via the angularis oculi, opthalmic and emissary veins. In humans changes in heat loss from the face have a powerful effect on thermoregulation that may be caused by a change in hypothalamic temperature (Baker 1982). Within the cavernous sinus the carotid artery forms a sigmoid siphon which augments the surface at which arteriovenous heat exchange can occur and a cooling of the arterial blood ascending to the brain can take place (Maron et al 1977).

10.3.2 - Mechanism of Brain Cooling in Humans:

"Brain temperature can be affected by local cooling of the face and is therefore largely independent of core temperature generally" (Cabanac & Caputa 1979a).

Baker (1982) describes how venous blood cooled by evaporation at the (facial) skin surface reaching the cavernous sinus is able to either exchange heat with the arterial blood supplying the brain or directly cool the base of the brain via conduction. The extent of brain cooling depends on the rates of evaporation and blood flow.

Caputa et al (1978; in Cabanac & Caputa 1979b) demonstrated that in humans during hypothermia, facial venous blood flows strongly to the cavernous sinus through the angularis oculi and the opthalmic veins. Local heat exchange between the arterial blood passing to the brain and the cooled venous blood returning from the facial skin is then possible. They also found that in mild hypothermia blood flow from the cavernous sinus to the facial venous network was slow. In contrast, during hyperthermia flow was rapid and directed from facial veins to the cavernous sinus.

Cabanac & Caputa (1979b) studied subjects sitting in a heated bath experiencing facial fanning. The fanning cooled venous blood profusing the cavernous sinus and hence the blood of the internal carotid artery. Crawshaw et al (1975; in Cabanac & Caputa 1979b) demonstrated that local cooling of different areas of skin of mildly heat stressed humans produced cutaneous cold sensations and was immediately followed by a decrease in the rate of sweating. Forehead cooling was found to be twice as efficacious on sensation and three times as efficacious in inhibiting sweating, relative to the cooling of other skin areas of the torso and limbs. They proposed that there could be a higher density of thermal sensors in the skin of the forehead. Selective cooling of the brain may be the cause of this sweating inhibition.

"This local effect of facial cooling on the human brain temperature during exogenous and endogenous heat stress is comparable to the local effect on brain temperature of evaporation from the upper respiratory tract of panting mammals...." (Cabanac & Caputa 1979a).

10.3.3 - Brain Cooling During Exercise:

"....thermoregulatory processes during exercise relate only to brain temperature and not to body temperature generally" (Cabanac & Caputa 1979a).

Nielsen (1970; in Cabanac & Caputa 1979a) found that in humans the increase in core temperature during exercise is proportional to work load and largely independent of ambient temperature. Selective brain cooling under conditions of hyperthermia appears to be advantageous because muscular hyperthermia is favourable for the efficiency of physical activity and work (Asmussen & Boje 1945), and cerebral tissue is especially heat sensitive when examined both *in vivo* (Carithers & Seagrave 1974) and *in vitro* (Burger & Fuhrman 1964). (all in Cabanac & Caputa 1979a)

The selective brain cooling mechanism determines the apparent upper resetting of core temperature during exercise, while brain temperature remains precisely regulated and constant. Tests on subjects pedalling on a bicycle ergonometer with their faces fanned and insulated indicate that "during exercise the body temperature which determines the intensity of the physiological responses to thermal stresses, and is therefore the regulated variable, is that of the brain" (Cabanac & Caputa 1979a).

Selective thermal cooling of the large human brain prevents cerebral overheating during heavy exercise in cool and moderate ambient conditions. This mechanism is negligible during rest in hot environments (Cabanac & Caputa 1979b). Maron et al (1977) measured the core temperature of a marathon runner at up to 41.9 degrees centigrade. Ambient temperature was only 18.8 degrees and no signs of heat induced illness were seen. However, it would appear impossible for cerebral integrating function to remain undisturbed if brain temperature rose by as little as 5 degrees. The face of running humans is an excellent heat exchanger due to its rich vascularisation and higher sweating rate (Hertzman et al 1953; in Cabanac & Caputa 1979a) as well as its better exposure to air movements relative to other skin surfaces.

"....an open loop increase in deep trunk temperature, proportional to muscular thermogenesis, occurred under conditions of efficacious head heat dissipation, while brain temperature was defended at a much lower level. Thus, selective brain temperature regulation during exercise....is probably a general feature of temperature regulation in exercising mammals" (Cabanac & Caputa 1979a).

10.4 - Influences on Skull Form Other than of Brain Size:

Various factors are quoted by Gibson (1984) as affecting skull form:

- Masticatory function - tooth size, muscle strength and angle of action all correlate with head shape (Sassouri & Forest 1971).
- Increased trends towards brachycephalisation are seen in the fossil record in conjunction in changes in both tooth size and muscularity of the head; but in the absence of brain size or climatic change (Carbon 1976).
- Dental-anthropological analyses have explained Eskimo skull form on the basis of masticatory stress (Hylander 1977).
- Altered respiratory patterns drastically affect skull shape and facial form e.g. the development of adenoids which cause children to breath through their mouths produces long heads and faces. Removal of the adenoids reverses this growth trend. (McNamara & Ribbens1979).

Given the capacity and importance for heat transfer between the face and the base of the brain, the size of fluid spaces in the cranium may have dominant roles in brain thermoregulation according to Girgis & Spencer (1984). Hence, the noted variation in cranial capacity relating to climatic adaptation may be more dependant on the size of these spaces, than actual brain size. Basicranial morphology may also be influenced by their size.

10.5 - Brain Thermoregulation During Exercise Among Neanderthals:

"The basic problem is that the [cranial/cephalic] index increases not only under conditions of cold (as expected), but also increases under conditions of severe heat (when unexpected). Our interpretation is that a climatic explanation cannot be the sole adaptive factor. It may not even be the most important" (Beals et al 1983; p 436).

It has been well documented that the brain is a highly metabolic organ, generating heat as a by-product, and hence energetically costly to maintain (section 10.1 & table 2). In light of this, brain dimensions would logically have an impact on the regulation of its temperature, a larger brain producing more heat and a more spherical one conserving more heat by minimising the surface area to volume area. But, how can the conflicting discoveries in the above statement be accounted for in these terms?

Temperature regulation during exercise in the cold might be a possible and plausible answer. In extremely hot conditions loosing metabolic heat from the brain through the scalp is obviously an important factor in its temperature regulation, whether highly active or otherwise. However, the mechanisms for brain cooling involving heat exchange in the cavernous sinus would be largely redundant in hot conditions as the face is exposed to heat stress (sections 10.3.2 & 10.3.3). In the cold it is a little harder to fathom why brain cooling would be necessary, considering the emphasis placed by some on morphological adaptations to retain heat (sections 6.1 & 6.2.1).

In cold ambient temperatures during exercise the physiological mechanisms of heat generation should be compounded, in theory. Skin thermoreceptors will be registering 'cold' and sending nervous impulses to stimulate internal heat generation (section 6.7.2). At the same time raised levels of muscular activity as a consequence of strenuous exercise will also be producing heat as an indirect but functionally beneficial consequence (section 6.7.5). Thus, in Neanderthals core temperature could be raised substantially by the summed effects of these metabolic processes. Brain cooling would therefor be important despite a low ambient temperature, and practical because of it cooling the face. Given the high exercise levels the Neanderthals apparently reached (section 9.11.3) the cavernous sinus would have been vital as a thermal buffer between core and brain. If the Neanderthals were indeed engaged in activity patterns involving intermittent short bouts of intensive activity and relatively inactive periods, then coping with the resultant fluctuations in temperature may have been an influential selective force for the expansion of the cavernous sinus.

10.6 - The Neanderthal Basicranium:

There is heterochrony of Neanderthal traits during growth whereby basicranial traits appear early on relative to facial ones which are more associated with the later eruption of the permanent dentition (Tillier 1989). DeBeer (1937; in Olson 1981) described the basicranium as being more conservative in morphological changes compared to other body parts that interact more directly with the environment. Ford (1958; in Olson 1981) first proposed an importance for the basicranium in phylogenetic reconstructions believing it to be only marginally influenced by extrinsic/genomic factors. These arguments imply that basicranial form is subject to predominantly genetic control.

Diagrammatic representations of the superior view of the cranial cavity's floor and its sinuses (see Bruni 1991 p 982) reveals that the cavernous/circular sinus sits above the sella turcica bone (positioned centrally). Inspection of recent human skulls and figures 1 & 2 reveals that this, in turn, lies above the region of the basicranium comprised of the basi-occipital (or the basilar portion of the occipital bone), sphenoid, and vomer bones (anterior to the foramen magnum and posterior to the palate). Since no Neanderthal endocasts of the area housing the cavernous sinus are sufficiently detailed, this region of the basicranium will be used here as a proxy for the morphology of the floor of the cranial cavity (assuming that there is a functional relation between sinus/brain morphology and basicranial dimensions).

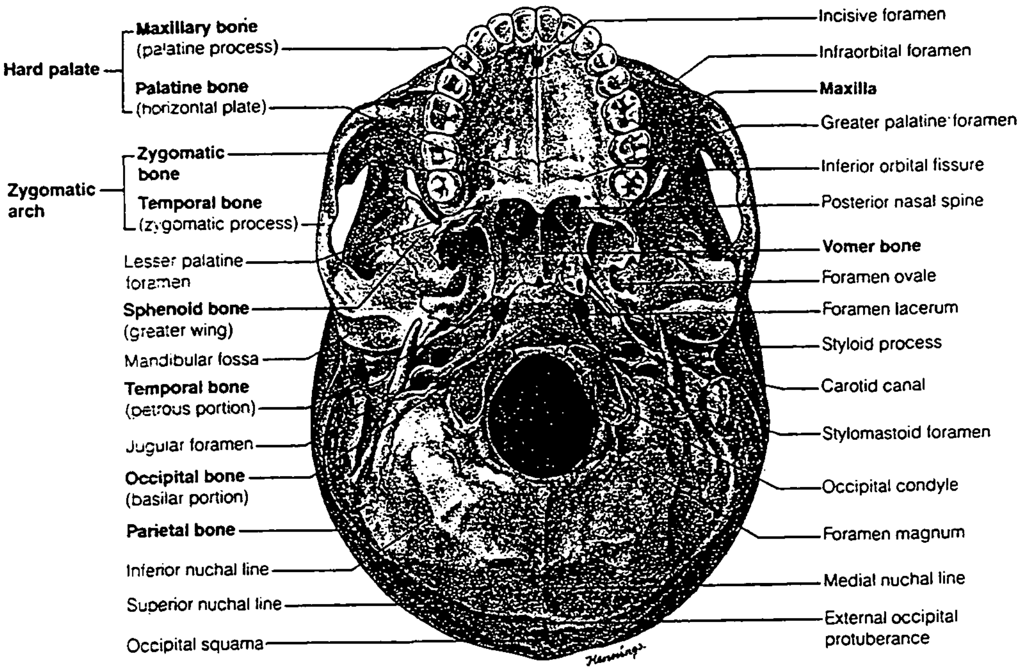

Figure 1: Inferior View of the Skull - The Basicranium (Reproduced from Gaudin & Jones 1989; p 137)

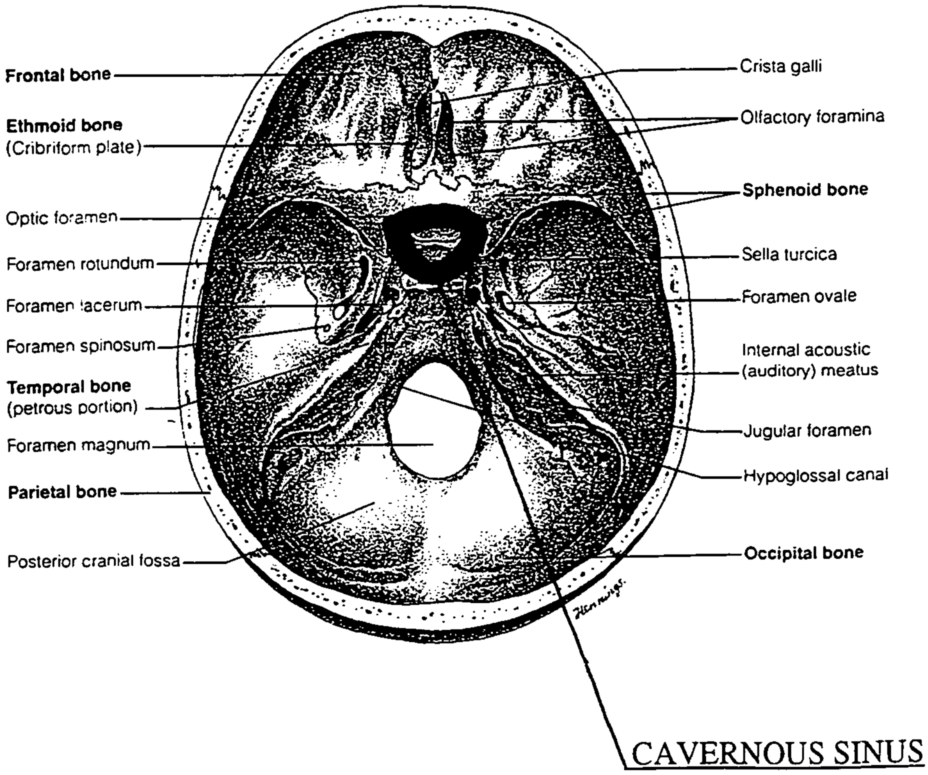

Figure 2: Superior View of the Floor of the Cranial Cavity (Reproduced from Gaudin & Jones 1989; p 137)

The juxtapositioning of the basi-occipital and the sphenoid determines the degree of basicranial flexion. Neanderthals have a very long and unflexed basicranium relative to that of both early and later modern humans. The unflexed nature of the Neanderthal skull contributes to its length by increasing the distance (antero-posteriorly) between the foramen magnum and the rear of the palate.

If the elevated demands of brain thermoregulation in Neanderthals did lead to the enlargement of the cavernous sinus, it could be possible that basicranial flexion was also influenced. It is logical that an increase in the size of the cavernous sinus would be accompanied by the lowering of the floor of the cranial cavity below in order to accommodate it. The degree of flexion would decrease as the basi-occipital and sphenoid bones moved downwards in order to create the necessary space above required by the larger cavernous sinus. Therefor, it is possible that the long unflexed basicranium, one of the defining characteristics of a Neanderthal skull, could be a consequence of such a morphological adaptation.

Significant basicranial flexion is first noted in *H erectus* (e.g. in KNM-ER 3733 by Laitman 1985; in Trinkaus 1987). According to Trinkaus (1987) this implies the emergence of "oral tidal respiration and the associated increased potential for voluntary pulmonary ventilation during sustained elevated activity". Therefore when compared to earlier hominids *H erectus* was capable of maintaining extensive movement across the landscape and greater activity levels in more arid environments during the more thermally (heat) stressful times of the day (section 4.4.3). But if this theory is correct then the unflexed nature of the Neanderthal basicranium would have hindered their respiratory, hence endurance capacity, further corroborating other lines of inquiry here (sections 9.11.3 & 12.2) proposing a pattern of frequent short sharp bursts to comprise the Neanderthals' daily exertions.

10.7 - Nasal Morphology and Activity Levels:

Living cold-dwelling populations have long narrow nasal openings. In stark contrast warm-dwelling populations have short broad noses. The Neanderthals had a strange mixture of nasal dimensions, theirs being both long and broad (Stringer & Gamble 1993). Trinkaus (1987; 124) pronounces the Neanderthals to have "....possessed among the largest nasal apertures known....[having] large nasal apertures, voluminous nasal cavities and projecting external noses....".

There is much debate over the precise adaptive significance of such an extreme morphology. Recent theories suggest that the Neanderthals' large nasal apertures would have functioned efficiently in facilitating substantial oxygen intake/carbon dioxide output volumes for their relatively large lung capacities, during bouts of heavy exercise, while simultaneously offering some form of temperature/moisture regulatory capacity (e.g. Trinkaus 1987; Jelinek 1994)

Enabling sufficient gaseous exchange would have indeed been important for a highly active group like the Neanderthals. If engaging in short powerful bursts of effort (section 9.11.3) this would have facilitated a more rapid recovery in terms of recuperating oxygen debt and warding off lactic acid build up in muscles, which causes cramp. Their large nasal apertures would also have enhanced both heat/moisture loss and the inhalation of cold/dry air. Controlling the temperature of inhaled air is difficult. A specific nasal morphology will only have a set, and probably limited, buffering effect regardless of whether the individual is active or inactive.

Wolpoff (1980; 289) stated that an expression of cold adaptation in the cranium is the "....further projection of the total face (separating the nasal passages from their usual close proximity to arteries supplying the brain)".

By distancing nasal passages from the arteries ascending to the brain, sufficient gaseous exchange is allowed (via the large nasal apertures), without the temperature oscillation accompanying the breathing cycle having a direct/significant effect on the temperature of the blood supply to the brain. Sensitive nervous control over blood flow between the skin of the face and the cavernous sinus will enable better regulation of blood temperature as it ascends to the brain. The effectiveness of this will be enhanced if interference from the temperature of air in the nasal passages is reduced.

During exercise, as core temperature rises, a high rate of blood flow from the cooled face will cool that of the cavernous sinus and internal carotid artery (which supplies the brain), hence prevent a significant increase in brain temperature. In the subsequent recovery period (as muscular activity and heat generation is reduced) this flow can be stemmed to enable heat generated in the body to reach the brain, via the ascending arterial blood flow, in order to prevent a rapid and/or excessive drop in brain temperature due to the cold ambient temperature.

So, rather than being a mechanism specifically for cooling brain temperature during exercise, the cavernous sinus in Neanderthals would have played a more general thermoregulatory role to buffer the brain from the fluctuation of extreme temperatures (both metabolic and ambient). Indeed the mid-facial projection which Wolpoff (1980) speaks of could be functionally linked to the proposals here regarding expansion of the cavernous sinus (section 10.6), with both offering physiological benefits for the Neanderthals in their daily subsistence activities in their cold environment.

CHAPTER 11

Thyroid Hormones and the Neanderthals:

In several sections thyroid hormones and their extracellular circulating levels have been implicated in changes within the human body designed to mediate internal demands and external conditions such that energy balance may be maintained. In living humans thyroid hormones have many physiological and metabolic functions, and affect nearly all the body's organs.

Thyroxin (T4) is the major hormonal product of the thyroid gland but is inactive. Triiodothyronine (T3) is the active form of the thyroid hormone. T3 is derived from T4 in the thyroid gland and other body organs. Activation and turnover rates are sensitive to various environmental and lifestyle stresses.

11.1 - Clinical Conditions Arising from a Malfunctioning Thyroid Gland:

There are two opposing instances of thyroid gland dysfunction, each with wide ranging consequences:

1. Hyperthyroidism (excessive production): Resting metabolism is raised by 50% or more (Durnin & Passmore 1967). This results in high body temperature, high oxygen consumption, and high caloric demands. Robbins (1991) states that under such conditions heart rate may increase to an extent whereby cardiac arrhythmia is induced, which can be fatal. Growth and development are not impaired.

2. Hypothyroidism (deficient production): In the young this causes cretinism, by retarding brain growth and mental development, and impairs physical/skeletal growth. This is both a direct and indirect result of low levels of active thyroid hormone (section 7.2). In adults it causes myxoedema, meaning that heart rate is slow, oxygen consumption is low, and resting metabolism falls to 50% of its normal level (Durnin & Passmore 1967). Robbins (1991) states that intestinal motility and body movement (muscular contraction and relaxation), thought processes and speech are all also

slowed as a consequence. Points relative to the discussion in this thesis are represented diagramatically in figure 3.

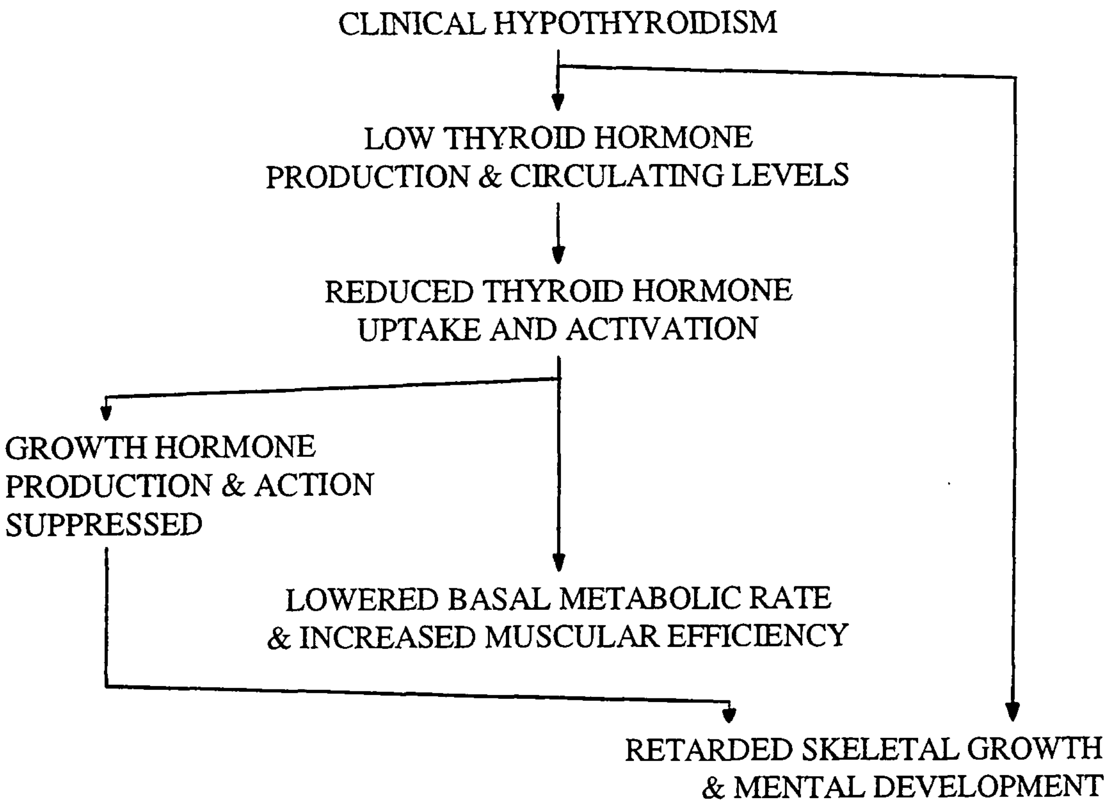

Figure 3: Physiological Effects of Clinical Hypothyroidism

11.2 - Neanderthal Metabolism and Thyroid Status:

The Neanderthals were glacial dwelling, hence suffered severe cold stress. They had high protein/low carbohydrate diets (at least on a seasonal basis) and suffered a significant level of nutritional stress. They were also highly active, being heavily muscled and robustly built accordingly. All three of these ecological/lifestyle components had implications and consequences in terms of the resultant thyroid hormone status and level of energy balance.

Non-shivering thermogenesis in order to increase metabolic heat production would have been an important mechanism for Neanderthals existing in low ambient temperatures (section 6.9). The accompanying high rate of thyroid hormone uptake by tissues would have lowered their circulating levels of the active hormone (uptake apparently outstrips production). As a consequence of this, the phenomenon of ageing bone loss may have been a reality for the Neanderthals in their cold and highly seasonal environment. Neanderthals also have 'cold adapted' leg (limb) proportions (i.e. shortened distally), but overall length is not exceptionally short compared to certain living human populations (sections 5.8 & 6.4).

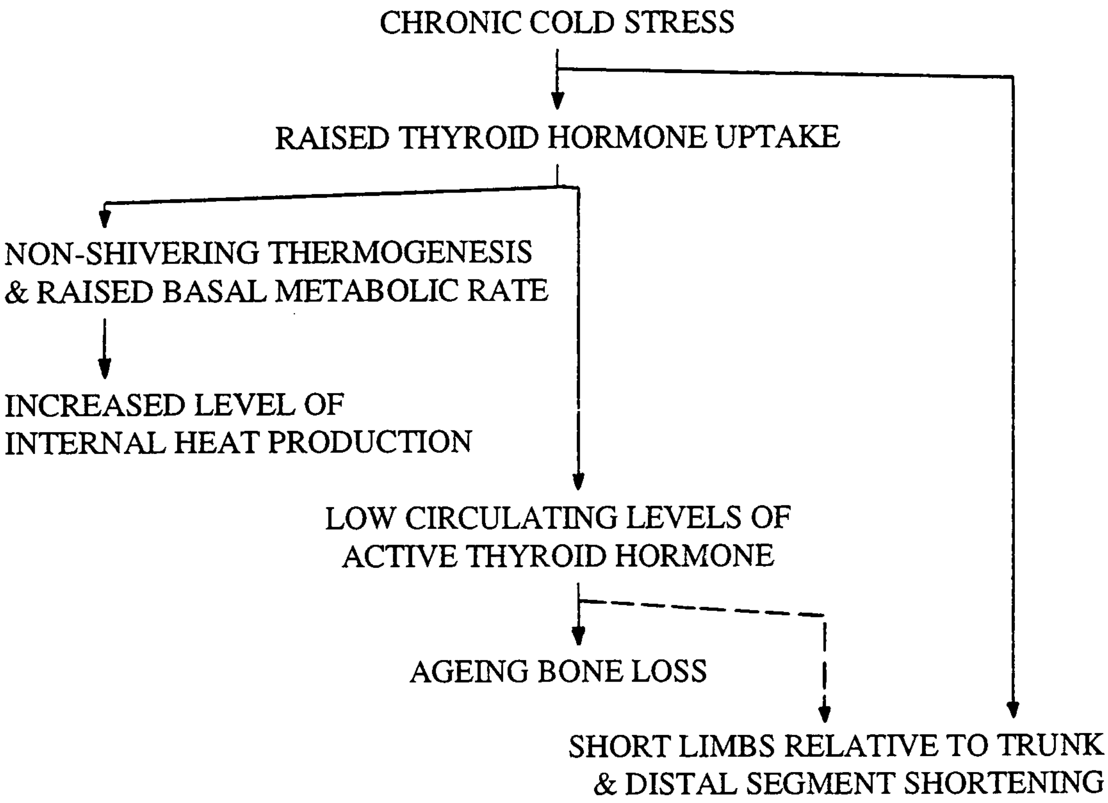

Figure 4: Physiological Effects of Chronic Cold Stress

The low energy nature of the Neanderthal diet due to the (seasonal) dearth of available carbohydrates and animal fat reserves would have suppressed both the production and activation of thyroid hormones. BMR is lowered and muscular efficiency increased, as a consequence of low circulating levels of thyroid hormones, under conditions of dietary energy deficiency in order to conserve energy for basic physiological functioning (section 9.6.1). The high protein content of the Neanderthal diet would have added to the physiological stress because of its high Specific Dynamic Action and calcium excretion in processing by the liver and kidneys (sections 7.8 & 8.5). Chronic Energy Deficiency during growth in humans today is seen to result in stunting, whereby their genetic potential for linear growth is not achieved. It is argued that leg length is disproportionately affected, and that this may have implications for the interpretation of Neanderthal stature (section 7.8). The key aspects of CED relevant to the discussion of Neanderthal stature are shown in figure 5.

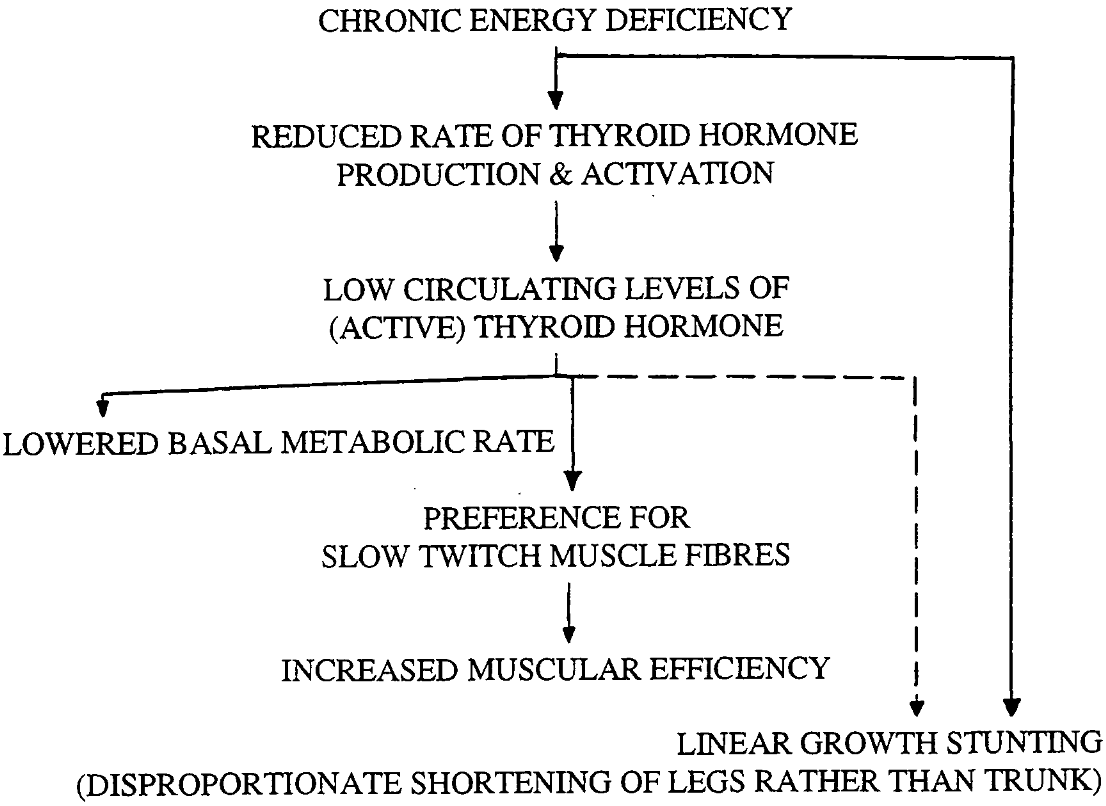

Figure 5: Physiological Effects of Chronic Energy Deficiency

A physically arduous lifestyle is accompanied by raised thyroid hormone uptake by skeletal muscles. Thyroid hormones stimulate the release of calcium ions from the sarcoplasmic reticulum and increase the rate of ATP consumption during muscular contraction. Thyroid hormones may also alter the proportions of the different types of fibre present in an individual's muscles, in favour of the fast twitch varieties with power generation rather than muscular efficiency being the priority. The large muscle mass of the Neanderthals is therefor indicative of a raised thyroid hormone uptake, increased metabolic activity, and a high proportion of fast twitch muscle fibres (section 9.11). This would lead to a reduced level of circulating active thyroid hormone, as is noted to occur with non-shivering thermogenesis. Figure 4 shows these physiological adjustments to such physical/biomechanical stress.

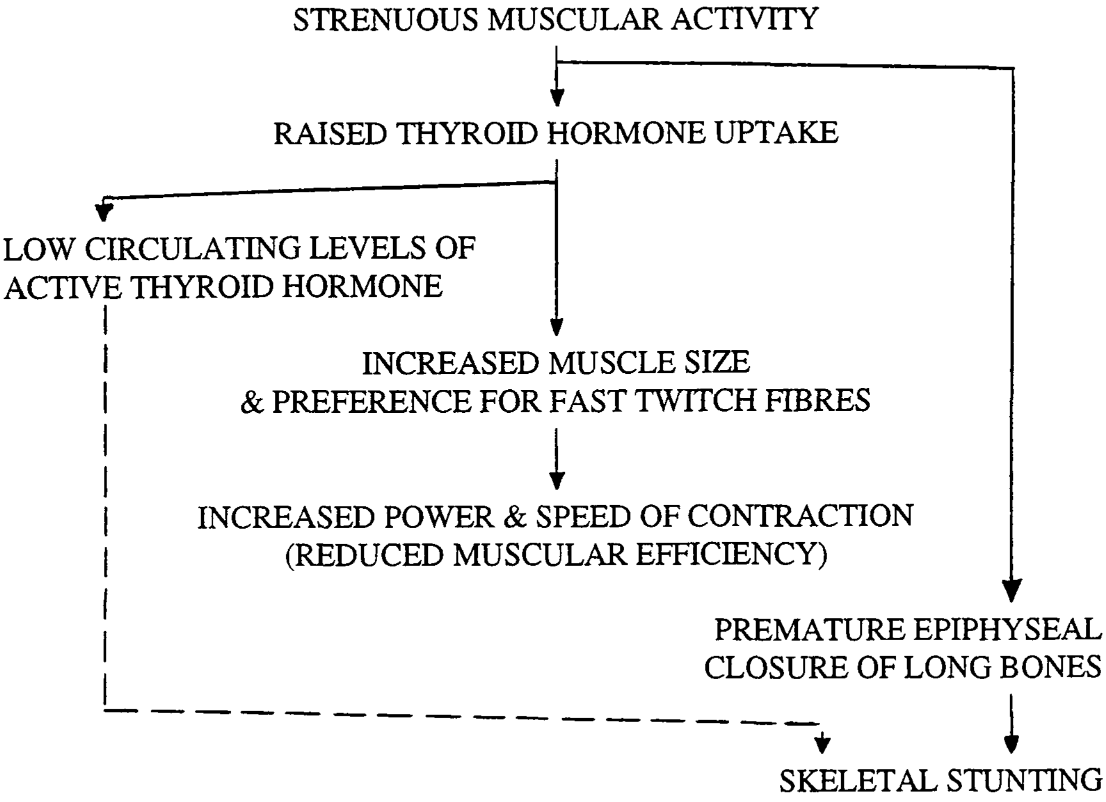

Figure 6: Physiological Effects of Strenuous Physical Activity

11.3 - Consequences of Thyroid Hormone Status for Neanderthal Growth and Stature:

In figures 4, 5 & 6 dotted lines are shown. These link the form of skeletal stunting noted in each case among living humans to the low level of circulating (or ‘free fraction’) active thyroid hormone which occurs in response to the pressure placed on energy balance by each of these stresses. These links, identifying the underlying causal mechanism for the stunting, have not been proved by direct testing. They are hypothesised here based on the observed consequences of a low level of thyroid hormone production/utilisation for growth and development in clinically hypothyroid individuals (figure 3).

The physiological responses to dietary energy deficiency and hypothyroidism clearly parallel each other. Both conditions leave the individual with a low circulating thyroid hormone level, reduced BMR, improved muscular efficiency, and a degree of stunting (if suffered during growth). As such the linking of thyroid hormone status and skeletal growth in the case of CED is highly likely (figures 3 & 4).

Certain consequences of non-shivering thermogenesis and recurrent physical exertion parallel those of hyperthyroidism. It is therefor harder to justify the links shown in figures 5 & 6. All three situations affect thyroid hormone status by increasing its turnover rate and thereby acting to increase the body’s energy consumption and metabolic processes.

The important difference is that in hyperthyroidism a high rate of production is the driving force, whereas in the other two it is uptake (and activation) of thyroid hormones. In the first case all tissues, organs and glands are awash with thyroid hormones and uptake is high in a simple response to excessive availability - the consequences are not desired. The contrast with non-shivering thermogenesis and strenuous physical activity lies in the high demand for thyroid hormones by the relevant tissues and organs in each case - the resultant hypermetabolism being vital for survival, generating heat or muscular power, respectively. In these instances production is seen to lag behind uptake, leaving a shortfall in circulating thyroid hormone levels. This difference will be enhanced if chronic dietary energy deficiency, hence reduced thyroid hormone production, is experienced simultaneously.

Other tissues, organs and glands will be deprived of stimulation by active thyroid hormone since availability is lowered, and they will become lazy in functional/metabolic terms. One avenue of thyroid hormone activity which is likely to be affected in this way is growth. Both directly and indirectly (via regulation of growth hormone production, by the pituitary gland, and its activity) thyroid hormones induce growth. Logically, in circumstances whereby there is competition for the available energy, a mechanism of differential distribution should operate, with preference being given to more physiologically vital operations, so that functioning can be maintained within the viable range.

It is argued here that in these cases of physiological adaptation (or coping) to heavy internal competition for energy, it is the limbs (long bones) which are most susceptible to being overlooked since not reaching their maximum genetic potential for growth is least detrimental to the survival of the individual. Growth of the trunk (and its internal organs - particularly in a cold environment since these are able to produce significant amounts of heat) and brain takes priority over that of the legs (limbs). The rationing mechanism acting to produce this outcome may be the balance of circulating active thyroid hormones.

It is possible that the ecogeographic clines in body proportions (today or in the past) are influenced to some degree by developmental plasticity in response to a low energy balance and associated thyroid hormone status induced by the cold and/or nutritional status and/or arduous activity regimes. In the case of the Neanderthals, who experienced all three stresses, each would compound the effects of the other two. The high rate of bone remodelling and high demands of mineralisation by the robust Neanderthal skeleton due to such biomechanical stresses (and the associated large muscle mass) and/or in response to a highly seasonal cold environment, may also have been a confounding variable (section 6.9).

It is therefor likely that the Neanderthal lifestyle incorporated the maintenance of a low /e level of circulating active thyroid hormones in response to a low/negative energy balance. This would have acted to constrain linear growth of the limbs as an energy conservation mechanism, such that physiological functioning of the major body organs and tissues (including brain) could be properly maintained. For the Neanderthal population to have survived as long as it did this mechanism must have been a successful adaptation to the stresses experienced.

The above is probably more relevant to European Neanderthals than their Southwest Asian neighbours. These Neanderthals clearly had longer legs (section 5.8), although still skeletally robust and wide-bodied, which is usually accepted as an ecogeographic cline related to temperature. However, as well as slightly higher temperatures, differential game availability may have also played a role, such that energy balance was improved and the pressures to conserve energy relieved. Thus, an increase in leg length would have been initiated as circulating active thyroid hormone levels were raised.

CHAPTER 12

The Neanderthals and Their Ecosystem:

The climatic and mobility hypotheses are commonly seen as competing with and being diametrically opposed to one another, with either thermoregulatory or locomotive demands dominating and shaping human body morphology (section 9.3.2). Previous discussions have had narrow foci (e.g. statistical analyses of limb lengths and climatic measures, such as mean temperature or humidity) in their assessment of the selective forces driving changes in body morphology.

Having short legs may be beneficial in terms of heat conservation but is not necessarily simultaneously detrimental to mobility. In both cases it should be noted that the range of Neanderthal total leg length lies above the means for living cold adapted Eskimos and Lapps, as well as highly mobile San bushmen in the Kalahari desert (sections 5.8 & 6.4). In the light of this, the fundamental premises of each argument have been reassessed, since several confounding (and significant) variables have been identified.

This paper has thrown different aspects of the environment (dietary balance, state of the landscape, as well as temperature), exercise behaviour (adeptness of different physiques - not just statures - to different activities and how specific activities influence physical development), and physiological factors (thyroid hormone status and energy balance with respect to these other points) into the fray. Thus a more rounded picture of Neanderthal ecology can be painted. A subsequent reconciliation of the conclusions drawn from this study with generally accepted interpretations of the archaeological record has also been attempted, and an alternative perspective on possible Neanderthal existence can be gleaned.

12.1 - Neanderthal Adaptation:

It may appear at first that morphological cold adaptation on a genetic level is the dominant driving force in determining Neanderthal body proportions. However, it is apparent that metabolic and hormonal adaptations to the cold and/or poor dietary quality and/or strenuous activity patterns during development would have had significant bearing on linear growth patterns and physical development (section 11.3). Morphological flexibility or phenotypic plasticity during growth, in response to these stresses, may have been a significant component in determining Neanderthal stature. The short stocky Neanderthals were indeed adapted for the conservation of body heat, but here it is argued that their stature may have been influenced, at least in part, by thyroid hormone status stemming from strong pressures on Neanderthal metabolic and physiological processes, rather than being under strict genetic control.

The Neanderthals were evidently successful hunters, at least of small-medium sized game. Looking at the mobility aspect of Neanderthal stature a paradox emerges: short limbs supposedly signalling reduced mobility but large muscles and robust bones attesting to significant activity. The Neanderthal physique was adapted to specific and stressful athletic feats, namely short and frequent bursts of high intensity exertion (section 9.11.3). The early development of features related to physical stresses, such as skeletal robusticity and marked areas for muscle attachment, appear at a young age in Neanderthals and therefor could be inherited (selected for at the population level) or /e indicative of the young being highly active (a phenotypic response in the individual). Either way the resultant physiological stresses on the individual would have been comparable. Regardless of its apparent thermoregulatory benefits, such a stocky physique is adaptive for the generation of athletic power and speed.

The arguments presented here (and chapter 11) relating to the potential for significant developmental or phenotypic plasticity to have operated among the Neanderthals are not intended to completely deny the influence of natural selection in determining the distinguishing morphological characteristics of the population. It is merely to acknowledge that various factors will have acted during Neanderthal growth and development to either enhance the genetically determined patterns or to relieve the necessity for extreme morphological adaptation under strict genetic control. If, as is suggested here, phenotypic plasticity indeed played a significant role among

Neanderthals, it would have enabled a degree of morphological flexibility to have been maintained.

12.2 - Hunting Practices of the Neanderthals Based on the Assessment of their Physiques and Proposed Activity Patterns:

The non-specialised species assemblages identified as associated with Neanderthals can be interpreted as a result of encounter tactics. Even the presumed specialised assemblages (in Late as well as Middle Palaeolithic) may simply be reflective of a natural bias in animal species in the area at the time (sections 4.3 & 4.4).

If the endurance capacities of the Neanderthals were indeed limited as their physique would suggest, chasing game randomly about the landscape was probably not their style. A hunting tactic involving the ambushing of prey in enclosed spaces would have been the option to which their physiques are best suited (section 4.3.1). Naturally abundant species, being more likely to pass into a suitable trap, would have been the dominant prey. Natural features being utilised as environmental weapons in the hunt may have included dense restrictive woodlands or riverine channels on the migratory routes of herds. The tracking or surrounding of a suitable quarry at a safe distance, would have been equally feasible (although impossible to discern directly from the archaeological evidence), with the Neanderthals biding their time until the right moment to pounce.

Walking to a suitable ambush location (or while tracking) would not have been energetically costly for hominids regardless of stature or weight, due to its high biomechanical efficiency (sections 9.1 & 9.7). In the case of Neanderthals valuable energy could have been conserved for the brief flurry of activity associated with the kill once an animal had entered the trap or been surrounded. Various aspects of Neanderthal anatomy and technology (i.e. high levels of skeletal trauma, high muscularity, asymmetrical upper limb strength, and spear technology) can give valuable insight into their kill methods. Rushing prey in close quarters is a possible interpretation incorporating all of the available evidence.

Neanderthal stature and muscularity would have been able to generate high speeds of movement and power for limited bursts of high intensity activity necessary for such a kill tactic. Considerable skeletal robusticity would have been required to withstand the physical abuse received from the cornered game, which in turn would account for the specific pattern and high severity/frequency of skeletal trauma observed among the Neanderthals. Upper body strength would also have been important in the handling aggressive game to prevent escape once initial wounding had occurred (chapter 5).

Neanderthals may have been pouncing on confined prey and stabbing it. This would have been a high risk tactic and as such is a rather extreme interpretation of the available evidence. Given the recently discovered wooden javelin-like spears in Europe, short-range spear throwing to wound prey before closing in may have been practised. The weight of the spears would have reduced accuracy at greater distances, and the general absence of hafting in the Middle Palaeolithic may have meant that laceration of the prey's muscle tissue was not totally disabling (section 3.7). Rushing wounded prey to prevent escape and deal the final blow in a contact situation would have been necessary, but done under conditions with reduced (although still significant) chances of injury.

12.3 - The Morphological Transition and the Replacement of the Neanderthals

Assuming that the first appearance of anatomically modern humans was Africa, rather than Southeast Asia, EAMH evolved in a hot open savannah environment (section 5.7). EAMH bodies were well adapted to dissipating heat, being tall and lean. They would have also had very different athletic capabilities, compared to those of the Neanderthals, probably being more adept at a 'middle distance' chase in the final stage of a hunt (the maintenance of a fairly robust frame is likely to have precluded a longer chase phase due to the energetic costs of transport - section 9.8).

Later, both populations were present in Southwest Asia. Each of them was able to survive in this region over a considerable time span, although the question regarding the permanence of settlement for either is heavily debated. It is possible that the environment here was more mixed relative to the extremes of Europe and Africa, or experienced oscillations in terms of the dominant ecosystem type (i.e. more wooded or open) coinciding with climatic cycles (i.e. colder and warmer pulses) in the run up to the last glacial maximum around 20,000ya. Shea (1989; p 622) suggests that a 'niche partitioning' system could have been operating in Southwest Asia. Although the proposed reason for this was slightly different to that argued below, it is agreed that the two populations remained largely separate on the basis of their ecological preference. Either way, both populations were able to survive here without significant alterations in skeletal morphology or significant technological advances, as both are associated with the Mousterian industry here (sections 2.2 & 3.3).

At the time of the transition both Neanderthals and EAMH inhabited western Europe, where both developed an Upper Palaeolithic industrial complex. As temperatures continued to drop, the environment underwent an important change: grasslands progressed southwards and replaced the arboreal landscape (section 2.6). Under such a scenario each population would have had a different adaptive problem.

The Neanderthals remained suited to the cold, but in a more open environment their physiques became maladapted for hunting activities. EAMH would have struggled in the cold but maintained their hunting capacity as they were familiar with hunting in such a landscape. As a consequence the 'classic' Neanderthal physique is seen to disappear around 30,000ya, or possibly slightly later. Regardless of the actual mechanism (i.e. extinction and replacement by EAMH, rapid substantial morphological adaptation by the Neanderthals, or a greater genetic contribution by EAMH in the hybridisation process) it is clear that as the maximum cold of the last glaciation approached in Europe, a physique closer in morphology to that of EAMH prevailed.

This implies that the Neanderthals became stressed to a greater extent under the environmental changes in Europe at this time than their EAMH counterparts. It would appear that the Neanderthal frame was less adept to hunting/subsistence in an open environment than the EAMH one was to withstanding the cold climate. The outcome of the environmental change was to alter the basis of Neanderthal subsistence. The

Neanderthal hunting technique, based on their short powerful physique, was no longer adaptive as the environment opened out. Late Neanderthal populations did cross the divide into the Upper Palaeolithic, but the associated technological advances must have failed to compensate for their newly deficient physiques.

The short and heavy physiques of the Neanderthals would have accrued increasingly vast energetic debts as hunting ranges had to expand, particularly in the realm of transport costs (but also possibly in biomechanical terms due to their accentuated distal limb shortening). In a closed environment where ambushing was possible, the Neanderthal kill tactics proposed here would have enabled a degree of energy conservation. This would not have been the case on a landscape where prey could not be trapped as easily and prolonged pursuit over greater distances was required for successful hunting. Competition from EAMH would also have enhanced the Neanderthals' adaptive problems.

This could be a possible explanation for the pattern of Neanderthal expansion into more southerly regions. The predominance of certain highly specific mechanisms of adaptation discussed here may have somewhat reduced the Neanderthals' flexibility. As conditions altered a degree of maladaptation seems to have ensued (section 12.3). The lines of inquiry here (with the backing the fossil record - sections 1.1 & 2.6) show that the last 'classic' Neanderthals (although not necessarily all, depending on whether hybridisation/continuation is recognised to have occurred in more central European areas) appear to have stayed with (or followed) their preferred woodland ecosystem as it shrank and disappeared with the approach of the last glacial maximum, remaining on the Iberian Peninsula (or pushing into Southwest Asia).

Muscular development, as it has a substantial phenotypic component, may have been able to adjust to establish a new balance between transport costs and power generation. However, body proportions would have had greater inertia to change due to the more conservative nature of genetic control and the fact that the metabolic/hormonal adjustments to the cold and nutritional stress would have continued and probably been enhanced. Thus with a theoretically limited option for morphological change, tracking woodland ecosystems as they moved southwards in accordance to glacial advances in northern areas of Europe would have been the simplest course of action available to the Neanderthal population.

In contrast, EAMH were able to survive and prosper in the cold even though their tropically adapted bodies underwent only limited proportional changes in limb length. Despite this anomaly they (or at least their physique) out-lasted the Neanderthals under increasingly cold climatic conditions, to which it is widely regarded that the Neanderthals were most strongly adapted. However, it was the increasing openness of the landscape, rather than the temperature, which likely proved to be the decisive factor in their survival. Rather than the explosive stop-start activities of the Neanderthals, EAMH were used to participating in more stamina orientated hunts across the African savannah which were more expansive in time and space.

In glacial Europe such long pursuits across the landscape would have increased metabolic heat generation directly, and indirectly as the fitness level attained would have raised BMR. This would have helped combat the cold to a degree, without the need to overcome the significant temperature oscillations to which the Neanderthals were subjected. However, the overarching explanation must be the improvements in artificial insulation and heat production (section 6.10.1). As the last glacial maximum approached (the Neanderthal form having already disappeared) the rate of technological advance and diversification is seen to increase within the archaeological record. It is not until later in the Upper Palaeolithic that the construction of tailored clothes/tents and thermally efficient hearths (as well as other advances including artistic endeavour) become established and widespread. The dating of this techno-cultural explosion is accepted as being considerably later than the archaic-modern morphological transition, roughly coinciding with the onset of full glacial conditions in Europe around 20,000ya.

Once in glacial Europe, under a novel set of selective pressures, EAMH techno-cultural capacities seemingly expanded/developed sufficiently to accommodate the thermally maladaptive nature of their physiques. Thus they were able to maintain a tall lean physique. Thus the associated athletic abilities used in successful hunting techniques on the African savannah would have easily been transposed on to the expanding tundra grasslands of Europe.

12.5 - Conclusion:

This thesis has proposed several new hypotheses to explain different aspects of Neanderthal morphology and their associated behavioural patterns from a physiological, rather than the customary archaeological/fossil, viewpoint. Thus, a broader picture of Neanderthal existence within their particular ecosystem has been developed. The wider context of their relationship with contemporaneous and subsequent EAMH populations at a time of substantial environmental/ecological change has also been discussed.

All the evidence suggests that the Neanderthals were highly adapted to a cold seasonal woodland niche. The Neanderthals (in particular the European group) successfully managed to maintain a positive energy balance and sufficient fertility for several hundred thousand years in the face of various rigorous physiological stresses. These were imposed by a harsh ecosystem which offered low energy availability while simultaneously demanding high energy output from its hominid inhabitants. A combination of the mediating influence of thyroid hormone activity, the resultant degree of proportional stunting, and possibly their specific activity (hunting) patterns seem to have successfully given the Neanderthals a significant capacity for energy conservation, and hence survival beyond 30,000ya.

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