Neanderthals (*Homo neanderthalensis*): An adaptive paradox

Zoe Gavan

Abstract

Neanderthals are widely believed to be a cold-adapted species due its unique craniofacial and postcranial characteristics (Harvati 2003), however in recent years this theory has come in to question (Churchill 1998; Holton and Fransiscus 2008; Rae et al. 2011). This essay reviews arguments that the morphology of Neanderthals are adaptations to a cold environment, and critically examines their validity. This essay begins by outlining the distribution and environment of Neanderthals from 300,000 to 30,000 years ago, provide an overview of Neanderthal derived morphological traits and discuss alternative arguments to the cold-adaptation hypotheses for these traits. The increased pneumatisation, prognathism, and the dolichocephalic cranium found in Neanderthals are unlikely to be a direct adaptation to cold climates. These findings are consistent with Neanderthal postcranial morphology, where body size and shape cannot solely be explained by adaptation to the cold. Instead, other theories are explored, such as increased mobility and activity, anterior dental loading, and hormonal anomalies. Evidence reviewed in this article indicates that the unique morphological characteristics of Neanderthals are likely to be the result of a combination of factors, and are not solely due to cold adaptation.

Keywords

Neanderthals, morphology, cranial, postcranial, cold-adapted

Introduction

During the mid- to late-Pleistocene, a distinct species of *Homo* emerged in Europe: *Homo neanderthalensis*, commonly known as Neanderthals. Inhabiting a wide range of environments and climates, this species has, for many years, believed to have been particularly biologically adapted to cold climates. The hypothesis that Neanderthals were a cold-adapted species rests primarily on interpretations of the cranial and postcranial morphology of fossilised Neanderthal remains (Burke 2012; Caldwell 2014; Churchill 2014). It is widely held that Neanderthals had enlarged paranasal sinuses and a wide nasal passage, which is thought to have played a significant role in their survival during periods of increased glaciation as an adaptation to a cold environment (Harvati 2010). However, recent evidence and analyses suggests that there may be other factors which account for this unique morphology (Stewart 2005). This essay will discuss the evidence for, and against, adaptation to cold climates in Neanderthals. It will outline the environmental factors surrounding the possible need for Neanderthals to adapt to the cold and will then examine the cranial and postcranial morphology of Neanderthals. The discussion of cranial morphology will focus primarily on the paranasal sinus and craniofacial pneumatisation, as these characteristics are most commonly associated with adaptations to climate (Rae et al. 2011). The discussion of postcranial morphology will focus on body proportions and limb length, due to their possible correlation with endothermic regulation (Pearson 2000). This essay will argue that cold adaptation is unlikely to be the sole explanation for the unique characteristics of Neanderthals.

Neanderthal distribution and environment

Neanderthals emerged around 300,000 years ago, during Marine Isotopic Stage 6 (MIS6), and survived through to approximately 30,000 years ago (MIS3). During this period, the climate fluctuated considerably (Finlayson and Carrión 2007; Churchill 2014) and Neanderthals lived through a series of glacial and postglacial stages, in which the climate was up to 25 degrees lower than worldwide modern averages during cool periods, but only 2 degrees lower during warm periods (Sørenson 2011).

Neanderthal distribution covers most of Europe. Fossil specimens have been found from Northern and Eastern Europe, as far south as Israel, with emerging evidence that Neanderthals may have made it as far east as modern Russia (Finlayson and Carrión 2007). The majority of fossil specimens have been found in southern and western Europe, where the climate was consistently warmer than other areas (Skrzypek et al. 2011; Benito et al. 2017). The fossil record indicates continual habitation in more temperate areas of Europe, and only temporary phases of occupation in northern and eastern areas, during warmer phases (Skrzypek et al. 2011). Furthermore, the Neanderthal diet has often been interpreted as consisting primarily of cold-adapted megafauna such as mammoth and bison (Hardy 2010). Further research into Neanderthal diets point to a wider variety of plant matter than previously supposed, which would not have been abundant in exceedingly cold climates. From the geographical distribution, diet, and climate reconstruction of the Neanderthal environment, it can be surmised that Neanderthals were capable of surviving in cold climates but were not necessarily restricted to cold areas (Papagianni and Morse 2013).

Were Neanderthals cold-adapted?

To understand whether Neanderthals were cold-adapted, we can start by considering how cold-adaptation is interpreted and understood through the fossil record. The most widely cited theories relating to possible cold-adaptation are Bergmann's (1848) and Allen's (1877) rules. These rules state that body size is directly related to climate, and that a smaller surface area-to-volume ratio is crucial in thermal regulation in endothermic species. Having a smaller surface area-to-volume ratio means the body retains heat more effectively. Research shows that Bergman and Allen's rules may apply to *Homo* species. For example, modern human populations living in warm climates have evolved to be tall and thin, and populations in cool climates are shorter and stockier (Weaver and Klein 2009). Similar to modern humans who live in cold climates, Neanderthals have also evolved a shorter and stockier body shape (Weaver and Klein 2009). Another significant argument for cold adaptation relates to the shape and size of the paranasal sinuses and nasal complex. Research has shown that enlarged nasal apertures, nasal passages, and paranasal sinuses are adapted to warmer climates; these features being smaller is better adapted to cooler climates (Hubbe et al. 2009).

An important caveat in interpreting the literature on the selective factors for Neanderthal cranial and postcranial morphology is that features that are often interpreted as adaptations to the cold in Neanderthals are frequently contrasted with anatomically modern human traits (Trinkaus 2003). For example, Neanderthals had more prognathic faces and a shorter, stockier body type compared to modern *Homo sapiens*. However, when compared to earlier specimens of *Homo sapiens* which often displayed significant morphological variation, the degree of prognathism is not substantially different from Neanderthal fossil specimens (Stringer 2016). This has led to a particular focus being placed on whether Neanderthals are better adapted to the cold when compared with later hominin species, instead of focussing on the Neanderthal characteristics alone and whether they are representative of adaptations to cold climates. To correct for this bias, this review compares Neanderthal characteristics with earlier, contemporary species of *Homo sapiens* where applicable, and compares Neanderthal attributes to modern human populations only when explaining or exemplifying particular endothermic rules.

Evidence from the Neanderthal cranium

To address the question of whether Neanderthals were a cold-adapted species based on evidence from the cranium, this paper will review two key cranial characteristics: midfacial prognathism and the overall size and shape of the cranium. The degree of midfacial prognathism has been chosen as many arguments about Neanderthals adaptation to cold climates rests on the morphology of the midface. The size and shape of the cranium has been chosen for review due to its relevance to arguments about endothermic regulation.

The mid-facial prognathism observed in Neanderthals is argued to be a result of enlarged development of the paranasal sinus (Márquez et al. 2014), which consists of four pairs of air-filled spaces in the cranium around the eyes and nose. The purpose and function of these air-filled spaces is not entirely understood, although it has been proposed that the paranasal sinus complex heats and adds moisture to the air inspired through the nasal cavity (Holton and Francisus 2008; Azevedo et al. 2017). Air traveling through a narrower nasal cavity is warmed and humidified more than air travelling through a wider nasal cavity. A narrower nasal cavity or smaller paranasal sinus would therefore lead to a smaller midfacial region, which would therefore be expected in species adapted to cold climates.

Neanderthal specimens often display a wide nasal aperture, which is in direct contradiction to theories of cold adaptation. A wide nasal aperture is indicative of a wide nasal passage and cavity, meaning the air inhaled is not heated or humidified as effectively as possible (Rae et al. 2011). Therefore, a wide nasal aperture in Neanderthals suggests that Neanderthals may not be cold-adapted. Alternatively, evidence suggests that the wide nasal aperture found in Neanderthals is associated with the late suturing of the maxilla in the species, which results in wide-set canines and overall widening of the face (Holton and Franciscus 2008). It is therefore possible that the midfacial prognathism commonly seen in Neanderthals may be a result of similar influences: late synostosis means that there is more time for the midface to grow and project, and this unique morphology is not necessarily a result of a potential increase in the size of the paranasal sinus (Holton and Franciscus 2008). Therefore, the argument that an enlarged paranasal sinus—as seen in Neanderthals—is an adaptation to cold climates does not withstand scrutiny. Data taken from x-rays indicate that the size of the paranasal sinus in relation to the cranium is comparable with that of more modern *Homo sapiens* samples from temperate climates (Rae et al. 2011), and other studies show that modern populations in cold climates demonstrate a more constricted paranasal sinus – in contrast to populations in warmer climates, who have a wider paranasal sinus (Noback et al. 2016). In species adapted to warmer climates, the paranasal sinus expands (Márquez et al. 2014). The exact nature and function of the paranasal sinus is not fully understood, and it may be that there is an, as yet unknown, function that help to answer the question as to whether this morphological region varies in response to climatic variation.

Scholars have suggested that the size and shape of the Neanderthal cranium is adapted to the cold (Weaver and Klein 2009). It has been argued that in a warmer climate, the cranium should be shaped to dissipate heat (i.e. have a larger surface area-to-volume ratio, following Bergman's rule), whereas in a colder climate, the cranium should have a smaller surface area-to-volume ratio in order to prevent the loss of heat (Beals et al. 1983). The Neanderthal skull is dolichocephalic, having an elongated, flattened cranium (Churchill 2014), meaning that Neanderthals would have a larger surface area-to-volume ratio and would therefore lose heat through the cranium more rapidly than populations with shorter, rounder skulls. This would indicate that the Neanderthal skull is not particularly adapted to cold climates. However, compared to contemporary hominin species that existed during the same time period as Neanderthals, Neanderthal skulls are *more* brachiocephalic in comparison. This could be seen as a possible transition to a more cold-adapted cranium shape in Neanderthals.

The Anterior Dental Loading Hypothesis has been suggested as an alternative explanation for the elongated shape of the Neanderthal cranium (Clement et al. 2012). This hypothesis states that the marked prognathism seen in Neanderthals is an adaptation to the application of heavy forces on the anterior teeth, which was subsequently balanced out by the elongation of the cranium (Lieberman et al. 2000). The anterior teeth may have been used for a range of cultural activities, such as making or using tools, as well as a result of diet and masticatory habit (Lozano-Ruiz et al. 2004). The size and shape of the cranium has been noted in Neanderthal fossil specimens of all ages, however, including infants (Weaver and Klein 2009). This would indicate that Neanderthal cranial shape is not solely the result of habitual lifestyle factors, and therefore cold adaptation cannot be ruled out as an explanation.

Evidence from the Neanderthal postcranial skeleton

To address the question of whether Neanderthal postcranial morphology is cold-adapted, the size, shape, and muscularity of the torso and limbs will be discussed. Neanderthal postcranial morphology is as distinctive as the cranial morphology in the archaeological record, being considerably more robust, shorter, and stockier than contemporary hominin species, particularly early *Homo sapiens* (Churchill 1998). Neanderthal body shape is stockier, compared to *Homo sapiens,* with comparatively short extremities. The torso is short and barrel-shaped, and judging by the muscle-attachment sites on several fossil specimens, both the torso and limbs were very muscular and powerful (Pearson 2000). According to Bergman and Allen's rules, it is certainly beneficial to have a smaller, more compact body in a cold climate. The apparent muscularity of the Neanderthal body could also have been beneficial in cold climates (Churchill 2014). High degrees of muscularity would be insulating as well as effective heat generators, albeit at a metabolic cost which is as yet unknown. Therefore, the overall size, shape, and body composition of Neanderthals is at the very least beneficial in a cold climate, and could potentially be seen as an adaptation to such.

Neanderthal limb morphology has been used to argue that Neanderthals are cold-adapted. Allen's rule specifically states that having shorter distal limbs is beneficial in a cold climate, and Neanderthal fossil specimens certainly conform to this rule. The bones of the forelimbs (radius and ulna) and lower legs (tibia and fibula) are considerably shorter than the upper long bones (Steudel-Numbers and Tilkens 2004) resulting in low crural and brachial indices. This is another example of conformation to Allen's rule, as it means a reduction in surface area-to-volume ratio. The relatively low crural and brachial indices of Neanderthals is also found in modern populations that live in some of the coldest climates in the world (Churchill 2014). The Neanderthal femur, radius, and ulna in particular are also bowed antero-posteriorly relative to anatomically modern humans (De Groote 2011), indicative of increased muscularity and power; this is supported by increased cortical thickness in the leg bones. The length, robusticity, and bowing of the Neanderthal limbs would have been beneficial in a cold climate, however it is unlikely that cold-adaptation is the sole explanation for these attributes in that this derived Neanderthal morphology has alternatively been posited to be the result of genetic drift (Weaver and Klein 2009) or increased activity levels (Steudel-Numbers and Tilkens 2004; De Groote 2011).

While the Neanderthal body shape would have been advantageous in colder climates, this does not necessarily indicate an evolutionary adaptation. Several theories have been asserted to explain the Neanderthal body shape, which relate to possible hormonal anomalies in Neanderthal growth patterns. It has been postulated that the timing and intensity of endocrine production (essentially certain growth hormones) may have caused accelerated growth rates of certain areas of the body, which could explain not only the general robusticity of the postcranial morphology but the midfacial projection of the crania as well (Maureille and Bar 1999). It is entirely possible that hormonal anomalies developed in response to cold environments; the two theories are therefore not mutually exclusive. It has also been suggested that the distinctive postcranial morphology of Neanderthals could be the result of a variety of other influences—increased carrying capacity and locomotion, or habitat vegetation density, for example (Stewart 2005).

The validity of using Bergman and Allen's rules to assess Neanderthals suitability to colder climates has also been questioned. The main criticism is that these rules should be used to compare *within* a species and not between different species (Stewart 2005). Interspecies comparison (between Neanderthals and *Homo sapiens*, for example) cannot provide an accurate reflection of whether a single species is cold-adapted (in this case, for the Neanderthals). On the other hand, intraspecies comparison of specimens from different climates or geographic locations would provide a clearer picture of whether Neanderthals are cold-adapted based on their body composition.

Discussion

This essay has presented evidence to show that the derived cranial and postcranial morphology of Neanderthals can be interpreted in a variety of ways. In considering Neanderthal cranial morphology, this essay reviewed evidence to show that the midfacial projection is not particularly advantageous in cold climates, nor is the widened nasal aperture or enlarged paranasal sinus (Rae et al. 2011; Márquez et al. 2014). It is therefore unlikely that these particular characteristics would have evolved as a product of a cold climate. The postcranial morphology would certainly be beneficial in a cold climate, according to Allen's and Bergmann's rules, and judging by the muscle attachment sites and thickness of the cortical bone in the long bones, it is certainly possible that at least some of these features were selected for in the genetic process. However, these characteristics could alternatively have arisen as adaptations to a number of factors, such as increased mobility and activity levels or genetic anomalies. Subsequently, a combination of any of these factors could provide the explanation for the distinctive morphology of the Neanderthal postcrania.

If Neanderthals were not a cold-adapted species, the unique cranial and postcranial morphology observed in this the species still requires an explanation. One possible explanation, posited by Weaver et al. (2007), is genetic drift; this is a chance process by which the frequency of alleles in the genetic loci can change, which can lead to random evolutionary possibilities. Recent findings have indicated that genetic drift may be more responsible for the differences in Neanderthal cranial morphology than the process of natural selection. Again, this is not to say that genetic drift is the *sole* cause of Neanderthal morphology. Other possible factors—such as population isolation resulting in genetic diversion or hybridisation between species or geographical groups—could all have contributed to Neanderthals displaying such unique morphology (Finlayson 2004).

It is evident from the fossil record that Neanderthals lived in a variety of climates, spanning a time frame in which the climate varied considerably (Finlayson 2004). It is well understood that Neanderthals utilised sophisticated stone-tool technology, were very competent hunter-gatherers, and were resourceful in exploiting their environments for survival (Hoffecker 2005; Papagianni and Morse 2013). Given this archaeological evidence, it may not have been necessary for Neanderthals to drastically adapt to the cold environment they inhabited, casting further doubt that the derived morphology found in Neanderthals are an evolutionary response to their cold environment.

Conclusion

The main argument for Neanderthals being cold-adapted relies on the size and shape of the paranasal sinus and midfacial pneumatisation, and the size and shape of the body. The evidence examined in this essay indicates that the unique craniofacial morphology of Neanderthals may be the result of a variety of factors and did not necessarily evolve in response to a cold environment. In particular, the size and shape of the nasal aperture, nasal passage, and paranasal sinus appear to be better adapted to warmer climates, when compared with modern populations. There are a number of alternative hypotheses that could explain the midfacial pneumatisation of Neanderthals, including growth patterns and lifestyle factors.

Similarly, the postcranial morphology of Neanderthals could be the result of a number of genetic, environmental, or lifestyle factors. The size, shape, and body composition of Neanderthals may have been beneficial in a colder climate, but there is not enough evidence to show that these morphological features are an evolutionary response to a cold environment. By contrast, this essay has shown that there are several other factors that may have influenced the postcranial morphology of Neanderthals that are not related to climate, such as increased activity levels and locomotive demands.

These hypotheses are only relevant if it was indeed necessary for Neanderthals to adapt to their environment – a topic that needs more research itself. Furthermore, issues relating to genetics, natural selection, and life histories still need to be explored further in order to understand the extent of influence on Neanderthal morphology. While there are aspects of Neanderthals that could be seen as being cold-adapted, it is more likely that these characteristics are a result of a number of factors and may not have been specifically selected for. Therefore, the theory that Neanderthals were a cold-adapted species requires more evidence to be convincing.

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