Independent roles of climate and life history in hunter-gatherer anthropometric variation

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Citation

Abstract
We investigated the role of two competing ecological pressures (climate and life history) in hunter-gatherer anthropometrics. Data on weight and stature were compiled for 47 male and 37 female populations. Additional measurements (relative sitting height, BMI, and surface-to-mass ratio) were also compiled or calculated. Body size and shape correlate with temperature as predicted by Bergmann's and Allen's rules, but we found that effective temperature is a better predictor of size than the commonly used mean average temperature. We also found that while life expectancy demonstrates a significant correlation with size, it does not correlate with body shape. Life expectancy retains its significant association with body size after controlling for latitude, suggesting that latitude and mortality levels have independent effects on body size. We conclude that patterns of variation in hunter-gatherer anthropometrics have been influenced by at least two distinct selection pressures: climate and life history.

INTRODUCTION
Ecological variability is a key force behind human adaptation and diversity. Climate in particular is believed to account for many aspects of variation among human populations. However, climate does not act alone to determine human adaptation. The effect of external environment on human variation can also be attributed to one of its most powerful but least discussed aspects, namely the determination of disease prevalence mortality rates, and their consequences for growth, development and life-history. In the following, we assess the relative importance of climate variation and mortality on current diversity in body size and shape among hunter-gatherers.

CLIMATE AND HUMAN ADAPTATION
For the majority of organisms, external temperature is the most influential climatic pressure. Our bodies need to establish a thermal equilibrium between internal and external environments, and consequently thermoregulatory mechanisms have evolved. A key determinant to thermoregulatory mechanisms in animals is the amount of surface area available for heat radiation. In cold climates, species and populations tend to exhibit a decreased amount of surface area per unit of body mass by which heat could escape. Conversely, hot external environment is associated with increases in surface area per unit mass in order to facilitate heat exchange. Based on this principle, two hypotheses were formulated to predict how morphology should respond to temperature. Bergmann suggested that within warm-blooded species or populations, body size should increase according to a decrease in external temperature, since tall, linear builds create a higher surface-to-mass ratio compared to the frame of a short and stocky individual. Allen's rule, on the other hand proposes that warm-blooded species should exhibit reduced limbs and other bodily extremities at lower temperatures, in order to reduce the ratio of surface area to mass and therefore heat loss. Thus, the rules are complementary in predicting changes in body size (Bergmann) and body shape (Allen) as two different ways of modulating the surface-to-mass ratio according to external temperature.

Two key studies have significantly developed our understanding of morphological diversity as a response to climatic variation. Roberts, by correlating average stature and weight of 116 male and 33 female population samples with mean annual temperature of their respective regions, detected a significant negative relationship between body mass and environmental temperature as predicted by Bergmann's rule. Additionally, Roberts found that the impact of temperature on body mass was independent of stature. The second study was carried out by Katzmarzyk and Leonard. By adding more samples and new
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anthropometric variables, they found significant correlations not only between temperature and body size, but also between temperature and body shape. In both men and women, weight, BMI (body mass index) and relative sitting height were found to correlate negatively with mean annual temperature, whereas the surface-to-mass ratio correlated positively with environmental temperature. This seemed to confirm that populations in cold climates are on average larger, minimise surface-to-mass ratios, and have relatively shorter legs. However, Katzmarzyk and Leonard also found that each anthropometric measurement correlated less strongly with mean annual temperature than previously estimated by Roberts, suggesting that there must be factors other than climate possibly exerting influence on human body size and shape. We discuss in the following another factor potentially determining variation in human body size, namely the expected risk of death faced by individuals.

DISEASE AND MORTALITY

Environmental pressures also restrict the health status and life expectancy in small-scale societies through an array of pathogenic constraints. The vulnerability of hunter-gatherers to infection stems from a variety of both lifestyle and environmental factors that allow pathogens to not only establish themselves quickly, but to also spread efficiently. The hot and humid environment of certain tropical areas, for example, is highly conducive to the development and life cycle of several pathogens and intestinal parasites. At the other end of the climatic spectrum, populations inhabiting Polar regions are likely to come into contact with wild animals, including mammals and fish, and are exposed to a range of zoonotic infections such as hydatid disease.

In addition to short-term effects on health and growth of individuals, disease prevalence and mortality rates have been also linked to long-term, adaptive changes. Zoologists have been drawing their attention to the importance of mortality rates and life expectancy as variables explaining adaptive differences among species, and more recently this view has been introduced into anthropological studies. According to Life History Theory, high mortality rates have the effect of reducing expected longevity and reproductive spans in populations. In the long run, this would favour selection for early reproduction, as a way of minimising the chance of reproduction before death. But since the beginning of reproduction as a rule tends to determine growth termination in mammals, the theory also implies that mortality rates indirectly define adult body size. Applied to humans, this view implies that variation in body size ranging from Pygmies to tall African Pastoralists such as the Hadza from Tanzania would reflect differences not in external temperature, but in externally imposed mortality rates experienced in their respective environments: high mortality would imply small size, whereas low mortality would imply larger body size.

Although mortality risk seems to be an additional selection pressure possibly conflicting with those of climatic constraints, no study has compared the contribution of the two factors. Furthermore, the effect of mortality rates on body shape remains unexplored. This study has addressed two key ecological pressures – climate, and mortality rates – as mechanisms to explain the variation observed in hunter-gatherer anthropometrics. This study will test the effects of mortality rates on body size and shape of hunter-gatherers in comparison with climate.

MATERIALS AND METHODS

Sampled populations. Data on hunter-gatherer populations have been continuously utilized in the study of human evolution due to the presumed similarities between their lifestyle and our ancestors; it is argued that as a species we have lived by a hunter-gatherer subsistence for 99% of our evolutionary past. Furthermore, they present a particular advantage when studying behavioural implications on anthropometrics due to their lack of nutritional diseases observed in populations that moved into agriculture. Populations were also selected for their geographical location, to ensure a broad spectrum of data, both anthropometrically and climatically. Ultimately, as many populations as possible have been included in this study to ensure a more detailed analysis. Maps with locations of the samples populations are shown in figures 1 to 6.

Figure 1

Figure 1: Locations of Arctic and sub-Arctic population samples.
Anthropometrics. Data were obtained for a total of 41 hunter-gatherer populations, of which there are 10 Arctic, 3 South American, 3 North American, 7 African, 8 South Asian, 6 Australian, and 4 Pacific Island populations. A full list of references with the sources of data for each of the populations included in the study can be provided by the authors on request. Mean population values of stature,
weight and sitting height were compiled from the literature, and from those three other anthropometric variables were calculated. Body mass index or BMI (mass/stature²) measures the distribution of weight per unit of stature, providing an estimate of shape and a tool for testing Allen’s rule. The second derived measurement was relative sitting height (RSH), or the ratio of sitting height to stature. Finally, the surface-to-mass ratio was estimated using the surface area equation proposed by Dubois and Dubois, as recommended by Houghton, namely

\[ SA = 0.00718 \times \text{mass}^{0.425} \times \text{stature}^{0.725} \]

Climate. Mean annual temperature (MAT) data were supplied by Binford and climatic atlases. A second estimation of temperature is effective temperature (ET). Devised by Bailey to provide an estimation of an area’s “ambient warmth”, or the amount of solar energy available in a given location, it was first introduced into anthropological literature by Binford. ET is calculated from a formula combining the mean temperatures (°C) of the warmest (MWM) and coldest (MCM) months of the year:

\[ ET = \frac{[(18 \times \text{MWM}) - (10 \times \text{MCM})]}{(\text{MWM} - \text{MCM})} + 8 \]

Also included in this study are measurements of latitude (°N/°S) obtained from online world atlases. Our analyses did not differentiate between northern and southern latitudes since they reflect the same distance to the equator and are supposed to reflect approximately similar temperatures and climatic conditions.

Mortality rates. A separate analysis was carried out a group of twelve (one male and eleven female) population samples, chosen for the availability of data on life expectancy at age 15 (utilized in this study as a proxy for mortality rates). Data for this analysis were taken from Walker et al.

RESULTS

Temperature and Body Size. Bergmann’s rule suggests that the relationship between temperature and body size should be negative. To test this, bivariate correlations were carried out between mean annual temperature and environmental temperature and the dependent variables of stature and weight (Table 1).

<table>
<thead>
<tr>
<th></th>
<th>MAT</th>
<th>ET</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stature</td>
<td>( r = -0.149 ) (( p &lt; 0.05, n = 76 ))</td>
<td>( r = -0.359 ) (( p &lt; 0.001, n = 79 ))</td>
</tr>
<tr>
<td>Weight</td>
<td>( r = -0.462 ) (( p &lt; 0.001, n = 65 ))</td>
<td>( r = -0.705 ) (( p &lt; 0.001, n = 59 ))</td>
</tr>
</tbody>
</table>

Overall, size showed significant negative correlations with the temperature variables (ET in special), although stature demonstrated a weaker association. Out of all the temperature variables, ET was revealed to have the most effect on body size (Figure 7). There was no difference in significance level of correlations when analyses were done separately for males and females (data not shown).

Temperature and Body Shape. In order to test Allen’s rule, which dictates that body extremities should be relatively reduced according to a decrease in temperature, body shape variables (relative sitting height, BMI and surface-to-mass ratio) were correlated with temperature variables.
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Figure 10
Table 2: Bivariate correlations of temperature and body shape, combined sexes.

<table>
<thead>
<tr>
<th></th>
<th>MAT</th>
<th>ET</th>
</tr>
</thead>
<tbody>
<tr>
<td>RSH</td>
<td>$r = 0.767 (P&lt;0.01, n=16)$</td>
<td>$r = 0.781 (P&lt;0.01, n=16)$</td>
</tr>
<tr>
<td>BMI</td>
<td>$r = 0.541 (P&lt;0.01, n=65)$</td>
<td>$r = 0.683 (P&lt;0.01, n=59)$</td>
</tr>
<tr>
<td>SA/Mass</td>
<td>$r = 0.502 (P&lt;0.01, n=65)$</td>
<td>$r = 0.674 (P&lt;0.01, n=59)$</td>
</tr>
</tbody>
</table>

Overall, body shape demonstrated a notably stronger association with temperature than body size. RSH in special was affected by environmental temperature, as shown by the higher values of $r$ (Figure 8). As expected, RSH and BMI were found to correlate negatively with temperature, whereas surface-to-mass ratio exhibited a positive relationship. Analyses carried out for males produce similar results; in the case of females, the relationship between temperature and RSH was rendered non-significant, most likely due to the highly reduced sample size ($n=5$).

Figure 11
Figure 9: Plot of effective temperature versus relative sitting height, combined sexes ($n=16$).

Latitude and Temperature Variation. Co-ordinates of latitude were used to measure their association with temperature variables (Table 3).

Figure 12
Table 3: Bivariate correlations of climate and biogeography.

<table>
<thead>
<tr>
<th></th>
<th>Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAT</td>
<td>$r = 0.951 (P&lt;0.01, n=76)$</td>
</tr>
<tr>
<td>ET</td>
<td>$r = 0.940 (P&lt;0.01, n=70)$</td>
</tr>
</tbody>
</table>

Overall, latitude was found to correlate extremely highly with climate – both the linear associations and significance levels for these relationships were considerably strong. Ultimately, the results show that latitude is an efficient proxy for climate and temperature in special.

Biogeography and Body Size. Given the strong association between latitude and temperature, it should be expected that body size would correlate with latitude too (Table 4).

Figure 13
Table 4: Bivariate correlations of body size and latitude, combined sexes.

<table>
<thead>
<tr>
<th></th>
<th>Latitude</th>
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</thead>
<tbody>
<tr>
<td>Stature</td>
<td>$r = 0.278 (P&lt;0.05, n=76)$</td>
</tr>
<tr>
<td>Weight</td>
<td>$r = 0.574 (P&lt;0.01, n=65)$</td>
</tr>
</tbody>
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As predicted, there were significantly positive correlations found between body size and latitude. Weight was more affected by latitude than stature (Figure 9). Very similar results are obtained when males and females are analysed separately (data not shown).
Biogeography and Body Shape. Overall, body shape was more affected by latitude than body size, with RSH demonstrating an especially strong correlation (Table 5 and Figure 10). In the analyses by sex, the only change is that the correlation between latitude and RSH in females is no longer significant, most likely due to the reduced sample (n=5).

Figure 15
Table 5: Bivariate correlation of body shape and latitude, combined sexes.

<table>
<thead>
<tr>
<th></th>
<th>Latitude</th>
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</thead>
<tbody>
<tr>
<td>RSH</td>
<td>$r=0.771$ ($P&lt;0.01$, $n=16$)</td>
</tr>
<tr>
<td>BMI</td>
<td>$r=0.592$ ($P&lt;0.01$, $n=65$)</td>
</tr>
<tr>
<td>SA/Mass</td>
<td>$r=-0.581$ ($P&lt;0.01$, $n=65$)</td>
</tr>
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</table>

Furthermore, partial correlation was performed in order to separate the effects of latitude and temperature. While the correlation between latitude and the five anthropometric variables (weight, stature, RSH, SA/Mass ratio and BMI) remains significant after controlling for either temperature variable (MAT and ET), controlling for latitude negates all significant associations with one exception (MAT and body weight: partial $r=0.296$, $P<0.05$, $n=62$). Similar results applied when each sex was analysed (data not shown). Overall, the results show that latitude has the dominating effect on the body size and shape of individuals, since controlling for it negates almost all significant association between anthropometry and temperature.

Effects of Mortality Rates on Body Size and Shape. Based on the reduced sample for which mortality data were available, bivariate correlations were carried out between anthropometric variables found to have the most significant relationships with temperature (weight, BMI and SA/Mass) and life expectancy at age 15 (Table 6). RSH was omitted from the following analyses due to the unavailability of data within the reduced sample.
Interestingly, results showed that life expectancy correlated only with body size; no significant relationships were detected with body shape. Figure 11 illustrates the linear relationship between body size and life expectancy.

### DISCUSSION

The current study has found, in agreement with previous studies by Roberts and Katzmarzyk and Leonard, that human morphology varies according to temperature variability. Bergmann and Allen rules, which have been used as foundations for the analysis in previous study, are still valid predictions in so far as a sample of populations ranging from equatorial to polar is considered. Body weight in both sexes was found to be more affected by temperature than stature. Whereas previous studies focused exclusively on the effects of mean annual temperature on body weight, we showed that effective temperature was found to be the most influential. Since effective temperature (ET) provides an estimation of the solar energy within a given area, this suggests that weight is more affected by the level of local solar radiation than simply an average measurement of annual temperature.

One of our findings is that body shape is more affected by temperature than body size in both males and females. As predicted, as temperature of each region decreased, relative sitting height (RSH) increased indicating a shortening of the lower limbs, body mass index (BMI) increased indicating a higher ratio of mass to stature, and surface-to-mass ratio (SA/Mass) decreased illustrating a decreased amount of surface area available for each unit of body mass. A possible explanation for the stronger association between temperature and body shape could be taken from Schreider’s notion that the ratio of surface-to-mass is a more appropriate measurement of an individual’s thermoregulatory capabilities than absolute body size.

As expected, latitude exhibited extremely strong negative correlations with the two temperature variables, providing an correlation is even higher than the bivariate correlation. In this reduced sample, latitude does not show significant relationships with size and shape, which may also be explained by the fact that the samples are mostly tropical with latitudes ranging from 3.82° S (the Hadza from Tanzania) to 25.7° S (the Ache from Paraguay). However, if we use our larger sample (n=49) of tropical populations (living in areas below 30° latitude), there is still no significant correlation between latitude and either body mass (r=0.270, P= 0.056), BMI (r=0.071, P= 0.620), or SA/Mass (r=-0.163, P=0.253). Conclusively, to understand the anthropometric variation among hunter-gatherers, factors such as mortality risk in addition to temperature and climate must be taken into account.
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acutely sensitive proxy for climatic variability. The fact that latitude has an unequivocal control over the direct and indirect effects of climate supports previous suggestions that biogeography is a significant ecological constraint to human populations. When analysed with latitude, both body size and shape were highly affected. As expected, populations inhabiting higher latitudes were found to have a larger body size, but the effects of latitude were considerably more pronounced for body shape. The results substantiate Terrell’s claim that biogeography is an essential component to our evolution anthropometric variation of hunter-gatherers.

One of the most significant findings of the current study is that life expectancy, reflecting mortality rates, has no significant correlation with body shape, although we confirmed the previous finding of Migliano and Walker et al. that life expectancy has a significant effect on body size and growth. This suggests that body size and shape of small-scale populations are under different selection pressures. Overall, results indicate that body shape may have evolved under the selective pressures of climatic variability, while body size seems to be mostly subject to the selective pressures of life history and mortality rates.

Ultimately, to understand the global variation of hunter-gatherer groups, factors other than climate need to be considered. Such suggestions have already been put forward by previous studies. Katzmarzyk and Leonard, for example, found that the secular trends over the past fifty years have had a substantial effect on global anthropometric variation, especially within the tropics where they found regression slopes to be far weaker than those published originally by Roberts. Whereas Katzmarzyk and Leonard concluded that these trends most likely reflected the impact of acculturation and lifestyle change in hunter-gatherer populations, the current study proposes that life history constraints in the long run have also influenced hunter-gatherer anthropometric variation.

References


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