



Humans preserve non-human primate pattern of climatic adaptation

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ABSTRACT

There is evidence for early Pleistocene *Homo* in northern Europe, a novel hominin habitat. Adaptations enabling this colonisation are intriguing given suggestions that *Homo* exhibits physiological and behavioural malleability associated with a 'colonising niche'. Differences in body size/shape between conspecifics from different climates are well-known in mammals, could relatively flexible size/shape have been important to *Homo* adapting to cold habitats? If so, at what point did this evolutionary strategy arise? To address these questions a base-line for adaptation to climate must be established by comparison with outgroups. We compare skeletons of Japanese macaques from four latitudes and find inter-group differences in postcranial and cranial size and shape. Very small body mass and cranial size in the Southern-most (island) population are most likely affected by insularity as well as ecogeographic scaling. Limb lengths and body breadths show group differences that accord with the expectations of thermoregulation across the whole range of latitudes. Postcranial size appears to vary more than shape, yet there is also evidence that limb segments follow Allen's rule in the forelimb at least, suggesting differing climatic signals in different regions of the skeleton. In contrast to other intraspecific studies of catarrhine ecogeography, the results presented here demonstrate non-allometric latitudinal patterns in craniofacial shape in Japanese macaques, which align closely with what is seen in cold-adapted humans. These insights begin to provide a comparison for hominin adaptation to similar habitat diversity and the role of biological adaptation in shaping the evolution and dispersal of *Homo* species.

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1. Introduction

1.1. Hominins in Northern Europe

Footprints found in 2013 at Happisburgh, Norfolk, provide evidence of hominins in northern Europe as early as ~850 ka (Ashton et al., 2014). This cool, continental and very seasonal climate (Parfitt et al., 2010; Ashton and Lewis, 2012) would have presented a novel set of challenges to hominins adapted to tropical Africa, including key stressors such as very low temperatures, increased seasonality, snow cover/precipitation, a shorter growing season and shorter day length (Ashton and Lewis, 2012; Hosfield, 2016).

How northern European Early Pleistocene populations would

have adapted to this environment is an open question. As hominins, with inherently flexible cognition and behaviour, behavioural and technological coping mechanisms would be expected, yet there is no evidence for great technological sophistication at this time and in this place. The oldest technology at Happisburgh is Mode 1, simple flake tools, and there is no evidence of structures (Ashton et al., 2014). Furthermore, despite continuing debate, it seems likely that control of fire was not mastered in Europe until the middle Pleistocene, at about 4–300 ka (Roebroeks et al., 2011). In terms of mitigating behaviour, migration on a scale large enough to avoid the cold seems unlikely, especially for the entire group, including the young, old, and pregnant females (Hosfield, 2016). Range expansion is possible, however, as are changes in diet either through dietary expansion (Buck and Stringer, 2014; Buck et al., 2016; Hosfield, 2016) or the consumption of greater amounts of meat and fatty tissues (Cordain et al., 2000). The extent of clothing in the middle Pleistocene is unknown, and the technology for tailored clothing is absent from the archaeological record (Gilligan,

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2010), but coverings of some kind seem likely, as for the later Neanderthals (Wales, 2012). If earlier hominins had similar thermoregulatory systems to present day *Homo sapiens*, it seems doubtful that with such a simple suite of technologies, behavioural adaptation would have buffered environmental stress sufficiently. If this is the case, biological adaptations would also have been required to allow the colonisation of this new climatic niche.

1.2. Biological adaptation to climate in hominins

Adaptation to climate is one of the key determinants of animal form and some of the most well-known and robust thermoregulatory patterns in morphology throughout the mammal class are Bergmann's (Bergmann, 1847) and Allen's (Allen, 1877) rules (Ashton et al., 2000; Meiri and Dayan, 2003). Bergmann's rule states that, within a species, individuals from higher latitudes will be larger (Bergmann, 1847) and Allen's states that those same cold-adapted individuals will have shorter appendages, including limbs and tail (Allen, 1877). The relationship between surface area and heat loss underpins these rules; endothermic animals produce their own heat internally and heat loss is directly proportional to surface area. Depending on surrounding temperatures, it is beneficial to either conserve or lose internally-generated heat and animal body proportions correspond accordingly. As with many other mammal species (Katzmarzyk and Leonard, 1998; Ashton et al., 2000; Meiri and Dayan, 2003), obedience to Bergmann's and Allen's rules can be seen in differing body proportions between populations of recent *H. sapiens* from different climates. Brachial and crural indices, bi-iliac breadth and rib cage shape have a close relationship with mean annual temperatures and populations living in cooler areas tend to have more barrel-shaped chests and broader hips (Ruff, 1994, 2002; Ruff et al., 1997; Franciscus and Churchill, 2002; Stock, 2006).

Climate is also an important selective pressure on human cranial shape; in fact, adaptation to extreme cold stress is thought by some to be the only non-neutral signal in recent *H. sapiens* craniofacial morphology (Roseman, 2004; Roseman and Weaver, 2004). *H. sapiens*, neurocranial shape and size seem to vary with climate in accordance with Allen's and Bergmann's Rules; crania are larger and more brachycephalic in cold climates (Beals, 1972; Beals et al., 1984; Nowaczewska et al., 2011). Cold-adaptation has also been inferred in greater facial breadth and reduced facial projection (Hubbe et al., 2009; Betti et al., 2010; Evteev et al., 2014, 2017), in accordance with Allen's rule, and in the shape of the nasal apparatus (Carey and Steegmann, 1981; Franciscus and Long, 1991; Betti et al., 2010; Noback et al., 2011). In cold climates the nasal aperture is generally narrower in relative terms (Weiner, 1954; Franciscus and Long, 1991; Hubbe et al., 2009; Evteev et al., 2014) and the internal nasal cavity is configured to increase contact time between the air and highly-vascularised nasal mucosa (Noback et al., 2011; Evteev et al., 2014, 2017). This morphology is thought to be an adaptation to optimise air conditioning. A close relationship between climate and nasal morphology is to be expected, as inspired air must be warmed to body temperature to avoid damaging respiratory tissues and to enable the proper functioning of the nasal cilia and mucosa, whilst expired air can be an important source of heat and moisture loss (Negus, 1957; Carey and Steegmann, 1981). For each of these cranial regions, the majority of differences seem to be driven by populations from very cold climates, and the signal becomes weaker or disappears if those samples are removed (Roseman, 2004; Harvati and Weaver, 2006; Hubbe et al., 2009; Betti et al., 2010; Relethford, 2010; Foster and Collard, 2013).

Climatic effects on hominin skeletal morphology have also been inferred in the fossil record, particularly with regards to Neanderthals in glacial Eurasia (Coon, 1962; Brose, 1967; Churchill, 1998;

Wolpoff, 1999; Steegmann et al., 2002). In the cranium, increased mid-facial prognathism was historically seen as an adaptation to increase the distance between the respiratory apparatus and arteries serving the brain, thus reducing the cooling effect of inspired air on the cranial blood and delicate cerebral tissues (Coon, 1962; Brose and Wolpoff, 1971; Wolpoff, 1999), whilst the large nasal aperture has been attributed to the need to warm and condition air (Coon, 1962; Churchill, 1998; Wolpoff, 1999). The relationship between greater prognathism and cold-adaptation is dubious, since it is the exact opposite of the trends described above for *H. sapiens* and also for other mammals, such as experimentally cold-adapted rats (Steegmann and Platner, 1968; Rae et al., 2006, 2011). The evidence of whether the Neanderthal nose is cold-adapted is still debated (see Churchill [2014] for a review), some elements of Neanderthal nasal morphology appear to optimise inspired air passage for more efficient warming, as in cold-adapted *H. sapiens* (de Azevedo et al., 2017; Wroe et al., 2018). The great breadth of Neanderthal noses, however, is still puzzling when compared to narrower noses in cold-adapted recent humans, macaques, and rats (Steegmann and Platner, 1968; Rae et al., 2003, 2006, 2011), and may be due to constraint and integration with other cranial structures.

In contrast to the debate over Neanderthal cranial morphology, there is substantial agreement that many of distinctive Neanderthal postcranial traits are climatic adaptations (Trinkaus, 1981; Holliday, 1997; Churchill, 2014). Holliday has shown Neanderthals to have body proportions similar to those of modern humans from very high latitudes, but even more 'hyperpolar' (Holliday, 1997). Neanderthals have short limbs and especially short distal limb segments relative to trunk height or proximal limb segment length, following Allen's rule. They have long trunks and high body mass also obeying Allen's and Bergmann's rules (Holliday, 1997). The extreme postcranial robusticity and larger joint diameters seen in Neanderthals compared to *H. sapiens* are likely linked to colder temperatures via their relationships with body mass and proportions (Ruff, 1994).

1.3. The relative importance of biological adaptation in hominins

The above evidence demonstrates that hominins adapt physically to the climate as other mammals do, following ecogeographic rules such as Bergmann's and Allen's. What is unknown is the extent which this adaptation is of the same magnitude and follows the same patterns as in other primates and whether the hominin pattern of climatic adaptation is conserved or derived. Though humans display considerable phenotypic diversity, we are remarkably genetically homogenous compared to other primate species (Kaessmann et al., 2001; Bowden et al., 2012) and from what we know of genetic variation in other hominin species, it appears they were even more so (Meyer et al., 2012; Castellano et al., 2014). It has been suggested that this dichotomy between variation in phenotype and genotype arises from a human evolutionary strategy characterised by flexibility and adaptability, making humans consummate generalists (Wells and Stock, 2007; Stock, 2008; Antón et al., 2016). This hyperadaptability, varying physically and behaviourally whilst largely buffering the genotype, would have facilitated dispersal into novel habitats and has thus been described as constituting a "colonising" niche (Wells and Stock, 2007).

If the exploitation of a colonising niche is a human trait, when did it begin? Is it a trait of the primate order, a trait of the tribe hominini, a trait of the genus *Homo*, or a trait of the species *H. sapiens*? Adaptability would have been particularly important during periods of climatic instability (Vrba, 1985, 2015; Foley, 1987; Potts, 1998, 2013). Regional variation in *Homo* during one such

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