Them and Us:

Neanderthal predation and the bottleneck speciation of modern humans

Danny Vendramini*

*Independent scholar. Correspondence to: PO. Box 924 Glebe. Sydney, NSW. 2037 Australia.
Ph: 612-9550 9682. Email: dv@amaze.net.au

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Abstract

Based on a reassessment of Neanderthal behavioural ecology it is argued argues that the emergence of behaviourally modern humans was the consequence of systemic Neanderthal predation of Middle Paleolithic humans in the East Mediterranean Levant between 100 and 45 thousand years BP. ‘Neanderthal predation theory’ proposes intraguild predation, sexual predation, hybridisation, lethal raiding and coalitionary killing gradualistically reduced the Levantine human population, resulting in a population bottleneck <50 Kya and precipitating the selection of anti-Neanderthal adaptations. Sexual predation generated robust selection pressure for an alternate human mating system based on, private copulation, concealed ovulation, menstrual synchrony, habitual washing, scent concealment, mate guarding, enforced female fidelity, incest avoidance and long-term pair bonding. Simultaneously, intraguild predation, lethal raiding and coalitionary killing generated selection pressure for strategic adaptations, including cognitive fluidity, male aggression, language capacity, creativity, increased athleticism, enhanced semantic memory, group loyalty, male risk-taking, capacity to form strategic coalitions, guile, conjectural reasoning and manual dexterity. Nascent fully modern human phenotypes were fixed during the population bottleneck by genetic drift and dispersed via global migrations. The new anti-Neanderthal species - *Homo sapiens sapiens* - agonistically replaced Neanderthals and Neanderthal-human hybrids, firstly in the Levant, then progressively throughout Europe and western Asia.

Introduction

Despite recent advances in radiometric dating, extraction and analysis of mitochondrial and nuclear DNA and the discovery of new Middle Palaeolithic (MP) and Upper Palaeolithic (UP) contexts, significant aspects of human evolution, behaviour and morphology remain poorly understood. Although isolated occurrences of UP behaviour appear in the African fossil record as early as 300 Kya, (McBrearty and Brooks, 2000), it was not until 46 Kya., (Tostevin, 1999) in Eurasia, that the UP began its rapid florescence to fixation and dispersal to Europe, (Bar-Yosef, 1998).

To further this debate, palaeoanthropologists have traditionally relied on fossilised skeletal remains and artefactual evidence notwithstanding that *Homo sapiens* are also distinguished by a plethora of non-skeletal, soft-tissue features and behaviours that do not preserve or result in physical artefacts, and therefore tend to be excluded from the debate on human origins. Significantly however, these microevolutionary phenotypes collectively distinguish humans from other primates and represent a macroevolutionary event – the speciation of archaic hominids into fully modern *Homo sapiens*. Therefore, understanding why these soft tissue morphologies and behaviours emerged, and how they contributed to inclusive fitness in the ancestral environment, may explicate modern human origins. The challenge is to identify what Bowlby, (1982) called the 'environment of evolutionary adaptation' - the ecological conditions that generated selection pressures for these novel features in humans but in no other primate species.

The pace of the UP transition

Any unified theory of human origins must not only explain the macroevolutionary magnitude of human evolution but also the singular pace of its florescence and fixation. The putative earliest Levantine UP culture, dated to 46-47,000 BP at Boker Tachtit in Israel, and Ksar Akil in Lebanon, (Bar-Yosef, 1996, 2000) spread to Europe (to Bacho Kiro in Bulgaria) within 3000 years (Kozlowski, 1982, 2000). Kuhn et. al., (2001) assert that UP ornament technologies dispersed "essentially simultaneous" to three continents.

The reasons most frequently cited for the rapid fixation of the Eurasian-European UP is the putative selective advantage conferred by qualitative improvements in UP procurement strategies compared to the MP. However, this has been challenged by Kaufman, (2002) whose examination of faunal assemblages from the two periods in the Levant revealed no significant differences in hunting effectiveness. See also Grayson and Delpech, (1994), and Stiner, (1994). Moreover, while the transition to UP undoubtedly resulted in minor increases in reproductive fitness, hominids had survived 6-7 million years (since diverging from family *Pongidae*) without UP culture. Furthermore, a mosaic of UP behaviour appears sporadically throughout Africa between 300 – 40 Kya, yet did not become fixed throughout Africa or proliferate across the world. It did not, as Bar-Yosef, (2002) noted, affect the general trend of human evolution. As it was only the Eurasian UP that fixed and dispersed to Europe, Africa, Asia and the Americas, it suggests the ecological factors that drove the UP transition to fixation in Eurasia were absent or insufficiently robust in Africa, resulting in the sporadic and haphazard mosaic of African hominid evolution demonstrated by the archaeological record.

Did climate stress play a role?

One plausible ecological factor is climate stress. Extreme climatic conditions and fluctuations (such as those precipitated by droughts, floods, volcanic eruptions and asteroid strikes) can increase competition between individuals and result in rapid evolutionary change and even speciation events. For example, the six year ‘volcanic winter’ that Ambrose, (1998a), argues followed the Toba volcanic eruption in western Sumatra 73 Kya may have impacted on population densities in the northern hemisphere, (Rampino and Ambrose, 2000, Ambrose, 2003. , but see Lahr and Foley, (1998), Oppenheimer, (2002), and more recently, Petraglia, et. al., (2007) for a contrary view.

However, it is difficult to comprehend what adaptations against atmospheric opacity, airborne dust and food shortage could have resulted in modern human morphology and behaviour. Population reduction precipitated by the Toba event would be unilateral and indiscriminate, denying NS a significant role. In addition, there is a chronological 26,000 year discrepancy between the Toba event (73 Kya.) and the appearance of the UP at Tachtit Boker (47 Kya.) Finally, based on a review of marine oxygen-isotope data from deep-sea sediment cores, Shea, (2001) concludes, “the MP/UP transition in the Levant is not correlated with any major shift in the global oxygen-isotope record of climate change.” For these reasons, it is unlikely the Toba event precipitated the UP revolution in the Levant.

While McGarry, et. al., (2004) have shown the climate of the Levant became cooler and dryer between 50-45 Kya. climate fluctuations have been relatively common throughout the evolutionary history of *homo* and previous fluctuations have not been associated with MP-UP transitions. Moreover, scenarios that attribute the emergence of the human UP to the advent of cooler, dryer conditions in the Levant must also explain why it exerted no impact on Neanderthal evolution.

If climate stress was not a factor in the emergence of modern humans in the Levant, what plausible alternatives remain? Extrapolating NeoDarwinian theory, it is my view that there is only one other ecological dynamic capable of initiating a speciation event within the limited time frame. Only one environmental factor could compel NS to confer art, language, organization, symbolism, long-term episodic memory, forward thinking, exceptional intelligence and innumerable other uniquely human cognitive traits on one primate species while the other 192 remained unaffected. That single factor, in my view, is predation.

The predation hypothesis

Because predation generates both interspecies and extraspecies competition, and competition is the engine of NS, the predator-prey dynamic is one of the most influential ecological mechanisms in the animal kingdom (Taylor, 1985). Selection pressure generated by predation has been instrumental in the evolution of a wide range of phyla, so it is entirely possible that predation may also have been a causative factor in the abrupt emergence of modern humans.

Significantly however, there are two aspects of predation dynamics - predator and prey - and evolutionary scenarios based on humans as predator - ‘man the hunter’ (Washburn and Lancaster, 1968; Ardrey, 1977; Peterson and Wrangham, 1997.) although deeply embedded in anthropological thinking, do not satisfactorily explain our unique evolutionary trajectory (Tanner and Zihlman, 1976; O'Connell, et. al, 2002; Sussman, 1999; Hart and Sussman, 2005.) However, the abrupt transition from MP to UP, our novel physical appearance, and our singular behavioural repertoire do appear consistent with the view that *H. sapiens* evolved - for a period of time - as a prey species. That is to say, the defining morphological, behavioural and emotional characteristics of *Homo sapiens* may be the adaptations of a prey species to systemic long term predation by a single predator.

On the basis of dispersal patterns of early human populations, correlated against the archaeological and trophic records of the Late Pleistocene Epoch, hunting patterns, habitats, climate and human-Neanderthal interaction scenarios, it was concluded that Neanderthals (*Homo Nenderthalensis*) were the singular Pleistocene predator of archaic humans. This paper will examine the proposition that Neanderthals subjected Early Modern Humans (EMHs) in the Levant to both low intensity cannibalistic and sexual predation over many thousands of years.

Neanderthal Predation theory

Accordingly, the core hypothesis to be elaborated and tested here argues that between 100 and 48 Kya, when Neanderthals and EMHs occupied contiguous areas of the East Mediterranean Levant, Neanderthals periodically hunted, devoured, abducted and coercively mated with EMHs. The sustained ecological and evolutionary impact of this multifaceted predation generated selective pressures, initially for defensive phenotypes against Neanderthal predation, and subsequently for offensive phenotypes, and cumulatively, these adaptations transformed EMHs into fully modern s*apiens*.

Neanderthal Predation (NP) theory is derived from a reassessment of *Homo Neanderthalis* as the pre-eminent Eurasian apex predator. It views Neanderthals as an environmental stressor, generating specific selection pressure on EMHs to affect evolutionary change. Although some aspects of this scenario are speculative and rely in part on circumstantial evidence, the revised evolutionary scenario is nevertheless consistent with current stratigraphic data and corroborated by genetic evidence from extracted ancestral nuclear and mitochondrial DNA (mtDNA) and generates a number of predictions that may be used to empirically test the veracity of the hypothesis.

Chronological and demographic context of Neanderthal predation

The first test of the hypothesis is to demonstrate that early MP humans and Neanderthals contemporaneously coexisted within the same geographic and chronological context, and that the duration of the cohabitation was theoretically sufficient to effect the speciation of EHMs into *Homo sapiens*. Late Pleistocene dates from Skhul and Qafzeh EMHs and Amud, Kebara and Tabun Neanderthal assemblages (all from Mt Carmel) convincingly demonstrate penecontemporaneity and geographic overlap between EMHs and Eurasian Neanderthals in the Levant, (Bar-Yosef, 1986, 1987, 1996; Gilead, 1991; Jelinek, 1982; Tchernov, 1998; Arensburg and Belfer-Cohen, 1998; Shea, 2001; Kaufman, 1999, 2001.)

Determining the chronological duration of cohabitation is more problematic due to the imprecision of dates derived from thermoluminescence, questions pertaining to provenance, and the possible interstratification of stratigraphic levels relating to the Tabun C1 Neanderthal. If Tabun C1 derives from level C, as suggested by Alperson et. al., (2000) and which Mercier et al., (1995) dated using TL on flint artefacts at 171 ± 17 ka BP, it would suggest a possible 100,000 year co-habitation by early moderns and Neanderthals. Other scholars, namely Shea, (2003) argue that EMHs were present in the Levant from 130 Kya to 80 Kya., and that Neanderthals may have been present in the region 120 Kya. This dates the Levantine overlap at 40,000 years, while Grün and Stringer, (1991), Valladas et. al., (1987) and Trinkaus, (1991) argue the two species coexisted for 65 Ky. In all likelihood, there were multiple 'trickle' migrations into the area by both Neanderthals and early humans, driven, Shea (2003) suggests, by climatic variability and parallel migrations of fauna into the Levant from Africa. While the duration of Neanderthal-EMH cohabitation in the Levant remains equivocal, for the purpose of this discussion, it is conservatively estimated to have occurred between 100-50 Kya., providing a 50,000 year period of potential predation - sufficient time for speciation to occur in the EMH population of the Levant.

Neanderthals: a reassessment

It is axiomatic that two bipedal MP hominids sharing the same ecological niche, and competing ostensibly for the same resources would disrupt the ecological homeostasis and generate intraspecific competition. However, NP theory additionally argues that competition was generated primarily by Neanderthals via predation, which exerted a functional constraint on Levantine early moderns that resulted in a speciation event. The hypothesis is not supported by the current model of Neanderthal behavioural ecology, which does not accommodate a robust predatory component. However, a reassessment of Neanderthal behavioural ecology and morphology based on recent palaeontological and archaeological evidence demonstrates (at least circumstantially) that Neanderthals were an apex predator and subjected Levantine EMHs to systematic long term sexual and cannibalistic predation. The reassessment will focus on ten aspects of Neanderthal ecology (Figure 1) and is consistent with the growing acknowledgement, based on lithic artefacts, abundantly preserved faunal remains, and carcass utilization of prey species, that Late Pleistocene Neanderthals were skilled hunters rather than opportunistic scavengers (Stiner 1994; Jaubert, et. al. 1990; Gardeisen, 1999).

Figure 1. ASPECTS OF NEANDERTHAL ECOLOGY UNDER REASSESSMENT

Periglacial adaptations	Carnivory
	Cannibalism
	Morphology: pelage, gait, craniofacial morphology
Predatory adaptations	Nocturnality
	Visual perspicacity
	Olfactory acuity
	Coalitionary killing
	Lethal raiding
Primate-hominid homologies	Sexuality
	Territoriality

It is also consistent with considerable research over the last decade that recognises the cognitive and behavioural complexity of Neanderthals (Wynn and Coolidge, 2004; Kolen, 1999; Vaquero, et. al., 2001; Marean and Assefa, 1999; D'errico, et. al., 2003).

Periglacial adaptations

Neanderthals were the only hominid species to evolve in a climate of seasonally lethal cold (Steegmann, Jr. et. al., 2002). Their periglacial European environment has been described (Shea, 2001) as one of the harshest and most inhospitable habitats ever occupied by hominids. During their 350,000 year occupation, Neanderthals acquired a range of novel morphological and behavioural adaptations to cold climate, including short distal limb segments (Trinkaus, 1981), the shape of the femur and pelvis (Weaver 2003; Russ, 1994) large nose, and compact torsos, all features believed to minimise heat loss (Trinkaus, 1986, 1989; Churchill, 1994). While Steegmann, Jr. et. al., (2002) propose a number of physiological climatic adaptations, (Figure 2), they stress the role of behaviour in cold resistance has not been addressed and remains one of the great puzzles of Neanderthal climatic adaptation.

Figure 2: NEANDERTHAL COLD CLIMATE SELECTION (Adapted from Steegmann, Jr. et. al., 2002)

High muscle mass	Effective insulator, providing 88% of insulation at rest.
Vasoconstriction	Diverts blood to maintain temperature around essential organs
Subcutaneous fat	Passive insulation against deep body heat loss.
Cold acclimatization	Decline in shivering and increase in nonshivering thermogenesis.
Brown adipose tissue (BAT)	Maintaining BAT into adulthood
Craniofacial morphology	Nasal adaptations are thought to play a major role in cold climate adaptations but precisely how remains little understood.

Carnivory

Steegmann, Jr. et. al., (2002) conclude that Neanderthals could only tolerate the cold climate if they could consume an adequate amount of energy. This highlights the need for protein and fat in cold climate ecosystems which has been amply demonstrated, (Cachel, 1997). A high protein, high fat, animal meat diet was therefore almost certainly another functional constraint imposed by the periglacial European environment. Kuhn and Stiner, (2006) show that few plants could survive in the cold climate and those that did were not nutritious enough, or required too much effort to collect and process relative to their low nutritional yields. Given that fishing was not generally practised during the MP (Bar-Yosef, 2004), and no Neanderthal contexts unequivocally reveal fishing technology, the only means by which Neanderthals could procure a constant supply of fresh meat was by proactively hunting terrestrial prey. The abandonment of the ancestral omnivorous diet in favour of carnivory would establish an ecological divide between *Homo Neanderthalis* and EMHs, with profound implications for modern humans.

Neanderthal carnivory is supported by data derived from carbon and nitrogen isotopes of bone collagen that reveals the percentage of plant foods in their diet was close to zero (Vincent and Laurent, 2006). Strontium-calcium and barium-calcium ratios extracted from 40 Saint-Césaire Neanderthal samples by Balter et. al., (2001) similarly shows of Neanderthal diet comprised approximately 97% (in weight) of meat. See also Lalueza-Fox and Pérez-Pérez, (1993); Fizet et. al., (1995); Lalueza, Perez and Turbon, 1996; Geist, (1978, 1981); and Richards, et al., (in press). The new consensus, exemplified by Bocherens, et. al., 1999; Fizet, et. al., 1995; and Pettitt, (2000 is that Neanderthals were exclusively carnivorous, subsisting only on a diet of animal flesh. Drawing on isotope analysis of mammal bone from the Vindija Neanderthal Cave, Croatia Richards, et al., (2000), draws the parsimonious conclusion – that Neanderthals were top-level carnivores.

Archaic humans, by comparison, maintained their African omnivorous diet, from which approximately 50% of energy intake was supplied by uncultivated fruits and vegetables (Eaton, 2006).

Behavioural implications of Neanderthal carnivory

The data demonstrating Neanderthal obligate carnivory warrants a critical revaluation of Neanderthal ecology and behaviour. As meat-eating predators, NeoDarwinian theory predicts that just as wolves, lions, hyenas and other carnivorous pack-pursuit predators evolved specialised sensory, behavioural, attitudinal and morphological adaptations to enhance capture rates, so too did Neanderthals. The massiveness of the trunk and limb bones of Neanderthals -indicative of superior strength compared to modern humans (Trinkaus, 1978; Trinkaus and Howells, 1979) may be interpreted as one such adaptation. Also typical of carnivorous predators engaged in hunting large, dangerous animals Neanderthals sustained a disproportionately high number of physical injuries during their short lives (Pettitt, 2000; Trinkaus and Zimmerman, 2005; Trinkaus, 2005;) which Berger and Trinkaus, (1995) argue are indicative of a violent and predatory lifestyle. These lines of evidence are also consistent with the observation by Trinkaus, (1983) that almost every adult Neanderthal skeleton provides indications of trauma, and the interpretation by Zillikofer, et. al., (2002) that some trauma injuries resulted from interpersonal violence. (See also, Shea 1998.) Judging by the pattern of fractures (Zollikofer, et. al., 2002), and their use of flint tipped thrusting spears to capture a range of dangerous prey species, including mammoths and woolly rhinos (Schmitt, Churchill and Hylander, 2003; Berger and Trinkaus, 1995; Hardy et. al., 2001) Neanderthals were courageous and adept close-quarter hunters.

Although they possessed the extrinsic physical appearance of bipedal hominids (albeit, their skeletons were adapted for greater musculature and robusticity than early humans) it is suggested Neanderthal behaviour was more analogous to pack-pursuit, social carnivores such as canids and felines. As both ambush and pursuit predators, Neanderthals would have to acquire inter-group communication skills, ferocity, aggression, viciousness and guile, plus specialist hunting strategies to maximise their capture rates. Although these behaviours do not fossilize, specialised hunting behaviours have been convincingly inferred from anatomical and archaeological data (Hoffecker and Cleghorn, 2000; Pettitt, 2000; Chase, 1989). Neanderthals hunted in organised packs and developed individualised strategies for each prey species they stalked (Gaudzinski and Roebroeks, 2003; Jaubert, et. al., 1990; Miracle, 2000). Furthermore, citing evidence of greater spear point production by Eurasian Neanderthals than by Levantine EMHs, Lieberman and Shea, (1994) and Shea, (1998) conclude Neanderthals were more predatory than EMHs.

The reassessment of Neanderthals as the Levantine apex carnivore reflects the growing consensus that Neanderthals were not dim-witted scavengers, but intelligent, adaptable and formidable pack predators.

Cannibalism

The suggestion that Neanderthal behaviour was analogous to that of social carnivores such as hyenas, wolves and lions and that their prey included EMHs needs to be corroborated by archaeological evidence. At issue is the central question – did Neanderthals also hunt and consume humans? Support for this hypothesis derives from a number of Neanderthal sites revealing evidence of perimortem modifications of hominids, (Figure 3) which confirm what Gorjanovíc-Kramberger, (1906) proposed over a 100 years ago; Neanderthals, at least periodically, practised dietary cannibalism. (See also Defleur, et. al., 1993).

Figure 3: NEANDERTHAL SITES WHERE CANNIBALISM HAS BEEN REPORTED

SITE	COUNTRY	REFERENCE
Krapina	Croatia	Russell, 1986; Fernández-Jalvo, et al., 1996
Vindija	Croatia	Malez and Ullrich, 1982
Marillac	France	Vandermeersch, 1980
Combe Grenal	France	Hughes, et. al., 1951
Macassargues	France	Mort, 1989
El Sidrón	Spain	Rosas, et. al., 2006
Les Pradelles	France	Mann, et. al. 2005
Zafarraya	Spain	Hubin, et. al. 1995
Moula-Guercy	France	Defleur, et. at. 1999

Within the ecological context of energy expenditure and provisioning in the challenging glaciated ecosystems of Europe where Neanderthals evolved, resorting to dietary cannibalism if only during periods of food stress would be a beneficial strategy and consistent with strong evidence of human cannibalism by ancestral hominids at Gran Dolina, Sierra de Atapuerca, in Spain dated to 780,000 years BP (Fernandez-Jalvo et. al., 1999). The alternative explanation – that Neanderthal cannibalism was ritualistic may be discounted as ritual cannibalism requires cognitive precepts hitherto only associated with UP culture.

Having adapted over 350,000 years to demanding glacial and periglacial European habitats, where food provisioning was capricious, and their principal diet was animal meat, it is parsimonious to suggest that when Neanderthals colonised the Levant refugia, no edible, economically procurable species was off the menu. Bone assemblages in Neanderthal contexts reveal they hunted the most hazardous species; including mammoths, giant cave bears, bison, antelope, woolly rhinos, wild boar, wolves and lions. Because Neanderthal were extracting maximum nutritional sustenance from each carcass, and hunted every edible animal species in their territory, then in the absence of cultural, moral and religious constraints against cannibalism (to date only attributed to fully modern humans) it is reasonable to conclude that Eurasian Neanderthals also hunted humans, if only during periods of trophic stress.

The predation hypothesis gains support from Gause's Law of competitive exclusion (Gause, 1934) which states that two species with similar trophic and ecological requirements cannot both indefinitely occupy the same environment. Applied to the Levant, a predicted outcome is that Neanderthal encroachment into archaic human habitat in the Levant would generate competition for the same resources and promote ecological instability. As Grün and Stringer, (2003) note, EMHs and Neanderthals possessed similar needs for food and shelter. They were competing directly for the same prey species (Shea, 2003, 2003b), and presumably for the same cave sites, fresh water, flint, chert and ochre. As the physically superior hominid, who had evolved the predatory instincts, strength, ferocity and ‘lethality’ to pursue and subdue a wide variety of prey over hundreds of thousands of years in the most demanding environment on Earth, it is plausible to conjecture that Neanderthals rapidly asserted a strategic dominance over EMHs. This supports the view that EMHs in the Levant, estimated by Shea, (2003) to have numbered between 5,000 – 10,000 individuals, opportunistically provided Neanderthals with an additional prey species that could be exploited as required.

Intraguild predation

The presence of two analogous MP hominid predators in the Levant also raises the possibility that their ecological interaction was moderated by intraguild predation, which is defined by Polis, et. al., (1989) as the killing and consumption of an intermediate predator by a top predator from the same guild – for example, the killing of cheetahs (*Acinonyx jubatus*) by lions (*Panthera leo*) (Morin, 1999.) Intraguild predation (or interspecific killing) is a taxonomically widespread phenomenon among mammalian carnivores (Rosenzweig, 1966). Palomare and Caro, (1999) found 97 pairwise predatory interactions between mammalian carnivore species, involving 27 killer species and 54 victim species. They report that mammalian carnivores account for up to 68% of known mortalities in some species. Significantly, the top predator does not always consume the intermediate predator. Of 21 cases of intraguild predation in the Palomare and Caro, (1999) study, the top predator species consumed their prey (wholly or in part) in only 10 cases. For example, while spotted hyenas (*Crocuta crocuta*) consumed all the cheetahs they killed, lions were not observed eating cheetahs. This indicates that the evolutionary function of intraguild predation may be to reduce competition for a shared prey resource (Eaton, 1979).

Given the ubiquity of intraguild predation among mammalian terrestrial predators, it may be assumed its evolutionary origins are of sufficient antiquity to apply to Neanderthal-EMH interactions in the Levant, strengthening the case for an adversarial relationship between the guilds based on competition for shared resources.

Territoriality

The use of physical force, threat, or advertisement to defend an area is a ubiquitous feature of chimpanzee society (Herbinger, Boesch, and Rothe, 2001). Male chimps at Gombe, Tanzania, patrol the borders of their territory at least twice a month, and intruders are often violently attacked, and in some cases, killed. These attacks support the view that intergroup violence in defence of territory is a persistent feature of chimpanzee societies (Wilson, et. al., 2004; Wrangham, 1999). Perhaps the most singular aspect of chimpanzee territoriality is the violence of their hostility towards neighbouring communities (Hamburg, 1974; Bygott, 1972; Teleki, 1975). This adds weight to Wrangham’s contention, (Wrangham, 1999) that chimpanzee territory size is correlated to fitness. However, while common to many primate species, (Bates, 1970) territoriality is not universal among primates (King, 1976). Other analogues for the study of Neanderthal territoriality may therefore be required. Several scholars (Schaller and Lowther, 1969; Thompson, 1975), have suggested that social carnivores, by virtue of their group dynamics, dominance hierarchies, land tenure systems and co-operative hunting techniques, provide better analogues than primates for the study of hominid behaviour. The assertion that Neanderthals were pre-eminent social predators condones the use of this analogue.

Ecological studies reveal that territoriality is not only more prominent among social carnivores such as lions, hyenas and wolves, but also far more violent (Schenkcl, 1966; King, 1975; Kruuk, 1972; Mech, 1970) with chimpanzees among the most violent of the social carnivores (Goodall, 1977; Kutsukake and Matsusaka, 2002; Hiraiwa-Hasegawa, et. al., 1986; Watts, et. al. 2006). While this evidence does not permit a conclusion to be drawn in respect of Neanderthal territoriality, it raises the likelihood that if Neanderthal behaviour was typical of that of other social carnivores, they would defend their territory aggressively, and this would have impacted directly on early human ecology in the Levant.

Coalitionary killing and raiding behaviour

Lethal violence, other than for consumption, while not infrequent in the animal kingdom, is almost always dyadic (Wrangham, 1999). A rarer form of lethal violence has also been observed; ‘coalitionary violence’, characterised by lethal violence between groups, or violence directed by a group towards an individual. Coalitionary violence has been periodically observed among spotted hyenas (,*Crocuta crocuta*), wolves (*Canis lupus*), lions (*Panthera leo*) and cheetahs (*Acinonyx jubatus*) - all social predators - but is most common among chimpanzees and humans (Wrangham, 1999). Among habituated chimps so far studied, no lethal case of dyadic violence has been reported; all lethal attacks have been attributed to groups. Victims may include members of the same group, but more frequently tend to be members of neighbouring communities. Typically, a coalitionary assault lasts at least ten minutes, during which the assailants hold down the victim and continue to bite, strike, tear and drag until the victim is killed or immobilised (Goodall, 1986).

A related aggressive behaviour, also the preserve of social predators, is ‘lethal raiding’ which entails the intrusion by groups of males into a neighbouring territory, specifically to conduct a surprise attack, extract casualties, and retreat to the home territory (Wrangham, 1999; Kelly, 2000; Gat, 1999). Lethal raids have been observed among wolves (Mech, et. al.. 1998) and spotted hyenas (Goodall, 1986), but again chimpanzees and humans are the most frequent exponents of lethal raiding by males.

Lethal raids are not escalations of current conflicts, acts of self defence or food procurement expeditions (Wrangham, 1999). In all observed cases of chimpanzee raiding, the males encroach in unusual silence, in single file into a neighbouring territory, until they locate and capture a vulnerable individual which is then killed. In this respect, Wrangham, (1999) describes chimpanzee lethal raiding as akin to predation.

No consensus has emerged to account for coalitionary killing, lethal raiding and intergroup aggression among chimpanzees (see van der Dennen, 1995 for a review). A number of researchers have proposed that lethal raiding and coalitionary killing in contemporary chimpanzees represents an extreme form of sexual competition, aimed at killing rival males and gaining access to sexually mature females from neighbouring communities (Manson and Wrangham, 1991; Boesch and Boesch-Achermann, 2000; Goodall, 1986). It may be significant that all-male groups of wild chimpanzees at Gombe, Tanzania have been observed violently appropriating and abducting females from other groups, resulting in prolonged fighting and skirmishes lasting several days (Bygott, 1979; Mohnot, 1971). However, their obvious resemblance to human patterns of intergroup aggression and warfare are so striking, many researchers argue they are linked by functional homologues and behavioural continuity (Trudeau, et. al. 1981; van Hoof, 1990; Boesch and Boesch-Achermann, 2000; Otterbein, 1985; Ghiglieri, 1988; Manson and Wrangham, 1991; Alexander, 1989).

Otterbein, (1997) draws on the evidence of warfare among primates, prehistoric hominids, early agriculturists, and contemporary hunter-gatherer societies to conclude that coalitionary killings and intergroup warfare by males has been a ubiquitous feature of human ancestry for over 5 My. If the propensity for coalitional killing and lethal raiding in modern humans and in our most proximate relative, the chimpanzees are valid analogues for intergroup aggression by hominids and early humans, then it is requisite to extend the analogue to Neanderthals. In the Levant, the presence of a less aggressive, sexually compatible hominid species and the margin of safety this ‘soft target’ provided may have additionally encouraged Neanderthal male aggression and lethal raiding.

Significantly, if the portrayal of Neanderthals as a proficient spear-wielding apex predator-carnivore is accurate, then lethal raiding and coalitionary killing by Eurasian Neanderthals would result in significantly more EMH casualties than an equivalent raid by contemporary chimpanzees (which do not use weapons) or MP humans. Furthermore, if Neanderthal raiding also encompassed a sexual component, then the asymmetrical depletion of human males, the transfer of fertile human females to Neanderthal camps, and the opportunistic mating of human females in oestrus would additionally dilute and deplete the human population.

Sexuality

Because modern humans are predisposed to monogamy, pair bonding, romantic love, sexual modesty and private copulation, this does not merit ascribing these behaviours to Neanderthals. As it is *Homo sapiens* who are anomalous – the only primate to develop a novel mating system - it is apposite to draw on nonhuman primate sexual analogues to speculate on Neanderthal sexuality. In the absence of evidence of specific functional constraints acting on Neanderthal sexual morphology and behaviour (as occurred with EMHs) it should be assumed that the Neanderthal mating system conformed to primate sexual orthodoxy.

Given that ovulating chimpanzees and bonobos copulate with alacrity with multiple partners (in public), do not fall in love or form lasting pair bonds, (Fisher 2004), it is likely that Neanderthal sexuality followed suit. Primate sexual arousal is moderated by female primates in oestrus displaying conspicuous and unambiguous signs of ovulation. With each cycle, the female genitalia becomes tumescent and the increased blood flow turns the tissue purplish pink - advertising the advent of oestrus. This is accompanied by a pheromonal scent and vaginal discharges that initiate competition between males for access to fertile females. This suggests that Neanderthal copulation was similarly initiated by visual cues and pheromonal scents and would be highly motivated but perfunctory and mechanistic. Significantly however, as members of the same clade and possessing homologous sexual proclivities, Neanderthal males would be receptive to the same sexual advertisements in human females. That is to say, human females in oestrus would also have attracted Neanderthals in the region. Because of Neanderthals' superior sensory modalities, olfactory and pheromonal attraction may have occurred over considerable distances.

This posits that Neanderthal and human males competed for the same human females, and that this directly contributed to the enduring antipathy humans felt towards Neanderthal. To Neanderthals, competition for human sexually mature females would represent an adaptive adjunct to their mating system, while for Levantine EMHs, it was endured as deleterious sexual predation.

Nocturnality and its functional constraints

Carnivorous predation imposes dietary restrictions which require carnivores to expend significant resources on hunting. Because terrestrial prey are easier to capture at night when they are sleeping or resting, most mammalian terrestrial predators are nocturnal. It is likely then, that in addition to diurnal hunting, Neanderthals also adapted to nocturnal hunting during their European sojourn. This hypothesis is testable because it predicts that like other nocturnal hunters, Neanderthals acquired specialist morphological and behavioural adaptations to enhance prey capture in low-light conditions, including increased olfactory, auditory and nocturnal visual acuity. Several lines of evidence supporting the hypothesis are here reviewed.

Visual perspicacity

Just as the visual systems of primates evolved to meet the challenge of their arboreal habitats (Elliot Smith, 1924; Le Gros Clark, 1959; Crompton, 1995;) so too, nocturnal primates acquired specialist adaptations to increase retinal image brightness in low light conditions (Cartmill, 1972; Heesey, 2003; Ravosa and Savakova, 2004). These adaptations contributed to prey capture by facilitating improved identification of prey and stereoscopic depth judgements (Cartmill, 1972; Allman, 1977). Based on a review of comparative data, Callum and Kirk, (2007) report 'that nocturnal visual predation had a putative selective influence on the early evolution of the primate visual system.' To maximize visual sensitivity, nocturnal primates acquired allometrically larger pupils and corneas (relative to the focal length of the eye) than diurnal species of similar size. To accommodate these larger eyes, Kirk, (2006b) reported that nocturnal primate species have larger orbital apertures relative to diurnal species.

If Neanderthals were nocturnal hunters, then larger corneas and optical orbits (eye sockets) would be a feature of their cranial morphology. While eyes do not fossilise, orbits do, and even a cursory comparison between Neanderthal and human orbit size reveals Neanderthals orbits were substantially larger. (Figure 4) To date, no explanation has been suggested for this novelty.

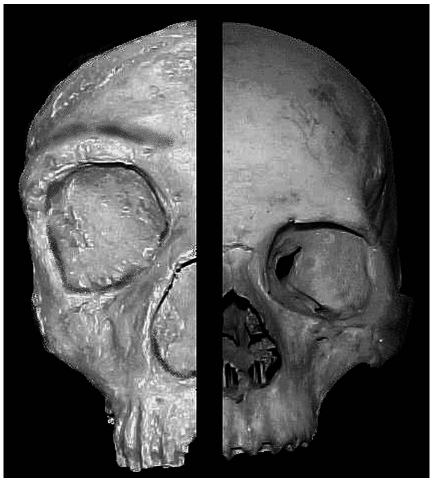

Figure 4. Comparison between orbit size of Gibraltar Neanderthal specimen (left) and EMH skull (right) reveals substantially different orbit size.

Another adaptation common to most nocturnal animals is the multifocus lens that utilises concentric zones of different focal lengths to improve focus in low light. However, as Malmström and Kröger, (2006) recently demonstrated, multifocus optical systems cannot function with round pupils. They require slit pupils to facilitate the use of the full diameter of the lens in low light. In considering whether Neanderthals evolved larger eyes with slit pupils, it is noteworthy that the optical orbits of Neanderthals are larger (and rounder) than humans, which is indicative of an adaptation to environmental conditions different from humans. Moreover, if Neanderthals evolved acute nocturnal visual acuity in Europe, it would additionally need to prevent retinal damage caused by sunlight reflected off snow, which was a ubiquitous feature of the European landscape during their tenure. Significantly, one of the added advantages of slit pupils is that the iris muscles can be closed tighter and exclude considerably more light than round pupils. Nocturnal predators such as lions, tigers, owls, cats, alligators, crocodiles acquired slit pupils to protect their retinas from strong sunlight.

As to whether the slit pupils were horizontally or vertically aligned, the fact that nocturnal primates, *Aotus trivirgatus*, and *Galago garnetti* have vertically aligned slit pupils is telling. Vertically aligned slit pupil work in conjunction with the animal’s eyelids to block out even more sunlight. When the animal squints, its horizontal eyelids close at right angles to the vertical slit pupil, blocking out considerably more light than if they were both aligned horizontally. Given this, it is likely that Neanderthal pupils were also vertically aligned.

The theory that Neanderthal eyes were adapted to nocturnal predation additionally implies the emergence of a larger visual cortex to process low-luminosity visual precepts. In primates, the primary visual cortex is located in the occipital lobe. Significantly, the pronounced posteriorly-directed projection of the occipital lobe is a ubiquitous feature of Neanderthal cranial morphology. This ‘bunning’ is absent in the human skull, suggesting that the Neanderthal bun may have evolved partially to accommodate an expanded visual cortex. However, for alternative explanations for Neanderthal occipital bunning; see Geist, (1978), Lieberman, et. al., (2000), and Smith and Green, (1991).

Physical appearance

It has generally been assumed that because humans and Neanderthals are phylogenetically derived from a common ancestor, ergo, their outward appearance would also be analogous, (Strauss, Jr. and Cave, 1957). Modern pictorial and three-dimensional representations of Neanderthals typically portray them as beetle-bowed, large nosed, but clean shaven versions of modern humans. There is of course, no evidence to substantiate this popular anthropomorphic assumption (Berman, (1999). An alternative view derived from

NeoDarwinian theory offers a more parsimonious view of hominid visual appearance; unless causal factors rendered it advantageous to alter the external appearance of Neanderthals, the primate morphological status quo - established by NS over millions of years - would prevail. That is to say, in the absence of robust selection pressures, Neanderthal external morphology and appearance would retain the visual characteristics of common hominid, hominin and primate ancestors. This suggests the hairless face, brown eye scleras, flat nose, wrinkled facial skin and thin black lips (that protected ancestral primates from sunburn and melanomas) would all be retained in European Neanderthals.

Pelage

If all contemporary terrestrial mammals living in periglacial ecosystems have selected for thick body fur, it suggests the iconic view of Neanderthals almost as devoid of body hair as moderns humans is an anthropomorphic artefact and needs to be re-examined. Cold adapted extant primates, in particular, Japanese macaques (*Macaca fuscata*) and gelada baboons (*Theropithecus gelada*) demonstrate that not only do cold climate primates acquire thicker, longer pelage, but additionally an annual 'winter coat.' This is consistent with European osteological, fossil and cave art evidence that reveals long thick pelage was a ubiquitous feature of Late Pleistocene terrestrial mammals (Figure 5), Russell, (1966); Ling, (1970); Stiner, (1999); Nagel, (2003).

Figure 5:

EUROPEAN PLEISTOCENE MAMMALS WITH LONG DENSE COATS

Woolly Rhinoceros	*Coelodonta antiquitatis*
Woolly Mammoth	*Mammuthus Primigenius*
Musk oxen	*Ovibos moschatus*
Cave Bear	*Ursus spelaea*
Eurasian cave lion	*Panthera leo spelea*
European bison	*Bison bonasus*

The possibility that Neanderthals relied on cultural means of insulation against the cold to any large extent is also unlikely as this would require needles to sew garments, and to date, needles have not been recovered from Neanderthal contexts. Furthermore, thermal garments need to be adequately maintained as wet clothes can increase heat loss by a factor of five (Osborn, 2004; Stenton, 1991; Curtis, 1995), and it is debatable whether Neanderthals possessed the cognitive capacity to support cultural insulation to any large extent.

Finally, when culturally insulated fully modern humans finally entered Europe, they were able to colonise the coldest parts of Europe and Siberia. Humans lived as high as latitude 60° North, but significantly, European Neanderthals rarely strayed above 50 ° North

(Hoffecker, 2004). Similarly, Davies and Gollop (2003) found that European Neanderthals avoided areas where the winter temperatures fell below -8° C, and preferred summer temperatures between 12° and 25° C. While there may be several reasons for this, one of them is that modern humans could live in sub -10° C temperatures because they fabricated tailored garments and Neanderthals did not. This would indicate that -8° to -10 ° C was the insulation limit of their body hair.

These data are consistent with the hypothesis proposed here that Neanderthals not only retained the ancestral primate pelage as a cold climate adaptation to periglacial Europe, but that it increased in length and thickness to facilitate thermoregulation and heat retention. Furthermore, the thick body fur of primate ancestors may have been bolstered by a seasonal 'winter coat.' These conclusions redefine what Neanderthals looked like, suggesting their visual appearance was more analogous to an upright chimpanzee or gorilla than a modern human.

Nasal morphology

Although it is generally assumed that Neanderthal noses looked similar to human noses, albeit, larger and broader, this assumption also lacks evidential corroboration. A large protruding appendage like a nose is more prone to frostbite - this is certainly the case in modern humans in cold climates (Lehmuskallio, et. al., 1995) so Neanderthals may have retained the flat nose of ancestral chimpanzees and gorillas to minimise frostbite in their periglacial European habitat.

Olfactory acuity

Mammalian predators typically rely on scent to locate and track prey - particularly at night and in marginal conditions – so it may be expected that Neanderthals also acquired enhanced olfactory functionality. Ergo, this would require additional olfactory neurons and consequently, a larger nose. The prediction that Neanderthals evolved larger, more sensitive noses than humans is circumstantially supported by comparative studies that reveal Neanderthal had larger nasal apertures compared to humans. If, as has been suggested, Neanderthals retained the flat primate nose to minimise frostbite, then the additional olfactory neurons, turbinal bones and Epithelial tissue required to enhance Neanderthal olfactory acuity would need to be accommodated internally. This I suggest, would result in midfacial prognathism, which would explain the so-called Neanderthal 'snout' (Boule, 1921; Tattersall and Schwartz, 1998), with its anterior nasal aperture and dentition and retreated zygomatics that are characteristics of the species.

Applying the reassessment to human evolution

The data presented in this reassessment of Neanderthal behavioural ecology and morphology concludes that because *Neanderthalensis* was the only hominid species to evolve outside Africa - in a unique periglacial European environment - the variety of phenotypes derived from their environment is unique among hominids, with no analogue in modern primates. This suggests the anthropomorphic view of Neanderthals as analogous to modern humans is inherently flawed and may have obfuscated our understanding of Neanderthal evolutionary patterns (and by extension) human evolutionary patterns as well. Setting aside this anthropomorphic bias, Neanderthals emerge as a tenacious territorial defender, a rapacious sexual competitor, and an formidable natural predator of early humans. While they possessed the cognitive functionality, communications and forward planning of MP hominids, and the outward appearance of a robust bipedal primate, behaviourally Neanderthals resembled modern social carnivores such as lions, wolves, hyenas and leopards. This is in keeping with Shea's description of Neanderthals (Shea, 2004) as 'wolves with knives'

By comparison, analysis of the human Palaeolithic diet reveals EMHs did not hunt large dangerous prey (instead, maintaining an omnivorous diet) indicating Levantine humans were not a predatory clade and therefore did not acquire the behavioural adjuncts to support exclusive predation. This is consistent with the view of Simeons, (1960) that archaic humans were the most timid of mammals, and of Scott, (1974, 1976, 1981) who argues that hominid survival required extreme timidity and a wariness of potential dangers.

To define the combined impact of Neanderthal sexual predation, dietary cannibalism, lethal raiding, coalitionary killing, intraguild predation, territoriality and sexual competition, the term 'multidimensional predation' is appropriate. Sexually mature human females (as sexual partners), infants, and juveniles (for consumption) would be a focus of multidimensional predation because they were easier to capture and transport. The hypothesis that Levantine archaic humans were subject to multidimensional predation by Eurasian Neanderthals generates four outcomes (Figure 6) that can be tested against reliable palaeontological, archaeological and genetic datasets.

Figure 6

PREDICTED OUTCOMES OF MULTIDIMENSIONAL PREDATION

	HYPOTHESIS	PREDICTED OUTCOME
1	Hybridisation	Interbreeding as a consequence of sexual predation should be evident in the fossil record as evidence of hybridisation of both Levantine clades.

2	Collapse of the EMH population in the Levant.	Evidence of a population bottleneck, or near extinction event
3	Defensive and offensive adaptations against NP would emerge	Morphological and behavioural evidence of adaptations that arose as direct or indirect consequence of NP
4	Speciation	Collectively, macroevolutionary adaptations to NP would constitute a speciation event.

Hybridisation

Because both species were derived from a homologous genus (Scott, 1976) it predicts that sexual predation by Neanderthals would result in hybridisation of the two Levantine clades and that skeletal evidence of this hybridisation may be evident in the Levantine fossil record. The hypothesis would be supported by evidence of the Eurasian Neanderthal clade diverging from the classic European Neanderthal clade, and the Levantine humans displaying a mosaic of Neanderthal traits. Specifically, the hypothesis predicts that Eurasian Neanderthal specimens (represented by assemblages from Tabun, Amud, Kebara and Shanidar) would reveal some human features while EMHs, represented by the Skhul and Qafzeh assemblages would be characterised by a number of Neanderthal features – in short – the hypothesis predicts the Levant was characterised by two variable hominid populations – indicative of admixture. The hypothesis additionally predicts that interbreeding and hybridisation were consequences of coercive copulation by Neanderthal males, and that humans would not willingly interbreed with Neanderthals. This predicts that hybridisation did not occur in Europe between UP humans and Mousterian Neanderthals.

Recent analysis of amplified mtDNA from European Neanderthals (from Germany, France, Belgium, Russia, Croatia and the northern Caucasus) confirms that little or no admixture occurred between European Neanderthals and EMHs (Krings, et. al. 1997, 1999; Pääbo, et. al. 2004; Serre, et. al., 2004; Currat and Excoffier, 2004; Green, et. al., 2006; Götherström, 2000), and furthermore, that morphological claims of hybridisation, such as the Cioclovina calvaria from Romania, have likewise been refuted (Harvati et al. 2007). Although the possibility remains that Neanderthal DNA was erased by genetic drift or the influx of EMH genes (Nordborg, 1998; Krings, et. al. 1997; Enflo, et. al. 2001), the single remaining archaeological claim of European hybridisation is the Lapedo Child from the Lagar Velho rock shelter in Portugal, which Duarte et. al., (1999) argue to be a Neanderthal-human hybrid. This has been challenged by Tattersall and Schwartz, (1999), but see Trinkaus and Zilhao, (1999) for a rebuttal.

In respect of the Levant however, although tests have been conducted on samples from Eurasian Neanderthals (notably Amud from Israel and Dederiyeh from Syria) to date, no Eurasian Neandertals have yielded any form of DNA, (Pääbo, 2007, personal correspondence,) so the veracity of the hybridization hypotheses cannot be tested by genetic comparison. In the absence of material amenable to amplification from Eurasian Neanderthals, or from Skhul or Qafzeh EMHs, testing the Levant hybridisation hypothesis must rely on other methodologies.

A number of researchers (notably McCown and Keith, 1939; Dobzhansky, 1944), have noted morphological similarities between Eurasian Neanderthals and early human assemblages from Levantine contexts and interpreted this as evidence of interbreeding between the species. The mosaic nature of both early modern humans and Neanderthals led to the early view (still maintained by a minority of researchers) that all these Levantine assemblages form part of a single highly variable population (Corruccini, 1992; Wolpoff, 1996; Clark and Lindly, 1989). Certainly, the Skhul early human fossils from Mt Carmel (arguably the earliest representatives of modern humans) share many skeletal features with Eurasian Neanderthals. While Skhul 4 and Skhul 9 are generally deemed to be early human, cranial features such as mandibular prognathism and supraorbital ridges are considered by Corruccini, (1992) to be more Neanderthal-like than modern human. And in respect of the Tabun C2 specimen from Mugharet-et-Tabun, Israel (represented by a single mandible) although it is generally considered to be a Neanderthal (Stefan and Trinkaus, 1998; Harvati, Gunz and Nicholson, 2006), in the view of Quam and Smith, (1999) its distinct similarity to the Qafzeh and Skhul mandibles argues for a phylogenetic connection between them. Accordingly, Quam and Smith conclude the possibility of hybridisation in Eurasia cannot be excluded.

Based on an extensive re-evaluation and comparison of Neanderthal specimens from Israel (Tabun, Amud, Kebara), plus Shanidar (from Iraq) with the Skhul and Qafzeh EMH assemblages, Arensburg and Belfer-Cohen, (1998) reported a distinct resemblance between the groups: ‘both groups display a similar pattern of marked morphological variability. In both groups, specimens display numerous plesiomorphic traits as well as many that are common to both archaic and modern *Homo sapiens*.’ Their conclusions reveal ‘numerous incongruences, such as assumed ‘Neanderthals’ lacking specific Neandertal traits and AMHS manifesting Neanderthaloid features.’

While the prediction of hybridisation in the Levant cannot be resolved unequivocally until DNA is extracted from Levantine samples, the available lines of evidence appear to support the view that hybridisation occurred between Neanderthals and EMHs in the Levant.

Population bottleneck

NP theory predicts that multidimensional dietary and sexual predation by Neanderthals would precipitate a gradualistic depletion of the population of Levantine humans, resulting in a population bottleneck – or near extinction event. This would continue until the scarcity of humans rendered continued predation uneconomic, allowing the prey population to recoup its numbers in accordance with the Lotka-Volterra predator-prey model (Lotka, 1925; Volterra, 1926, Abrams, 2000). Because alternative terrestrial prey were available to Eurasian Neanderthals, their own population would not decrease in correspondence with the collapse of the human prey population as predicted by the standard Lotka-Volterra cyclical model. Rather the Levantine human population reduction would be linear. A second testable prediction argues that although NP commenced circa 100 Kya., low population densities, migratory patterns and the habitation of different ecological niches meant the demographic bottleneck did not reach its nadir until 60 - 50 Kya.

As a population bottleneck between 60-50 Kya provides arguably the only ecological scenario capable of generating sufficiently salient and protracted selection pressure to initiate the speciation of modern humans and to fix it through genetic drift, the prediction of a recent severe population bottleneck <50 Kya. provides two predictions that can be empirically tested. The null hypothesis - that a population bottleneck did not occur <50 Kya - is falsified by three lines of evidence:

- the archaeological record of the Mediterranean Levant
- comparative genomic data
- the homogeneity of human morphology and behaviour

The archaeological record of the Mediterranean Levant

A recent population bottleneck is in agreement with the archaeological record of the Mediterranean Levant. Based on a review of Levant assemblages, Shea, (2003b) reports that between 80,000 and 50,000 BP, the population of archaic humans in the Levant was depleted to the extent that they effectively disappear from the fossil record. While the absence of artefacts in Levantine contexts may indicate humans migrated out of the area, or were replaced by Neanderthals, it is also consistent with the view that the population (diminished by predation) was so small, it could not be detected in the fossil record due to insufficient sampling. Indeed, it is salutary to note that the complete history of Neanderthal and human occupation of the Levant over nearly 300,000 years – are represented by diagnostic skeletal remains that originate from only eleven stratigraphic horizons (Hovers, 2006.) Moreover, if EMHs had been displaced from their cave sites by NP and forced to adopt a nomadic existence ‘below the Neanderthal radar’ to avoid capture, this would also contribute to the group’s ‘invisibility’ in the Levant archaeology.

Attempting to answer his own question, ‘What happened to the humans at Skhul and Qafzeh after 80 Kyr?’ Shea, (2003b, p205) notes that in their place, Neanderthal fossils appear (or reappear) in the caves once inhabited by early humans. Various theories have been proposed to explain the replacement (Figure 7), but the absence of hard evidence hampers the debate.

Figure 7:

EXPLANATIONS FOR THE REPLACEMENT OF LEVANTINE EMHS BY NEANDERTHALS

Holiday, (2000)	Attributes replacement to the growing intensification of Neanderthal settlements in the Levant.
Steegman et. al., (2002)	Asserts that cold adaptation traits would ensure Neanderthals were better able to survive as the climate became colder.
Shea, (2003b)	Posits innovative behavioural strategies may have provided Neanderthals with a competitive edge, including increased residential stability and subsistence intensification.
Lieberman, (1998)	Identifies increased mobility patterns of Neanderthals compared to humans as a causative factor.
Kaufman, (1991, 2001)	Considers the possibility of cultural assimilation between the two groups, raising the possibility of interbreeding

One scenario that has received little attention is violent displacement. The reason, according to Shea, (2003) is that the Levantine archaeological record lacks clear and unambiguous evidence of agnostic encounters between the two species. While Shea cautions that the absence of such evidence does not disprove lethal competition, he cites research that shows encounters between modern hunter-gatherers and large carnivores are dangerous and life-threatening (Van Valkenburgh, 2001; Keeley, 1996), to argue that Neanderthals and humans probably avoided each other.

Shea's speculation is based on the assumption that avoidance is derived from mutual fear, as between two equal adversaries. However, this would not apply to predator-prey interactions where avoidance is the antithesis of the predatory instinct. Moreover, predatory encounters would be unlikely to leave physical evidence as remains of Levantine humans would be consumed at the capture site or scavenged by wild animals.

Comparative genomic data

The bottleneck hypothesis is also supported by comparative genomic data from phylogenetic trees derived from amplified DNA. Gagneux, et. al., (1999) for example, compared an array of genetic markers from nine African or African-derived hominoids, including all gorilla, chimpanzee, bonobo and orangutan species, plus human and Neanderthal DNA. They found the species with the least genetic variation was humans, and that chimpanzees have four times more genetic diversity than humans. One single troop of West African chimpanzees contained twice the genetic variability of all extant humans. (See also Kaessmann et. al., 2001; Fischer., et. al., 2006; and Yu., et. al., 2004.) Gagneux suggested this indicated a demographic bottleneck had occurred in human evolutionary history. A human demographic bottleneck is also substantiated by linkage disequilibrium studies in the human genome by Reich et. al., (2001) who estimated the population of humans may have dropped to as few as 50 individuals for 20 generations. This datum supports NP theory's estimate of a single 'survivor tribe.'

Dating the bottleneck

In addition to predicting a demographic bottleneck, NP theory predicts when it occurred, and this can be used to further test the hypothesis. If as argued, NP was a causal factor in the human population bottleneck and in the speciation event it precipitated, it predicts the population reduction commenced shortly after <100 Kya (coinciding with the commencement of NP) and reached its nadir <50 Kya, prior to the appearance of IUP in the Levant. This finds agreement from data derived from 500,000 human single-nucleotide polymorphisms by Marth et. al., (2003) who conclude a population bottleneck occurred 1600 generations ago. At 25 years per generations, this provides a date of 40,000. MtDNA sequences analysed by Ingman, et. al., (2000) estimate the expansion occurred 1,925 generations ago, which dates the repopulation at 48,125 years based on 25 years per generation. Also using MtDNA data, Stoneking, (1994) argues a population expansion took place approximately 40 Kya. Linkage disequilibrium studies by Reich et. al.Reich et. al., (2001) show a severe botttleneck occurred 800 – 1,600 generatons ago, providing dates between 27,000 – 53,000 years ago. Whitfield et al., (1995) analysed a 100,000 nucleotide base pair segment of the Y chromosome in five ethnically distinct males. This estimates the most recent common human ancestor (MRCA) lived between 37,000 and 49,000 years BP. Similarly, Pritchard et. al., (1999), also using Y chromosome microsatellites to dated the MRCA between 46,000–91,000 years; while Thomson, et. al., (2000) date the MRCA to 59,000 years. After consideration of errors, these data agree with the archaelogical record of the disappearance of humans from the Levant between 80,000 and 50,000 BP, and the alternative hypothesis which estimates the bottleneck reached its nadir between 48,000 - 50,000 BP.

The homogeneity of human morphology and behaviour

A third argument for a bottleneck in recent human history is derived from the homogeneous nature of contemporary humans. Human nature is invariant across cultures and time, and human physiology is equally uniform, which indicates the present global population of humans is descended from a single founder population. Furthermore, this founder population must have emerged prior to the dispersal of anatomically modern humans 45 Kya.

Anti-Neanderthal adaptations

A focal tenet of the NP model is that the population of EMHs in the Levant, although severely reduced by the bottleneck, did not become extinct. It is reasoned that human survivors from across the Levant aggregated into a single survivalist population (or tribe) which became the founder population for all extant humans. That the Levantine human population emerged from the bottleneck and recovered its numbers is substantiated by fossil evidence that chronicles the reappearance of humans in the Levant after 50 Kya. (Shea, 2003b). All the evidence indicates that after 47 Kya. (post-bottleneck) Levantine humans were behaviourally modern, capable of language, complex bone and ivory tool manufacture, representational art, personal ornaments, musical instruments, trade, and enhanced cognitive function. NP theory argues these post-bottleneck UP Levantines were the founding population of modern humans.

This evolutionary scenario corresponds to the third predicted corollary of NP: that as the population of Levantine humans was reduced by NP, selection of ‘anti-Neanderthal’ defensive and avoidance adaptations occurred, which were fixed by drift during the bottleneck. This is consistent with observations that selection occurs in prey species to mitigate the impact of predators on fitness (Cott, 1940; Abrams, 2000). The more deleterious NP became, the more selection pressure manifested for anti-predator adaptations, which contributed to runaway selection. This paper argues that collectively these nascent human adaptations constitute a speciation event.

It is further suggested that all four Darwinian mechanisms of evolution (natural selection, sexual selection, artificial selection and genetic drift) contributed to the rapid florescence of these defensive adaptations, and correspond to an exceptionally rare biological phenomenon. In my view, this four pronged evolutionary imperative combine to create what might be termed ‘meta selection’ (Figure 8) – that exponentially increased selection pressures for macroevolutionary features that are now associated with *Homo sapiens*.

Figure 8:

META-SELECTION OF ANTI-NEANDERTHAL, PRO-HUMAN PHENOTYPES

Natural selection	In addition to selection for defensive and offensive phenotypes, NS also favoured ‘antipathetic phenotypes’ that indirectly contributed to fitness by differentiating members of the nascent human species from Neanderthal-primate homologs. As the distinctions between *them and us* became central to survival, features such as hirsutism, art, body adornment, dance and music, that accentuated the division between the species came under positive selection. This explains the seemingly arbitrary nature of many human phenotypes.
Sexual selection	Enmity between human prey and Neanderthal predator in the Levant exerted a functional constraint on human mate selection. Preference would be given to human mates who displayed ornaments dissimilar to Neanderthals, while individuals displaying Neanderthaloid ornaments would be sexually ostracised and their phenotypes lost.
Artificial selection	Artificial selection was exercised by Levantine hominids, vis-à-vis coercion, ostracism, banishment and lethal violence as an adjunct to NS and SS. Throughout the Late Pleistocene, coalitionary groups of human males increasingly utilised infanticide and homicide to eradicate Neanderthal-human hybrids, excessively hirsute individuals, deviant neonates, or indeed any individual who evoked the antipathetic emotional response of ‘Neanderthaloid.’
Genetic drift	The small bottleneck population of early humans in the Levant provided the ideal conditions for genetic drift to consolidate the macroevolutionary modifications caused by the three other evolutionary mechanisms. Had the Levantine human population been in regular contact with the outside world – if they had been exchanging genes with early humans in north Africa or central Asia - the impact of Neanderthal predation would not have been so acute.

This complementary process of selection against Neanderthaloid features while simultaneously selecting nascent human features constituted the first phase in the speciation of EMHs into fully modern humans. That is to say, the physical and behavioural features that distinguish modern humans appear to be vestigial structures selected in response to prolonged NP. These adaptations are summarised as:

1. Adaptations to facilitate differentiation and identification
2. Adaptations to counter sexual predation
3. Adaptations to avoid capture and restraint
4. Social adaptations
5. Adaptations against nocturnal predation
6. Adaptations against predation stress
7. Strategic adaptations

Adaptations to facilitate differentiation and identification

Predator identification and asymmetrical detection have a direct corollary to fitness, so features that visually differentiated EMHs from Neanderthals from a distance would come under robust selection. This nominates pelage, colouration, gait, posture, body shape and facial morphology as the prime loci of selection. (See Figure 9)

Figure 9

ADAPTATIONS TO FACILITATE DIFFERENTIATION AND IDENTIFICATION

ADAPTATION	COMMENT
Xenophobia	It became obligatory for Levantine EMHs to acquire an innate fear of hominid strangers. Thus, xenophobia acquired an adaptive functionality in respect of NP, facilitating hyper-vigilance for Neanderthaloid characteristics in extragroup conspecifics.
Denudation	Hair loss came under selection because it could be used to differentiate *them* from *us* over large distances. However, as denudation would increase the risk of hyperthermia and hypothermia, it is posited that gradualistic denudation was concurrently accompanied by the capacity to fabricate thermal garments. (See below.)
Cultural insulation	By dating the origin of mtDNA and nuclear DNA segments in a sample of head and body lice using molecular clock techniques, Kittler, Kayser, and Stoneking, (2003) estimated the emergence

	of body lice (and by inference, the human use of clothing) to 72 Kya (+/- 42 Kya). In a subsequent erratum, Kittler et. al., (2004) revised the date of the origin of human body lice to 107 Kya. These dates are in general agreement with NP theory.
Gait and posture	The distinctive human gait diverged form primate orthodoxy to differentiate EMHs from Neanderthals over long distances
Facial morphology: clear eye whites, protruding nose, unwrinkled skin, tumescent lips, facial flatness, small ears, pale skin, reduced brow ridges, pronounced chin and facial symmetry	Humans have sophisticated facial recognition networks derived from presapiens which generated selection for species-specific facial features to distinguish humans from Neanderthals
Spinal lordosis	Sexual selection for a curved spine to distinguish humans laterally; suggests that like modern primates, the Neanderthal spine was virtually straight. Rounded buttocks, I suggest, were selected for because they accentuated the curve.

Adaptations to counter sexual predation

Although the locus of sexual predation was primarily on post-pubescent females, competition for females and depletion of reproductive stock by Neanderthals impact on inclusive fitness. Enmity of Neanderthals and the vicissitudes of mate-guarding instilled in human males new, non-primate behavioural protocols that irreversibly altered the mating system of Levantine humans. Physiological and behavioural adaptations emerged to minimise or neutralise the deleterious impact of sexual predation. The resulting morphological and behavioural adaptations (Figure 10) were adaptive in two respects; they rendered human females less attractive to Neanderthal males, and secondly, they discouraged, prevented and punished extraspecies copulations by human females. These new sexual protocols form the basis of modern human epigamic behaviour, which is unique among the primates.

Figure 10

ADAPTATIONS TO COUNTER SEXUAL PREDATION

ADAPTATION	COMMENT
Private copulation	Public copulation would attract Neanderthals by virtue of their enhanced sensory acuity so became associated with increased risk and anxiety.

Habitual washing	If Neanderthals possessed hyper-olfactory and pheromonal acuity, able to detect ovulating human females over considerable distances, Levantine humans would learn to associate body odour with increased risk of predation. To prevent Neanderthals ‘sniffing about’, regular bathing and washing (concentrating on the vagina, anus and underarms) became a habitual behaviour, aimed primarily at minimising and masking telltale body odours and secretions
Scent concealment	Use of flowers and perfumes to mask female body odours
Stigmatisation of menstruation	If as suggested, Neanderthals were as adept at smelling blood as other predators, the monthly menstruation cycle of blood loss would become associated with increased anxiety, stress and depression, leading to the stigmatisation and ostracism of menstruating females for the duration of menstruation.
Oestrus synchrony	Selection of mutational alleles to facilitate hormonal-pheromonal synchrony of female menstrual cycles would be adaptive within the group context as it would reduce the group’s scent profile to a few days per month. Significantly, Matsumoto-Oda and Kasuya, (2005) have demonstrated that oestrus synchrony does not occur in populations of wild African chimp.
Concealed ovulation	Denied predatory Neanderthals the visual and olfactory epigamic cues that incited raiding behaviour.
Romantic love, recreational copulation, pair bonding	Romantic love predisposed pair bonded humans to practise recreational sex notwithstanding the loss of epigamic displays due to hidden ovulation.
Protuberant breasts	Although the breasts of primates swell marginally during lactation, on cessation, the breasts virtually disappear. As females do not generally mate while nursing infants, protuberant breasts advertise the female is infertile and sexually unreceptive (Etcoff, (1999). Within the ecology of the Levant, protuberant breasts would provide a false advertisement to Neanderthal males that would discourage epigamic advances. By acting as a deterrent against sexual assault by Neanderthals, protuberant breasts contributed to fitness and were selected for. Significantly, for a human male, bonded to his female partner by romantic love, breasts would not have been a disincentive to copulation.
Sexual jealousy, mate guarding and patriarchy	The loss of fertile human females to abduction and voluntary transfer to Neanderthal groups led to efforts by male coalitions to control women and their sexuality. In the context of NP, coercion and violence would be

	adaptive perceived as adaptive male strategies to prevent human-Neanderthal copulation and hybridisation.
Infanticide and femicide	Females who copulated with Neanderthals were at increased risk of male coalitionary violence. Hybrid neonates would be prone to infanticide.

Adaptations to avoid capture and restraint

The strategic advantage of Neanderthals over EMHs in proximate combat would induce selection for phenotypes facilitating capture avoidance and escape, (Figure 11). If athletic phenotypes to increase speed and manoeuvrability in response to NP occurred, they would almost certainly be associated with a concomitant reduction in skeletal robusticity. This predicts an abrupt shift to gracilization occurred in EMHs between 100-50 Kya. The prediction is supported by skeletal analysis of the Qafzeh-Skhul EMHs by Trinkaus and Churchill (1999) that demonstrates unequivocal evidence of gracilization. See also Weidenreich, (1945), Olivier, (1969), Frayer, (1980), and Trinkaus and Ruff, (1999b).

Figure 11

ADAPTATIONS TO AVOID CAPTURE AND RESTRAINT

ADAPTATION	COMMENT
Increased athleticism, reflex speed, increased agility, sprint speed.	Among the human genes that display the strongest evidence of a recent selective sweep are genes that encode structural components of muscle tissue (Ehmsen, et. al., 2002).
Long distance running, stamina and gracilization	Athletic phenotypes to increase long distance running and stamina would be associated with a concomitant reduction in skeletal robusticity

Social adaptations

Flocking, schooling and herding are common tactics adopted by prey species against predators. If Eurasian Neanderthals were the formidable adversary suggested, and like other mammalian predators, preferentially selected solitary individuals as prey, social phenotypes may be expected to have become fixed in the Levantine human population. (Figure 12) Concomitantly, infringements against the group would solicit negative consequences, thus leading to the fixation of an innate ‘tribal defence’ ethos.

Figure 12

SOCIAL ADAPTATIONS

ADAPTATION	COMMENT
Group living	‘Safety in numbers.’ Prohibition against solitary expeditions beyond the camp
Collective identity	Innate loyalty to the group
Them and us mindset	In-group distinguished from out-group
Conformity to shared ideals	Within the framework of NP, individuality was a maladaptive strategy
Male bonding	Proto-militaristic coalitions of young males
Aversion to woodland ecosystems	Archaeological evidence suggests that Neanderthals occupied the inland mountains and forests of the Levant, while humans tended to reside in the flat coastal plains. Humans would develop an innate trepidation of forests
Hierarchical social structure	Male dominated, patriarchy
Art, music, dance, body adornment	Because Mousterian culture did not accommodate art, body adornment, dance or music, these behaviours became associated with EMHs and were dispersed primarily via sexual selection.

Adaptations against nocturnal predation

This paper has argued that Neanderthals, like the majority of terrestrial predators, hunted nocturnally to exploit reduced prey vigilance during sleep and rest states. Typically, prey species subject to nocturnal predation acquire adaptations to offset the advantage conferred by nocturnality, and this generates a number of predictions that can be used to test the argument. Figure 13 outlines two possible early human adaptations against nocturnal predation.

Figure 13

ADAPTATIONS AGAINST NOCTURNAL PREDATION

ADAPTATION	COMMENT
Innate fear of the dark	If Neanderthal raiding occurred primarily at night, Levantine humans may be

	expected to have acquired an innate fear of the dark, plus an inhibition against venturing from their encampments at night.
Use of canines as guard dogs	NP theory argues that EMHs domesticated wild wolves <100,000 Kya. to exploit their superior olfactory and auditory senses as nocturnal guard dogs. This is consistent with the habit of some primate species to form polyspecific associations to increase vigilance against common predators (Stanford, 2002). The hypothesis is supported by mtDNA extracted from 162 wolves and 140 domestic dogs by Vila, et. al., (1997) that indicate dogs originated 100 Kya. providing good agreement with NP theory.

Adaptations against predation stress

50,000 years of predation stress would generate selection pressure for phenotypes to increase resilience and resistance to psychological stress. (Figure 14)

Figure 14

ADAPTATIONS AGAINST PREDATION STRESS

ADAPTATION	COMMENT
Enhanced central nervous system robusticity	The emergence of a 'predator proof' clade.
Psychological resilience	Resistance to stress-induced psychopathology
Capacity to maintain subliminal vigilance for Neanderthaloid cues.	Amygdala robusticity

Strategic adaptations

A central tenet of the NP argument is that despite a plethora of defensive adaptations (outlined above) to ameliorate the deleterious consequences of NP, the Levantine EMH population continued to decline, generating selection for a new form of offensive adaptation – what is here termed 'strategic adaptations.' Strategic adaptations' (Figure 15) may be defined as offensive phenotypes that contributed to the cessation of NP, the reversal of the ancestral predator-prey interaction between Neanderthals and EMHs, and allowed EMHs to out-compete and agonistically replace Neanderthals. Strategic adaptations constitute the major thrust of the human speciation event and provide the seminal features of the nascent *Homo sapiens* species.

Figure 15

STRATEGIC ADAPTATIONS

ADAPTATION	COMMENT
Language capacity	Communication conferred a strategic advantage in adversarial conflict so would be selected. Circumstantial support for the appearance of language 70-50 Kya. comes from Noble and Davidson, (1996, p217) who date the origins of human language between 100-70 Kya. These dates are supported by Lieberman, et. al., (2007) who demonstrate that fully human speech anatomy is not evident in the fossil record until the UP, 50 Kya.
High intelligence, conjectural reasoning, forward planning	
Aggression	The transformation from hominid timidity to a hyper-aggression was fundamental to the EMHs ability to engage Neanderthals agonistically
Organization	Capacity to form strategic coalitions facilitated the emergence of the first proto-armies
Courage, self sacrifice	The willingness to die in defence of the group is adaptive only within the context of deleterious NP
Creativity: primarily applied to weapons development, footwear, military strategies, etc.	NP theory posits that projectile point technology emerged after the bottleneck 50Kya- 47 Kya and was a singular factor in the reversal of the ancestral predator-prey dynamic. In support of this, aerodynamically streamlined lithic and bone projectile points have been recovered from a number of Levantine Initial UP sites, including Ksar Akil, and some of these points display damage similar to projectile point breakage in modern hunter gatherers' spears and to damage recorded by spear throwing experiments (Bergman, 1981; Bergman and Newcomer, 1983; Shea, 2003; Newcomer, 1987).
Manual dexterity	Weapons manufacture; hafting, blade production, arrow-making, etc.
Guile	The emergence of what Byrne and Whiten (1988) call, 'Machiavellian intelligence' would be an assert in interspecific proto-warfare
Improved semantic memory	
Consciousness	Ability to interpret intention from behaviour, abstract thought, empathy
Competitiveness	

Genocidal ‘them and Us’ mindsets	While predators normally only kill for food, the human capacity to ‘dehumanise’ Neanderthals to facilitate genocide was adaptive within the context of NP.

Speciation

The hypothesis - that the rapid florescence of strategic adaptations among Levantine humans not only reversed the predator-prey interaction but additionally dispersed Initial Upper Palaeolithic (IUP) phenotypes to fixation within the small Levantine population is corroborated by the Levantine palaeontological record, which according to numerous researchers, notably Shea, (2003), Bar-Yosef, (2002), and Kuhn, Stiner and Güleç, (1999), provides evidence of the earliest systemic transition from MP to IUP anywhere in the world. All of the fundamental indicators of modern behaviour, including prismatic blade technology, long distance raw material transfers, complex multicomponent tools (including bone and ivory tools) personal ornaments, specialized subsistence strategies, symbolic ‘notation’ systems, etc. are established and dispersed from the Levant before they appear in Europe or Africa.

The modern humans who emerged from the population bottleneck circa 47-50 Kya. ago were a transitional population characterised by hyper-aggression and a single specialised competence and objective – the agonistic replacement of all Neanderthals. That is to say, pervasive unidirectional selection transformed a timid MP hominid prey species into a formidable hyper-aggressive predator species – Cro-Magnon.

To complete the next phase of this revised Late Pleistocene evolutionary narrative requires only a cognizance of the singular enmity humans acquired towards Eurasian Neanderthals as a consequence of systemic predation over millennia. This provides a number of predictions that may be tested. Firstly, that Cro-Magnon males conducted an attenuated ‘proto-war’ against their natural enemy in the Levant. The object of this lethal aggression was not self defence, trophic requirements or territoriality, but the genocidal eradication of the Eurasian Neanderthal population. The prediction is supported by the chronostratigraphic record of Neanderthal extinction in the Levant; Shea, (2001); Mellars, (2006), Kozlowski, (2004), Bar-Yosef, (2000), Tostevin, (2003).

The second prediction is that hyper-aggressive Cro-Magnons would disperse into Europe from the Levant hunting and eradicating European Neanderthals and occupying their territory. This predicts a distinctive east-west pattern of Neanderthal extinction and replacement corresponding to the colonisation of Europe by Cro-Magnons. The absence of such an east-west pattern of replacement provides the null hypothesis. The fossil record reveals the IUP Aurignacian culture that first appeared in the Levant 47-45 Kya. dispersed via Turkey to south-eastern Europe by 43 Kya. (Mellars, 1992, 2004, 2006; Bar-Yosef, 2000; Kozlowski, 2004). The singular pace of this dispersal supports the premise that Cro-Magnons, unlike their MP predecessors, were not averse to risk-taking, exploration or territorial expansion. Furthermore, the archaeology reveals not only an east-west pattern of Neanderthal extinction but the simultaneous replacement by modern humans (Tattersall and Schwartz, 1999; Stringer and Davies, 2001; Bocquet-Appel and Demars, 2000). In their analysis of Neanderthal contraction and modern human colonisation of Europe, Bocquet and Yves Demars, (2000) demonstrate ‘a coherent pattern of invasion-contraction, moving chronologically from east to southwest.’

The genocidal model of Neanderthal extinction adds ‘motive’ to the competitive replacement hypothesis first proposed by Boule, (1912) which argues that Cro-Magnons agonistically replaced European Neanderthals after 40 Kya. See also Wendt, (1963); Bigelow, (1969); Gat, (1999); Birdsell, (1972); and Tattersall, (1995).

Augmented by UP strategic technologies, Cro-Magnons also dispersed from the Levant to colonise new and hitherto unexploited territories. This prediction is supported by genomic and archaeological data that reveals the modern human population in the Levant split into innumerable groups that dispersed north and west into Europe, south to Africa, and east, around the coast of India into eastern Asia, and eventually across the Bering Plain (Beringia) into the Americas, Cavalli-Sforza and Feldman, (2003), Karafet, et. al., (1999); Santos, et. al. (1999); Lahr and Foley, (1994, 1998); Maca-Meyer, et. al., (2001). Analysis of human Y-Chromosome haplotypes by Cruciani, et. al., (2002), also indicates a back migration to Sub-Saharan Africa from Asia.

The ‘back to Africa’ scenario proposes that introgression occurred between Levantine fully modern humans and MSA ancestral humans in Africa, and this is supported by Behar et al., (2008) on the basis of MtDNA analysis of Khoi and San (Khoisan) genomes that suggest they remained reproductively isolated from fully modern humans for between 50 and 100 Ky until introgression occurred during the Late Stone Age (LSA) approximately 40 Kya. The back-migration hypothesis is also supported by Olivieri et. al., (2006) on the basis of analysis of haplogroup diversity in mtDNA and on Y chromosome variation, which reveals the first UP cultures in Europe (the Aurignacian) and North Africa (the Dabban) both had a common source in the Levant. See also Bar-Yosef, (2002), Macaulay et. al., (1999), and Van Peer and Vermeersch, (1990). The chronological dating of the Levantine dispersal is also consistent with Olivieri, et. al., (2006) who applied mtDNA evidence to date the dispersal from the Levant into Europe and Africa to between 45-40,000 Kya.

Post Neanderthal human evolution

Palaeontological evidence confirms that from the Neanderthal extinction (<30 Kya) to the late Neolithic (2.5 Kya), Cro-Magnons underwent a population expansion and dispersal across six continents (Biraben, 2003) splitting into innumerable nucleus ethnic groups, hunter-gatherer tribes and proto nation-states. During this attenuated period of postNeanderthal expansion, I argue the selection of strategic phenotypes that initiated the Levant speciation event continued to direct the selection of anti-Neanderthal (fully modern human) phenotypes. That is to say, although Neanderthals no longer presented either a threat to human existence or a source of prey, and indeed, no longer existed in human memory, the psychoevolutionary legacy of the agonistic interspecific interaction remained a causative factor in the continuing evolution of *Homo sapiens.* A case is here made that the postNeanderthal phase of human evolution manifested principally vis-à-vis two evolutionary mechanisms: artificial selection (lethal violence, primarily by males directed at conspecifics and extraspecific hominids, and in particular females and infants); and by mate choice (sexual selection) whereby both genders preferentially selected human ornaments and rejected Neanderthaloid ornaments. This process continued into the late Neolithic, by which time, incessant internecine warfare by males removed the most deleterious hyper-aggressive phenotypes from the human genotype. This dates the modern human genotype to the Neolithic.

Recent sweeps of the human genome

The post-Neanderthal evolutionary model argues that modern human morphology and behaviour were consolidated into their extant form between 50 -2.5 Kya. This ‘late emergence’ model generates a testable prediction: that analysis of human mitochondrial and nuclear genetic sequences will reveal evidence of recent sweeps of the human genome. This appears to be the case. Analysis of single-nucleotide polymorphisms (SNPs) in disparate human populations has identified innumerable genomic locations that have experienced recent selective sweeps due to the accumulation of mutational alleles over the last 50,000 years. Most recently, analysis of 1.2 million SNPs in African-American, European-American, and Chinese populations by Williamson et. al., (2007) identified 101 regions of the human genome that had experienced recent selective sweeps. Indeed, they estimate that up to 10% of the human genome has been altered by recent selection, including genes involved in nervous system development and function, pigmentation, immune system, heat shock, and olfaction. Significantly, these are all genes predicted by NP theory to have come under selective pressure as a consequence of NP. Moreover, Williamson, et. al., (2007) estimates the sweep occurred during the last 15,000 to 100,000 years, providing good agreement with NP theory. The prediction that body hair and colouration came under intensive selection pressure appears to be supported by genetic analysis by Voight et. al., (2006) and Lamason et. al., (2005) that shows five genes regulating skin pigmentation (OCA2, MYO5A, DTNBP1, TYRP1 and SLC24A5) all show evidence of recent selection. See also Hawkes, et. al., (2007).

Conclusion

This paper attempts to demonstrate that the transition from MP hominid to fully modern human occurred as a consequence of prolonged cannibalistic and sexual predation by *Neanderthalensis* which precipitated a bottleneck speciation event <50 Kya. which extended into the Holocene. According to this scenario, the speciation of *Homo sapiens* is distinguished by two phases; the period of Neanderthal predation and hybridisation (Neanderthal ascendancy), during which demographic attrition of early humans precipitated the selection and fixation of defensive and strategic adaptations; and secondly, the post-bottleneck period (human ascendancy) characterised by sympatry and genocide. Subsequent to the extinction of *Neanderthalensis* sexual selection and artificial selection against Neanderthal phenotypes and in favour of nascent human phenotypes consolidated the human genotype into its extant form. While it is hoped this paper may provide a conceptional framework for a fresh debate on human origins, space precludes such a detailed discussion here. For that, see Vendramini, (in press).

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