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Does Climate or Mobility Explain the Differences in Body Proportions Between Neandertals and Their Upper Paleolithic Successors?

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European Neandertals and their Upper Paleolithic modern human successors differ substantially in various proportions of their bodies. As compared to Neandertals, Upper Paleolithic Europeans tend to have longer limbs, both absolutely and relative to estimated skeletal trunk height; narrower bi-iliac breadths, both absolutely and relative to femur length; and higher brachial and crural indices.[1–7] Although these differences hold generally, body proportions did change through time during the Upper Paleolithic and subsequent Mesolithic, with more recent groups approximating Neandertals more closely. In comparison with Early Upper Paleolithic humans (>20,000 years ago), those of the Late Upper Paleolithic (20,000 to 10,000 years ago) and Mesolithic (10,000 to 5,000 years ago) have shorter limbs, both absolutely and relative to estimated skeletal trunk height.[5,6] However, brachial and crural indices, which do not always reflect overall limb length, do not change much through time. Early Upper Paleolithic, Late Upper Paleolithic, and Mesolithic humans all have high brachial and crural indices; it is not until recent Europeans that lower indices appear.[5,6,8] During the Upper Paleolithic and into the Mesolithic there is a shift from relatively narrow bodies with long limbs to relatively wide bodies with short limbs, but not all proportions change at once.

In extant humans, as in other endothermic species, contrasts in body proportions similar to those between Neandertals and Upper Paleolithic humans appear to reflect, at least in part, population-level genetic differences produced over thousands of years by interregionally differing selection pressures due to variation in local climate.[1,5,7,9–17] For effective thermoregulation, in warm climates it is advantageous to have a narrow body with long limbs to dissipate heat, and in cold climates it is better to have a wide body with short limbs to retain heat. Thus, the body proportions of Early Upper Paleolithic Europeans appear to be a genetic signature of recent warm-climate ancestry and, conversely, lack of Neandertal ancestry, which is consistent with a predominantly African origin for all modern humans.[1,5,6,18] Under the "climate hypothesis," changes in body proportions during the Upper Paleolithic and into the Mesolithic would be explained as the gradual and mosaic adaptation over time to colder climates, possibly slowed by the increased cultural buffering of selection provided by Upper Paleolithic clothing and shelters.[1,2,5,6,18]

However, the climate hypothesis has been questioned.[8,19,20] The primary alternative is that differences in body proportions reflect adaptation to differences in mobility (see discussions in Trinkaus,[1] Finlayson,[19] Wolpoff,[20] and Holliday and Falsetti[21]). One variant of the "mobility hypothesis" posits that Neandertals could have played a substantial role in the ancestry of Upper Paleolithic Europeans if differences in body proportions originated *in situ* through selection for increased energetic efficiency during mobile foraging with the start of the Upper Paleolithic. Under this scenario, Neandertal body proportions could also still be adaptations to cold climates but, during the Upper Paleolithic, climatic selection was relaxed by increased cultural buffering and superceded by stronger selection for mobility. Under another variant, if Neandertals and modern humans coexisted for some time in Europe, then differences in body proportions between Neandertals and Upper Paleolithic modern humans could explain why modern humans were able to outcompete Neandertals as environmental conditions changed to those that favored mobile foraging.[19] Alternatively or additionally, Neandertal body proportions, along with other features of their skeletons, could have been shaped by selection for competence in foraging activities requiring substantial mechanical power[18,22] or locomotion over hilly terrain.[20] Neandertal body proportions could be the result of poor nutrition and health during the growth period,[20,23] but while certain anthropometric dimensions are readily affected by changes in nutrition and health, body proportions appear to be fairly stable (see discussion and references in Ruff[7]).

The "mobility hypothesis" has less empirical support than does the climate hypothesis, because no relationship can be found between body proportions and various measures of mobility in extant hunter-gatherer groups, even when controlling for the

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effects of climate.[21] This lack of a relationship is important, but the evidence would be more compelling if better data existed on hunter-gatherer mobility. In particular, data for logistical mobility (trips by small groups from a residential base), as opposed to residential mobility (movement from one residential base to another), is virtually nonexistent.[24,25] It is possible that no relationship has been detected between mobility and body proportions because of the poor quality of the data rather than because one does not exist. There are also potentially confounding factors to finding a relationship between climate and body proportions, but the relationship is still remarkably strong. This suggests that while mobility may well play an as yet undetected role in shaping body proportions, climate likely plays a much larger role.

There are also theoretical reasons why body proportions might be expected to reflect adaptation to climate more strongly than to mobility levels. Differences in body proportions between extant human populations appear to be genetically determined, at least in part, and are known to be present from a very early age (see discussion and references in Holliday[5] and Ruff[7]). Although climatic selection for interregional differences in body proportions may act on adults, it also has the potential to act on infants, particularly during extreme temperature periods in cold climates where the small body masses of infants would already make heat retention difficult. Thus, interregionally differing selection for body proportions that enhance thermoregulation has the potential to act on all age cohorts, starting from birth. On the other hand, selection for increased energetic efficiency during mobile foraging can act only on older age cohorts, because individuals in the youngest cohorts (infants) do not actively engage in foraging activities. In general, selection pressures that act only on older age cohorts are weaker, because by the time they act many individuals have already died, leaving fewer individuals whose mortality and fertility can be influenced.[26] In principle, selection for body proportions that enhance mobile foraging activities could override selection for body proportions that are advantageous for thermoregulation, but the cohort-specific mortality and fertility differential related to mobility would have to be much larger than the differential related to thermoregulation.

Nevertheless, there is some archeological support for differences in mobility, either residential or logistical, among Neandertals and Upper Paleolithic humans, and possibly for changes through time within the Upper Paleolithic and into the Mesolithic. Although there are some exceptions, the stone tools found in sites known or presumed to have been produced by Neandertals are predominately manufactured from local raw materials, coming from sources that are usually much less than 100 km away. This pattern appears to be fairly consistent across western, central, and eastern Europe.[2,27–29] In contrast, the sites of Early Upper Paleolithic humans often contain stone tools manufactured from raw materials coming from more than 100 km away. In some cases, marine shells from more than 500 km away are present.[2,27–30]

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The predominantly local use of resources by Neandertals may mean that Neandertals were not particularly mobile and inhabited territories less than 10,000 square km in size,[2] which is small for extant hunter-gatherer groups living in northern geographic regions.[25] Because of their diets high in meat, extant hunter-gatherer groups who live in northern geographic regions tend to be more mobile and inhabit larger territories than do their equatorial counterparts, who usually consume more plants.[2,25] There may also be evidence, both archeological and biological, that mobility decreased during the Upper Paleolithic and into the Mesolithic, as humans became increasingly sedentary.[31,32] If these inferred changes in mobility are correct, then the changes in body proportions from Neandertals to Mesolithic humans may be exactly what one would predict if selection for energetic efficiency in mobile foraging were shaping body proportions. It should be pointed out, however, that inferring the magnitude of selection from the archeological record is difficult. Raw material movement distances may reflect trade between groups rather than the mobility of one particular group, and mobility inferred from archeological data may not be tightly correlated with the daily movements of individuals. Like the data on extant hunter-gatherer mobility discussed earlier, archeological data on mobility could be a poor proxy for the intensity of selection for energetic efficiency in locomotion.

Differences in body proportions between Neandertals and Upper Paleolithic humans and changes through time during the Upper Paleolithic and into the Mesolithic likely would have had energetic consequences for mobile foraging. It is possible to quantify these energetic consequences using experimental data on walking in humans. If variation in lower limb length in humans has a predictable relationship with the energetic cost of walking, then it seems reasonable to conclude that variation in lower limb length would have had a similar relationship in Neandertals and Upper Paleolithic and Mesolithic humans.

From experiments on human subjects of varying leg length who walked on a treadmill at speeds near their

TABLE 1. ESTIMATED DIFFERENCES IN THE DAILY ENERGETIC COST OF FORAGING DUE TO DIFFERENCES IN LOWER LIMB LENGTH[a]

	Early Upper Paleolithic	Late Upper Paleolithic	Mesolithic
Neandertals	−78	−51	−28
Early Upper Paleolithic	*	+27	+50
Late Upper Paleolithic	*	*	+23

[a] Estimates in kCal day^{-1}; − indicates that the group at the top of the column has a lower cost than the group at the left of the row; + indicates the opposite.

energetic optimum, Steudel-Numbers and Tilkens[22] have estimated a multiple regression equation ($E = 8.301 - 0.1691 + 0.234$ m) relating the total energetic cost of transport (E, measured as oxygen consumption in ml O_2 m^{-1}) to lower limb length (l, femur length + tibia length in cm) and body mass (m, kg). The total energetic cost of transport includes postural and body maintenance costs over the distance traveled. The energetic cost in ml O_2 m^{-1} can be converted into kCal m^{-1}, because consuming 1 ml of O_2 corresponds to using 0.004801 kCal,[33] assuming a respiratory quotient (RQ) of 0.80.[34] Combining the equation in Steudel-Numbers and Tilkens[22] with these conversion factors and holding body mass constant, we estimate that a 1-cm decrease in lower limb length would increase the energetic cost of walking by about 0.811 kCal km^{-1}.

These calculations can be illustrated by considering two hypothetical individuals. Let E_1 and E_2 be the energetic cost of transport, l_1 and l_2 be the lower limb length, and m_1 and m_2 be the mass, respectively. If $l_2 = l_1 - 1$ (1-cm decrease) and $m_2 = m_1$ (equal mass), then $E_2 - \mathrm{E}_1$ is the energetic cost of transport for a 1-cm decrease in lower limb length, holding body mass constant. A daily estimate can be approximated using data on average foraging distances in extant hunter-gatherers. If we assume that an individual walks about 12.2 km day^{-1} (the average of round-trip foraging distances for Nunamuit, Australian, Anbarra, and Pume women and Nunamuit, !Kung, and Pume men from Binford[24]), then the daily energetic cost of a 1-cm decrease in lower limb length would be about 9.89 kCal day^{-1}. For comparison, the daily energetic cost of a 1-kg increase in body mass, holding lower limb length constant, would be about 13.7 kCal day^{-1}. These values should be interpreted cautiously because they are rough estimates with many unquantifiable sources of error, but they at least give a sense of the order of magnitude of the energetic cost of a 1-cm decrease in lower limb length. The cost is somewhere around 10 kCal day^{-1}, rather than 1, 100, or 1000 kCal day^{-1}.

Based on the lower limb lengths given in Holliday[6] (personal communication for the numerical values used to create his Fig. 5) and the preceding calculations, it is possible to quantify the differences in energetic cost of walking among Neandertals and Early Upper Paleolithic, Late Upper Paleolithic, and Mesolithic humans. As a starting point, we first assumed that there were no differences in body mass among the groups. Just considering differences in lower limb length, the shorter lower limbs of Neandertals would have cost them 78 kCal day^{-1} relative to their Early Upper Paleolithic successors (Table 1). There would have been less of a difference in cost between Neandertals and Late Upper Paleolithic or Mesolithic humans because lower limb length is shorter in these modern human groups (Table 1). Relative to the Early Upper Paleolithic, the shorter lower limbs of Late Upper Paleolithic and Mesolithic humans would have cost them, respectively, 27 kCal day^{-1} and 50 kCal day^{-1} (Table 1). Thus, the magnitude of the differences between the groups is on the order of tens of kCal day^{-1}.

So far, our calculations have ignored any potential differences in body mass among the groups. Although it may be reasonable to assume that Late Upper Paleolithic Europeans had about the same average body mass as Early Upper Paleolithic Europeans,[35,36] though possibly slightly lighter[31,37] or heavier,[12] Neandertals may have been about 15% heavier than these two modern human groups,[37] whereas Mesolithic humans may have been about 10% lighter.[31] These differences in estimated body mass are consistent with what we know about the body proportions in these groups. While Late Upper Paleolithic humans had shorter lower limbs than did their Early Upper Paleolithic predecessors,[6] these shorter lower limbs were compensated for by longer trunks, as evidenced by their lower ratios of femur length and tibia length to estimated skeletal trunk height.[5] These two groups had similar body breadths.[36]

If these inferred changes in mobility are correct, then the changes in body proportions from Neandertals to Mesolithic humans may be exactly what one would predict if selection for energetic efficiency in mobile foraging were shaping body proportions. It should be pointed out, however, that inferring the magnitude of selection from the archeological record is difficult.

The volume, and therefore mass, of the human body can be modeled as a cylinder[7,37,38] using the equation $V = \pi/4\ \mathrm{D}^2 L$, where V is volume (proportional to mass), D is bi-iliac breadth, and L is stature. Based on the cylindrical model, Early Upper Paleolithic and Late Upper Paleolithic humans

TABLE 2. ESTIMATED DIFFERENCES IN THE DAILY ENERGETIC COST OF FORAGING DUE TO DIFFERENCES IN BODY MASS[a]

	Early Upper Paleolithic	Late Upper Paleolithic	Mesolithic
Neandertals	−137	−137	−206
Early Upper Paleolithic	*	0	−69
Late Upper Paleolithic	*	*	−69

[a] Estimates in kCal day^{-1}; − indicates that the group at the top of the column has a lower cost than the group at the left of the row; + indicates the opposite.

would be expected to have similar average body masses. Neandertals are estimated to have lower limb to trunk proportions similar to those of Late Upper Paleolithic humans, with a relatively longer femur but a relatively shorter tibia (see Holliday's Tables 6 and 7), but shorter lower limbs,[6] which would appear to result in a shorter stature and thus a lower body mass than Upper Paleolithic Europeans. However, Neandertals probably had wider body breadths, as evidenced by estimates of their bi-iliac breadths,[4,7] than did their Upper Paleolithic successors. According to the cylindrical model, changes in breadth have a greater effect on body mass than does stature, because breadth is squared and stature is not in the formula for the volume of a cylinder. This theoretical argument is borne out by a much larger coefficient for bi-iliac breadth than stature in Ruff, Trinkaus, and Holliday's[37] multiple regression equation for predicting body mass from stature and bi-iliac breadth. Mesolithic Europeans had estimated lower limb to trunk proportions similar to those of Late Upper Paleolithic Europeans,[5] but they had shorter lower limbs[6] and narrower bi-iliac breadths,[31] which would have resulted in a lower body mass.

If we assume that Upper Paleolithic Europeans had average body masses of about 65 kg,[31,35–37] then a 15% larger body mass in Neandertals would be about 75 kg, and a 10% smaller body mass in Mesolithic Europeans would be about 60 kg. These values can be used, if only very roughly, to estimate the daily energetic cost for walking of differences in body mass among the groups. Based on body mass alone, Neandertals would have used about 137 kCal day^{-1} more energy in walking than Upper Paleolithic Europeans would have, while Mesolithic Europeans would have used about 69 kCal day^{-1} less than did their Upper Paleolithic predecessors (Table 2). If Neandertals actually had body masses closer to 90 kg, as Kappleman[39] estimated from orbital aperture area, then they would have used about 343 kCal day^{-1} more energy in walking than would Upper Paleolithic Europeans. Based on lower limb length and body mass together, Neandertals would have used about 215 kCal day^{-1} more energy than would their Early Upper Paleolithic successors (Table 3). Thus, the differences in energetic cost between Neandertals and the modern human groups, considering both body mass and lower limb length, would have been on the order of hundreds of kCal day^{-1}.

These estimates appear to be reasonable based on other lines of evidence. The percentage of the total daily energy expenditure accounted for by locomotion is only 8% to 14% even in fairly mobile terrestrial mammals such as carnivores or hamadryas baboons (*Papio hamadryas*).[40] Assuming that Neandertals and Upper Paleolithic and Mesolithic humans expended no more energy on locomotion than do these fairly mobile mammals and had a total daily energetic expenditure of no more than 4,480 kCal day^{-1} (the upper end of the range estimated for Neandertals by Steegmann, Cerny, and Holliday[41]), then their daily energetic expenditure on locomotion would be no more than 627 kCal. A similar estimate of 770 kCal is obtained using 5,500 kCal day^{-1}, which is the very heavy activity level value estimated by Sorensen and Leonard.[42] Given that the energetic costs of differences in lower limb length and body mass would be a fraction of the total daily energetic cost of locomotion, the estimates on the order of tens to hundreds kCal day^{-1} seem reasonable.

How do we reconcile evidence of the influence of climate on body proportions on the one hand with evidence, on the other hand, of possible differences in mobility among Neandertals and Upper Paleolithic and Mesolithic humans and the energetic consequences for mobility of differences in body proportions? It is noteworthy that almost all human skeletons from the Early Upper Paleolithic are substantially younger than 30,000 years old; most are closer to 25,000 years old.[43] Thus, even using the youngest estimates for the date of arrival of modern humans in Europe, about 36,000 years ago,[44] most Early Upper Paleolithic skeletons come from about 11,000 years after the earliest arrival of modern humans in Europe. In addition, modern human populations would likely have taken thousands of years to make their way from Africa into Europe, and body proportions took thousands of years to change during the Upper Paleolithic. So we have a situation in which most human skeletons from the Early Upper Paleolithic come from populations that were probably living in the fairly cold climates of Oxygen Isotope Stage (OIS) 3 for about 10,000 to

TABLE 3. ESTIMATED DIFFERENCES IN THE DAILY ENERGETIC COST OF FORAGING DUE TO DIFFERENCES IN BODY MASS AND LOWER LIMB LENGTH[a]

	Early Upper Paleolithic	Late Upper Paleolithic	Mesolithic
Neandertals	−215	−188	−234
Early Upper Paleolithic	*	+27	−19
Late Upper Paleolithic	*	*	−46

[a] Estimates in kCal day^{-1}; − indicates that the group at the top of the column has a lower cost than the group at the left of the row; + indicates the opposite.

15,000 years. The climate was probably not as cold as it was during OIS 4, OIS 6, and earlier cold periods that shaped Neandertal morphology, but it still seems somewhat peculiar that Early Upper Paleolithic body proportions show no evidence of adaptation to cold climates. Human populations living in the warmer parts of the Americas, who are fully modern in their ability to culturally buffer themselves from the environment, have had a similar amount of time to change their body proportions from the cold-adapted proportions of their ancestors to more warm-adapted proportions. There does appear to have been climatic adaptation in body weight and proportions, as measured by sitting height, in the time since the peopling of the Americas.[45,46] However, it is also true that some Native American groups living in warm climates retain fairly cold-adapted body proportions.[7,47] This suggests either that selection was weaker in New World environments or that some aspects of body form are evolutionarily conservative and have not had enough time to change.

Even though body proportions appear to change fairly slowly in Europe, on present evidence Holliday's[6] purely climatic explanation for differences in body proportions between Neandertals and their Upper Paleolithic successors and changes in body proportions during the Upper Paleolithic and into the Mesolithic cannot be rejected. However, we would like to conclude with an alternative explanation that may better account for the energetic costs for mobility of differences in body proportions. Differences between Neandertals and Upper Paleolithic humans in body proportions initially originated with climatic adaptation and the migration of Upper Paleolithic humans from warmer climates into Europe. Once Upper Paleolithic humans migrated to colder climates, there would have been selection against their elongated lower limbs. However, this climatic selection may have been mitigated by weaker but still consequential selection for energetic efficiency in mobile foraging. If later Europeans became less mobile, locomotor costs would have become a smaller fraction of the total daily energy expenditure, reducing selection for energetic efficiency in foraging. Further quantitative modeling of selection pressures may provide a means of distinguishing between these two alternatives.

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