Palaeoecological and genetic evidence for Neanderthal power locomotion as an adaptation to a woodland environment

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Abstract

The prevailing explanation for Neanderthal body form is the cold (glacial) adaptation hypothesis. However, palaeoecological associations appear to indicate a less cold woodland environment. Under such conditions, encounter and ambush (rather than pursuit) hunting – and thus muscular power and sprint (rather than endurance) capacity – would have been favoured. We hypothesise that the highly muscular Neanderthal body form reflects an adaptation to hunting conditions rather than cold, and here both review the palaeoecological evidence that they inhabited a mainly woodland environment, and present preliminary genetic analyses in support of this new hypothesis.

Key words: Endurance, power, running, encounter/ambush hunting, human evolution.

Introduction

Neanderthals have been widely considered to be a cold adapted human species living in the glacial environments of the Pleistocene (e.g. Trinkaus, 1981). Certainly many European Middle Palaeolithic sites that are thought to have been occupied by Neanderthals, are associated with the steppe tundra faunas of the Late Pleistocene. The remains of mega-herbivores such as mammoths, woolly rhino, bison, and giant deer, and carnivores such as cave bears, hyenas, and lions, are common in such sites (Kalke, 1999; Musil, 1985; Markova, 1995, Stewart *et al*., 2003a,b; Stewart, 2004).

This cold adapted view has incorporated explanations for various anatomical features that differentiate Neanderthals from modern humans. Examples include the relatively low brachial and crural indices of the limbs (Trinkaus, 1981, 1983; Holliday, 1997) and supposed higher cranial sinus volumes (Woolpoff, 1968).

More recently, the degree to which Neanderthals are thought to be cold adapted has been questioned. Biogeographical investigations suggest that they retreated south and west through time as climate in general cooled during Marine Isotope Stage (MIS 3) (Stewart, 2007) and that they were most common during interstadials both in NW and Southern Europe (Jacobi and Higham, 2011; Bradtmöller *et al*., 2012). Their anatomical features have also been questioned as indicative of cold adaptation: Analyses of the faces suggest that their sinus volumes were not larger than that of Anatomically Modern Humans (AMH), and that larger sinus volumes in mammals (including non-human primates) correlates with warmer temperatures rather than colder ones (Rae *et al*., 2011). Stewart (2005) also questioned the Neanderthal limb proportions as cold adapted and instead suggested locomotion as the main evolutionary driver. The form of locomotion favoured in wooded environments would have been more power-burst based, to facilitate encounter and ambush hunting. The latter was presented as evidence in support of the muscular Neanderthal body (Stringer and Gamble, 1993) being an adaptation to sprinting.

In this paper, we reconsider the ecological conditions in which Neanderthals preferentially lived in North West Europe, the area that saw the start of their demise. To that end, we review some of the latest views on the ecology of Neanderthals from Belgium, including both the palaeoecological data from Walou Cave and the ancient DNA (aDNA) data from collared lemmings *Dicrostonyx torquatus*, also from Belgium. Walou is probably the best and most recently published site available with a multi-proxy palaeoecological record covering the Neanderthal occupation of north-west Europe during MIS 3. Together with inferences based on collared lemming population data for the same region, we can reconstruct details of the environment in relation to global climate change that were not previously available. Complementing the ecological analyses, we exploit the availability of multiple full Neanderthal genomes published recently [See SI references] and present results of an exploratory genetic analyses, which are consistent with a power form of Neanderthal locomotion.

Neanderthal ecology

An understanding of Neanderthal ecology is critical in any discussion of their hunting and associated locomotion styles (Schmitt *et al*., 2003). Their geographical range encompassed Southern to Northern Europe and longitudinally from Britain to Siberia, with the north being preferentially occupied during warmer interglacials and interstadials (Prüfer *et al*., 2014; White & Pettitt, 2011, Gaudzinski-Windheuser *et al*., 2014; Knul, 2018). The northern margins are the areas where the limits of their ecological tolerance are best studied.

The timing of their last occupation of North West Europe was broadly MIS 3 (ca. 60–20 000 years ago), a period during the last glaciation when climate is known to have fluctuated greatly (Andersen *et al*., 2006; Svensson *et al.*, 2006). The ecology of the region during MIS 3 has been described as non-analogue (Stewart, 2005), including faunal and floral elements found today in the arctic, boreal, steppic as well as temperate zones (e.g. Bell, 1969). The general description of this biome has been steppe tundra, or mammoth steppe, and it has been characterised as having a high carrying capacity (Guthrie, 1990a,b).

There are, however, a variety of studies that raise doubts about this view of the nature of the MIS3 ecology, and particularly the degree to which these non-analogue ecologies are genuine. The most challenging criticism is that non-analogue ecologies are caused by mixtures of fossils from different times (Coope and Angus, 1975; Coope, 2000). While attempts to tease apart beetle fossil assemblages into distinct eco-climatological faunas and then reconstruct the climates they individually represent using the Mutual Climatic Range method (Coope, 2000) are questionable, Coope's principle concern regarding the non-analogue mixtures remains. There have been attempts to refute the mixed assemblage argument by dating the distinct ecological elements directly (Stafford *et al*., 1999). However, these were best achieved for MIS 2 fossil vertebrates when the associated date uncertainties are typically less than for MIS 3 (Higham *et al*., 2011; Stafford *et al*., 1999). Therefore, contemporaneity of non-analogue taxa in MIS 3 is difficult to show, although more recent model-based Bayesian treatments of dates may help overcome such issues (Blackwell and Buck, 2003; Bronk Ramsey, 2008).

With this in mind, it is interesting to consider one of the most important recent developments in Late Quaternary palaeoecology; the advent of population studies using aDNA (Hofreiter *et al*., 2012). This has provided insights into ecological changes that were not possible using conventional palaeoecological methods. Of particular note are studies showing population turnovers in species as varied as brown bear *Ursus arctos*, steppe bison *Bison bison*, collared lemming *Dicrostonyx torquatus*, water vole *Arvicola amphibius* and red deer *Cervus elaphus* (Barnes *et al*., 2002; Shapiro *et al*., 2004; Brace *et al.*, 2012; Brace *et al*., 2016; Meiri *et al*., 2013). Such studies have demonstrated that climate, and probably associated vegetation change, is likely causing significant mammalian population turnovers in at this time. Such population changes no doubt represent the finer details of biotic responses to climate change over Milankovitch and sub-Milankovitch time scales (Stewart, 2009).

The most illuminating study using aDNA is probably that of the collared lemming *Dicrostonyx torquatus,* where the population turnovers in Belgium appear to have taken place at interstadials (Brace *et al.*, 2012). This study indicates that collared lemmings became locally extinct as global climates warmed during Greenland Interstadials 12, 8? and 2 (GI-12, probable GI-8 and GI-2) and finally during the cold of Greenland Stadial 2 (GS-2) (See Figure 1). Climate presumably shaped vegetation in such a way that the collared lemming could no longer survive. Global cooling during the subsequent stadials saw a return of the species, albeit a genetically distinct population, and again presumably due to a return of their required vegetation. The last local extinction presumably involved the lower climatic tolerance limit of the collared lemming rather than the upper climatic limit. Since that study was published, it has been shown that this pattern of turnover is not confined to Belgium but is widespread and apparently synchronous across Northern Europe (Palkopoulou *et al.*, 2016). The contemporaneity of mammalian turnovers at a continental scale provides persuasive evidence that the phenomenon is due to the global climate change reflected in the Greenland Ice Core data.

So this previously invisible ecological change, where the collared lemming – one of the most arctic adapted species in North West Europe – experiences turnovers at interstadials, prompts a question over the contemporaneity of this species with some of the less arctic taxa. Neanderthals no longer need to be considered hyperarctic in nature (Stewart, 2005; Gaudzinski-Windheuser and Roebroeks, 2011). Furthermore, their possible general predominance during Greenland Interstadials (GIs) in North West Europe may signify that Neanderthals and collared lemmings were not contemporary. It may be that similar cold adapted species and less cold adapted taxa were generally not coeval and that these elements of the non-analogue communities of MIS 3 may not have been contemporaries. This in turn suggests that the nature of the MIS 3 non-analogue environment may have been over-stated; certainly for animals with the more extreme adaptations. This scenario is consistent with the hypothesis of Jacobi and Higham (2011) whereby humans in general, although they were principally discussing modern humans, were mostly present in North West Europe during the Late Pleistocene warmer intervals (e.g. GIs).

These finer details of MIS 3 ecology would not have been apparent without aDNA analyses of species coupled with AMS radiocarbon dating on the studied specimens and statistical correlations with global climate signals. However, the limited occurrence of Neanderthals in North West Europe during interstadials may be visible in the more conventional palaeoecological data. The analysis of small mammals from Walou Cave in Belgium has shown, for example, that the Mousterian archaeological layer (Layer CI-8) is the one with the richest fauna in the MIS 3 part of the sequence, with elements indicative of warmer and more wooded environments (Stewart and Parfitt, 2011; Figure 1). This is also the layer that yielded the *in situ* Mousterian archaeology and the Neanderthal tooth (Pirson *et al*., 2012). Other research of this sequence such as palynological and pedological analyses may be consistent with this result (Pirson *et al*., 2012), although they refer to the layer immediately below CI-8 (layer CII-1). Layer CII-1 is a soil although it only has the B horizon preserved. This suggest that the A horizon, which is the first to form during pedogenesis (Goldberg and Macphail (2006), is missing, presumably due to erosion. The presence of a soil containing tree pollen (Figure 1) beneath a layer with *in situ* Neanderthal remains and their associated archaeology, and a small mammal fauna typical of woodland, must surely indicate that these are contemporary. Pirson *et al.* (2012) consider that the Neanderthal layer (Layer CI-8) was formed during a cold open phase due to the pollen preserved in that level. It does, however, seem likely that the pollen in the CI-8 is not contemporary with the Neanderthal and other animal remains in that level. The original pollen contemporary with these remains is likely to have been lost during the removal of the fine grained material from the A horizon during erosion, while the heavier bones and stone tools remained. Therefore Layer CI-8 is best thought of as a palimpsest.

Relating Walou Cave to the results of the lemming aDNA study and the ice core data is complicated by the fact that the individual elements of the fauna in Layer CI-8 at Walou Cave are not directly dated but instead are dated stratigraphically in terms of their association with dates on material from that level. The date for that layer, based on a cave bear *Ursus speleaus* tooth, according to the most recent and most reliable date is 47,900 ± 3500 BP (OxA-21608) (Higham *et al*., 2014). There are a small number of collared lemming teeth recovered for that layer (Stewart and Parfitt, 2011; Figure 2) although they may not be contemporary with the warmer- and woodland-indicating species for the layer. The warmer environment-indicating elements in CI-8 appear to be contemporary with similar warm and woodland indications in the soil (Layer CII-1) below. The soil below has also been correlated with the regional Les Vaux soil (Pirson *et al*., 2012), which has been associated with GI12 and fits with the latest date for Layer CI-8. The over-riding indications from layers that seem to be informative for the Neanderthal occupation of Walou Cave are of an interstadial climate with woodland elements (Pirson *et al.*, 2011; Damblon, 2011; Stewart and Parfitt, 2011; Pirson *et al*., 2012). This is a similar, but distinct, interpretation of the small mammal fauna from CI-8 and its contradiction to the pollen from that layer as made by Toussaint *et al*. (2011). In that case the small mammals alone were reworked from the layer below. Here we suggest that many of the mammals and artefacts came from the level below. This would also signify that the Neanderthals at Walou Cave are contemporary with turnover A of the collared lemming presence in North West Europe (Brace *et al*., 2012) (Figure 1). Therefore, there seems to be an alternating occupation of Europe by Neanderthals and collared lemmings, living in more wooded interstadials and open cold episodes, respectively.

By combining the latest palaeoecological evidence from North West Europe, a coherent pattern begins to emerge. Humans, and Neanderthals in particular, appear to be predominantly found in warmer and more closed environments during MIS 3. The importance of this inference lies in its implications for the likely hunting mode used by Neanderthals; encounter and ambush hunting, which in turn would require burst-speed and power locomotion. The latter is consistent with the experimental and other findings suggesting that Neanderthals used thrusting rather than throwing spears, which would be preferential when hunting at close quarters (Schmitt *et al*., 2003; Gaudzinski-Windheuser *et al*., 2018).

Neanderthal functional genetics

The list of genomic variants associated with endurance or power/strength athlete status has grown considerably in recent years (Ahmetov *et al*., 2016), laying the foundation for a better understanding of the function of genes underlying athletic performance in modern humans. The availability of multiple Neanderthal nuclear genomes raises the possibility that these data can inform on the hypothesis that Neanderthals were proficient at burst-speed and power locomotion typically associated with elite sprinters today. However, it is important to note that any such inferences are necessarily constrained by the assumption that alleles associated with power in modern humans have the same phenotypic effect in archaic individuals. Furthermore, we caveat that we do not distinguish the varying effect strengths among the power-associated alleles considered in the following analyses.

First, we analysed 39 power-associated alleles reviewed in Ahmetov *et al.* (2016) (see SI Table 1) independently by comparing their allele frequencies in today's modern humans and Neanderthals (see SI for a description of the data and the statistical approach implemented to estimate and compare allele frequencies). As summarised in Figure 3, the majority of power-associated alleles considered here are inferred to have had higher frequencies among Neanderthals than modern humans. This is consistent with power-phenotypes being more frequent in the Neanderthal population than in modern humans.

Focusing on individuals rather than alleles, Figure 4 shows the fraction of power-associated alleles carried in modern humans (N=2504) and Neanderthals (N=9) based on genotypes at the 39 loci. Neanderthal individuals are inferred to have more power-associated alleles per individual on average than modern humans ($p=4.3 \times 10^{-6}$). This signifies that Neanderthals may have been more powerful on average than modern humans.

We re-iterate that the above interpretations of the genetic data both rely on the assumption that alleles associated with efficient power locomotion in modern humans have the same phenotypic effect in archaic individuals. In addition, these analyses will be affected by ascertainment bias. For example, it is possible that Neanderthals carried other private alleles associated with power or endurance locomotion (i.e. alleles that are not variable in modern human populations, and as such, cannot be statistically associated with locomotion traits). We have used a large (>2000 individuals) 'control' sample—but are aware that allele frequencies can differ substantially between modern day global populations. Nonetheless, the consistent pattern of 'power-related' allelic representation across multiple unlinked loci (many on quite different chromosomes) strengthens confidence in the inference. So, too, does the more recent data relating to the climate and environment in which such individuals lived. These analyses thus support (whilst not confirming) the hypothesis presented, and indicate a potentially valuable avenue for future research into hominin ecology.

Discussion and Conclusion

We question the long held view that Neanderthal anatomy is an adaptation to the cold environment they are perceived as preferentially occupying in the Pleistocene. First, there is mounting evidence that the habitat in the north of Europe preferred by Neanderthals is not the cold glacial of the Late Pleistocene but instead the more temperate episodes such as Marine Isotope Stage 5e or the warmer interstadials of MIS 3 such as GI12. The conditions during these times are also generally more wooded and richer in faunal diversity than colder phases of the Late Pleistocene. This in turn suggests that the thermoregulatory 'rules' used to explain the Neanderthal anatomy (large trunk and shorter relative limb proportions) are unlikely to have explanatory value in this case. Furthermore, association with denser vegetation suggests that their hunting strategy is more likely to be encounter or ambush in style than pursuit hunting. This hunting style is likely to have required a power mode of locomotion such as sprinting rather than an endurance-based long distance running pursuit mode. This power mode of locomotion is consistent with the simple observation that Neanderthals, like modern elite sprinters, are generally more muscular than most modern humans (Stringer and Gamble 1993).

To examine this hypothesis further using an independent data source, an analysis of the frequency distribution power-associated alleles in Neanderthal genomes was conducted. This is possible due to the publically available data and because the field of sports performance genetics has identified alleles associated with power versus endurance. The results of this analysis are consistent with Neanderthals being adapted to power-based locomotion, compared to modern humans.

The dominant paradigm of Neanderthal ecology and adaptation is based on thermoregulation. We identify a number of problems with this view. Despite the caveats of our genetic analyses and palaeoecological data, a new general view of Neanderthal ecology and adaptation is emerging where their anatomy is mainly shaped by locomotion and hunting rather than thermoregulation.

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Figure Captions

Figure 1. Greenland ice core (NGrip) (Svensson *et al*. 2006) derived temperature proxy record ($\delta^{18}O$) for MIS 3 with likely positions of collared lemming (*D. torquatus*) genetic turnovers (Brace *et al*., 2012) with the dominant episodes of human occupation in Belgium and occurrences of forested environments. Five collared lemming lineages with four turnovers took place, the first three during interstadials while the fourth was during the height of the LGM.

Figure 2. Walou Cave stratigraphic sequence (Pirson *et al*., 2012) with palaeoecological proxy data showing pollen (Pirson *et al*., 2012) and small mammal data (rodent palaeoecology summary diagram* and total small mammal species richness and turnover - Jaccard Index of similarity) (Stewart and Parfitt 2011). Also shown are the stratigraphic levels from which yielded *in situ* human occupation evidence as well at the Neanderthal tooth (Pirson *et al*., 2012). The level thought to represent the Les Vaux soil is also indicated. Ecological categories for the rodent palaeoecology summary diagram are: polar (*Dicrostonyx torquatus* and *Lemmus/Myopus*), dry continental (*Microtus gregalis*), humid continental (*M. oeconomus*), temperate grassland (*M. agrestis/M. arvalis*, *Arvicola amphibius*, *Microtus* (*Terricola*) sp.) and temperate woodland (*Clethrionomys* sp. and *Apodemus* sp.).

Figure 3. Histogram of the probabilities that the Neanderthal allele frequency (f_a) for 39 different power associated alleles is larger than the corresponding modern (global) allele frequency (f_m). See Supplementary Material for details on the Methodology.

Figure 4. Comparison of the fractions of power-associated alleles at 39 loci in 2504 modern individuals and 9 Neanderthals (*p*-value from Kolmogorov-Smirnov test). See Supplementary Material for details on the Methodology.

SI. Table 1. Raw data underlying the analysis summarised in Figure 3, including the probabilities for each if the 39 different power associated alleles that the Neanderthal allele frequency is larger than the corresponding modern (global) allele frequency**.**

SI.

Genetic Rationale and Methods

Only in a few—generally simple, *e.g.* Mendelian—cases the genotype-phenotype map, *i.e.* how exactly genetic information brings about phenotypic characteristics, is understood well enough to predict phenotypic characteristics based on a mechanistic understanding of the underlying biology. However, even in the absence of biological/physiological understanding an alternative supervised Machine Learning approach can be used to predict phenotypic characteristics based on DNA: given the alleles observed at relevant loci in the genome of individuals' whose phenotypic characteristics of interest are known, one can train algorithms to "learn" the association between genotype and phenotype and maximise classification accuracy on data not used for training. An example for the application of this paradigm is Forensic DNA Phenotyping (Kayser, 2015), which has been successfully used to predict pigmentation characteristics for example.

Here, we implement a less powerful version of the latter approach. We consider loci that have previously been associated to power athlete status (listed in SI Table 1) independently and establish the number of power-associated alleles per individuals at each of these positions. As already pointed out in the main text, we therefore treat alleles as if their effect strength on power athlete status is the same. Unlike machine learning approaches, we do not integrate the information to provide a final classification. Furthermore, in the case of archaic individuals like Neanderthals the analyses are based on the assumption that alleles associated with power in modern individuals had the same phenotypic effect in the past.

We analyse the genomes of eight Neanderthals [3-5] and one Neanderthal genome generated by merging genomic sequencing data from three different Neanderthal bone fragments [1], as well as 2504 modern individuals from populations world-wide sequenced by the 1000 genomes project [6].

Comparing allele frequencies between Neanderthal and modern populations is complicated by the fact that we only have nuclear genomic data for nine Neanderthals, *i.e.* 18 alleles, which means that the inference of an allele frequency has great uncertainty associated to it. Therefore, we implement an approach based on the beta-distribution that correctly accounts for the uncertainty when inferring frequency from counts. Note that we assume that the modern counts are large enough to neglect uncertainties. Given the number of power-associated and other alleles observed in Neanderthals, say c_p and c_o respectively, and the allele frequency in modern populations globally, say f_m, for each of the 39 loci, we compare the inferred allele frequencies by computing the probability that the power-associated allele frequency in Neanderthals, f_a, is larger than in modern humans as $P(f_a > f_m) = 1 - I(f_m; 1 + c_p, 1 + c_o)$ where $I(x; a, b)$ is the cumulative distribution function of the beta distribution with shape parameters a and b.

We kernel-smooth the distributions of fractions of power-associated alleles in Neanderthals and modern individuals for better visualisation only, the comparison with the non-parametric two-sample one-sided Kolmogorov-Smirnov (KS) test is based on the actual distributions of fractions. Kernel-smoothing and KS test were computed in R.

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