

Developmental Variation in Ecogeographic Body Proportions

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ABSTRACT While ecogeographic variation in adult human body proportions has been extensively explored, relatively less attention has been paid to the effect of Bergmann's and Allen's rules on human body shape during growth. The relationship between climate and immature body form is particularly important, as immature mortality is high, mechanisms of thermoregulation differ between young and mature humans, and immature body proportions fluctuate due to basic parameters of growth. This study explores changes in immature ecogeographic body proportions via analyses of anthropometric data from children included in Eveleth and Tanner's (1976) *Worldwide Variation in Human Growth*, as well as limb proportion measurements in eight different skeletal samples.

Moderate to strong correlations exist between climatic data and immature stature, weight, BMI, and bi-iliac

breadth; these relationships are as strong, if not stronger, in immature individuals as they are in adults. Correlations between climate and trunk height relative to stature are weak or nonexistent. Altitude also has significant effects on immature body form, with children from higher altitudes displaying smaller statures and lower body weights. Brachial and crural indices remain constant over the course of growth and display consistent, moderate correlations with latitude across ontogeny that are just as high as those detected in adults. The results of this study suggest that while some features of immature body form, such as bi-iliac breadth and intralimb indices, are strongly dictated by ecogeographic principles, other characteristics of immature body proportions are influenced by intrinsic and extrinsic factors such as nutrition and basic constraints of growth. *Am J Phys Anthropol* 148:557–570, 2012. © 2012 Wiley Periodicals, Inc.

A wide body of research has successfully explored the application of Bergmann's rule (1847) and Allen's rule (1877) to ecogeographic variation in human body proportions (Heirnaux and Froment, 1976; Trinkaus, 1981; Ruff, 1991, 1994, 2002; Holliday and Trinkaus, 1991; Holliday and Falsetti, 1995; Holliday 1997a,b, 1999, 2002; Katzmarzyk and Leonard, 1998; Pearson, 2000; Holliday and Ruff, 2001; Weinstein, 2005; Auerbach, 2007, 2010, unpublished data; Temple et al., 2008; Leonard and Katzmarzyk, 2010; Temple and Matsumura, 2011). In general, variation in human body proportions is congruent with the predictions of these rules: populations from high latitudes frequently display relatively wide bodies, high body masses for stature, short limbs relative to trunk length, and foreshortened distal extremities, whereas populations from low latitudes have relatively narrow bodies, low body masses in relation to stature, long limbs, and long distal limb extremities. This documented variation in adult human form is likely produced by selection for minimized surface area relative to volume for heat retention in cold climates and maximized surface area to volume for heat dispersal in warm climates.

With a few exceptions (Ruff et al., 2002; Ruff, 2007; Cowgill, 2008, 2010; Temple et al., 2011), however, little work has been conducted on variation in ecogeographic body proportions in immature populations. Clinal variation in adult morphology has been used to implicate selective pressures originating from climatic factors. The youngest individuals in a population may experience the

same climate-derived pressures, particularly in societies where cultural buffering is minimal and infant and childhood mortality is high. Moreover, infants appear to be sensitive to temperature fluctuations that would be comfortable for older individuals, and deaths in infancy and early childhood have frequently been attributed to exposure to extreme temperatures, even in climates that typically do not stress healthy adults (Mann and Elliott, 1957; Bower et al., 1960; Danks et al., 1962; Silverman and Agate, 1964; Cohen, 1977; Christensson et al., 1988,

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TABLE 1. Reported differences in immature relative to mature thermoregulation

Difference	Effect on thermoregulation
Heat stress	
Higher surface area to mass ratio	Greater heat loss in mild and cold environments, and possibly greater heat gain in very high heat
Lower sweating rate	Less heat lost via evaporative cooling in hot climates
Well-developed vasodilation	Effective shunting of blood from periphery to core, higher skin temps in heat stress
Lower blood volume and maximum cardiac output	Possible cardiac instability while active in heat stress
Smaller sweat glands	Lower sweating output
Lower sweat gland sensitivity	Higher sweating threshold
Greater oxygen cost of locomotion	Greater metabolic heat production during exercise
Cold stress	
Metabolically active deposits of brown fat in infants	Large increases in metabolic rate in infants in response to cold-stress (non-shivering thermogenesis)
Small body mass	More rapid cooling
Inability to shiver	Lack of heat generation through muscular activity
Limited subcutaneous fat	Relative lack of insulation

Adapted from Little and Hochner, 1974; Thomas, 1994; Falk, 1998.

1995; Kleemann et al., 1996; Dragovich et al., 1997; Adcock et al., 2000).

In addition, it has long been recognized that allometric changes in body proportions occur over the course of growth (Bogin, 1997). The human head is very large at birth, approximating 25% of body weight, and eventually decreases to only 7 to 8% of body weight (Jackson, 1928). In general, a superior-inferior gradient exists, with the human head reaching adult proportions first, followed by the torso, and lastly, the lower limb (Tanner, 1962), following a broader developmental pattern established in utero (Schoenwolf et al., 2009). After birth, however, the lower limb grows faster, shows greater relative growth, and attains peak growth velocities earlier than the upper limb (Johnston, 1962; Buschang, 1982; Jungers et al., 1988; Bareggi et al., 1996; Smith and Buschang, 2005). Lastly, distal limb segments grow relatively faster than proximal limb segments during the fetal period and adolescence (Robertson, 1955; Cameron et al., 1982). Given these evident proportional shifts, differences between the upper and lower limb, and changes over the course of growth, it is unclear when ecogeographic proportions are established and whether these are maintained throughout human ontogeny.

Physiology of thermoregulation in immature individuals

Adaptation to climate via body proportions in immature individuals is particularly important given that thermoregulatory systems in immature humans are different than those of adults. Table 1 summarizes suggested differences between immature and adult thermoregulation. Infant physiology in particular seems especially susceptible to cold stress, which is supported by studies implicating hypothermia as a leading cause of infant mortality in non-industrialized nations (Bruck, 1961; Little and Hochner, 1973; Thomas, 1994; Asakura, 2004; Braumgert, 2008; Mance, 2008). Researchers attribute this to several factors, including an underdeveloped muscular system that makes sustained metabolic increase through shivering impossible in young infants, and thus eliminates one of the major mechanisms of adult heat generation (Little and Hochner, 1973; Hack-

man, 2000; Asakura, 2004). In addition, while subcutaneous fat thickness increases rapidly during the first year of life, the fat layer of very young infants remains too thin to adequately insulate against cold (Bruck, 1961; Little and Hochner, 1973). Lastly, the surface area to volume ratio in infants can be twice that of adults in the same population due to their small body size (Smolander et al., 1992). These differences in body proportions, particularly when combined with a relatively large head, promote rapid heat loss during cold exposure in immature humans.

Conversely, a variety of thermoregulatory responses, some of which differ from those of adults, appear to compensate for the shortcomings noted above (Pawlowski, 1998). Well-developed vasoconstriction in infants restricts blood flow to the infant's periphery (extremities) and redirects it toward the core (trunk), which compliments voluntary muscle activity and changes in body posture that act to generate more heat (Himms-Hagen, 1995; Hackman, 2000; Baumgart, 2008). Most importantly, however, is the increased metabolic rate of infants, which can be elevated over adult levels by twofold or more (Bruck, 1961; Asakura, 2004; Baumgart, 2008). This increased metabolic rate is generated through nonshivering thermogenesis via the activation of metabolically active brown fat stores (Christensson et al., 1988; Hackman, 2000; Asakura, 2004). Nonetheless, it remains unclear if the various mechanisms of retaining and dispersing heat in infants interact to maintain temperature homeostasis as effectively as in adults.

In older children, most research has focused on heat tolerance, particularly while exercising (Gullestad, 1975; Drinkwater et al., 1977; Drinkwater and Horvath, 1979; Docherty et al., 1986; Davies, 1981; Delamarche et al., 1990; Falk et al., 1991, 1992; Meyer et al., 1992; Smolander et al., 1992; Armstrong and Maresh, 1995; Tsuzuki-Hayakawa et al., 1995; Shibaskai et al., 1997; Bar-Or, 1998; Falk, 1998; Inbar et al., 2004; Rivera-Brown et al., 2006; Falk and Dotan, 2008; Rowland et al., 2008). Many authors have noted that children do not perform as well while exercising in the heat as adults do, which has been linked to a number of factors (but see Rivera-Brown et al., 2006; Rowland, 2008; Rowland et al., 2008 for contrary evidence). The very high surface area to volume ratio in immature individuals

leads to effective heat loss in moderate temperatures, but several authors have suggested that, when ambient temperature is higher than body temperature, greater heat gain via radiation and convection from the environment can result (Docherty et al., 1986; Armstrong and Maresh, 1995; Inoue et al., 2004). In addition, lower heat tolerance may in part be explained by sweat glands in juveniles that are smaller and produce a lower quantity of sweat per gland, resulting in an overall lower sweating rate despite slightly higher densities of glands when compared with adults (Davies, 1981; Delamarche et al., 1990; Falk et al., 1992; Meyer et al., 1992; Armstrong and Maresh, 1995; Bar-Or, 1998; Inbar et al., 2004). Lastly, children do vasodilate quite effectively, possibly to compensate for their lower sweating rate, and display higher skin temperature due to vasodilation during exercise. This physiological response, though, may contribute to lower tolerance while exposed to heat during exercise, as large shifts in blood flow from the core to the periphery result in circulatory instability (Davies, 1981; Delamarche et al., 1990; Armstrong and Maresh, 1995; Tsuzuki-Hayakawa et al., 1995; Falk, 1998; Inoue et al., 2004).

The preponderance of physiological evidence, then, shows that immature individuals are more vulnerable to climatic extremes than adults, and that their thermoregulatory mechanisms are different from those of adults. An evaluation of ecogeographic body proportions across ontogeny could therefore augment current understanding of human climatic adaptation. Evolutionary processes will potentially act strongly on immature individuals, especially selecting against those individuals who cannot withstand extreme environmental pressures. Thus, morphological patterns in body proportions similar to those of adults should be present in immature individuals. However, it is unclear how ecogeographic variation in immature individuals interacts with allometric changes in body shape and maturity-related differences in thermoregulatory capacity.

Research questions

In comparative studies such as this one, the available data cannot conclusively assess whether selection has acted or is acting on the features in question. Instead, this research only evaluates the congruence of the observed data with expectations based on specific hypothesized selective pressures. Given this caveat, the research herein will investigate several questions using both anthropometric data from living children and skeletal data from archaeological samples by comparing the results to expected patterns: Does the body form of immature individuals relate to latitude and climatic variables in the same pattern as seen in adults? Is the strength of the relationship between body form and climate similar in both immature and mature individuals? Does this pattern fluctuate during ontogeny due to growth-related body form changes? If confounding effects resulting from differences in the physiology of thermoregulation, allometric changes through ontogeny, and other environmental factors (e.g., nutrition) are not systematically and significantly affecting immature individuals, body shape and proportions will match patterns predicted by ecogeographic models. Specifically, we expect:

- Weight, BMI, relative sitting height, and bi-iliac breadth will show positive correlations with latitude and temperature variables.

- Latitude and temperature will have no relationship with sitting height, leg length, and stature.
- Altitude should have low correlations with immature body proportions, outside of differences resulting from temperature variation (and assuming terrain is not a factor; see Higgins and Ruff, 2011).
- Intralimb indices will maintain a consistent relationship with latitude over the course of growth.

MATERIALS AND METHODS

Materials

In order to comprehensively explore the above research interests, two types of data were employed: anthropometric data from living individuals obtained from published literature, and skeletal data measured by two of the authors (LWC and DHT). Anthropometric data were taken from Eveleth and Tanner (1976) and supplemented with other published data. These were used to investigate variation in basic body proportions relative to latitude and climatic variables. Skeletal data obtained from immature individuals from archaeological assemblages were used to examine the general patterns of brachial and crural indices across ontogeny; these data are the most diverse set utilized to date for this purpose.

Anthropometric data. The anthropometric data set consists of previously published group means. The sample is comprised of 119 samples of immature male means and 116 samples of immature female means provided in Eveleth and Tanner (1976). These measurements were supplemented with data from immature Asian and African groups reported in the recent literature to account for a sampling bias toward European populations in Eveleth and Tanner, bringing the total sample to 153 male groups and 158 female groups. A sample of adult means (female $n = 46$; male $n = 46$) was assembled from Eveleth and Tanner (1976) in order to provide a standard against which the correlations between immature data and climatic variables could be compared. For this analysis, only Old World groups were utilized, as previous research in adults has indicated that Old World populations display the strongest and most consistent cline for ecogeographic body proportions (Ruff, 1994; Holliday, 1997a,b; Auerbach, 2007, unpublished data; Jantz et al., 2010). Not all ages were available in each data set collected from the published literature, therefore, group sample size varies by age. All anthropometric data (and references for the data sources other than Eveleth and Tanner, 1976) are available in an online Supporting Information Table.

Geographic location of each group was determined based on locations described in the original publications. The majority of group means included in this analysis were collected from individuals in a single city/locality. In instances where a single mean was provided for individuals from multiple closely associated cities, states, or regions, the midpoint of these areas was used to represent the group's location. Approximately 10% of the anthropometric data were collected from national studies of children. In order to reach a compromise between maximizing sample size and minimizing error, these data were only included if the country of origin did not exceed a latitude range of 10°. Groups lacking specific location information in the original publication were excluded from analysis.

TABLE 2. Skeletal sample description, immature sample size, date, latitude, and location

Sample	Original location	Approx. time period	Immature sample size	Adult sample size	Average latitude
California Amerindian	Northern California	500–4,600 BP	69	90	~ 39°N
Dart	Johannesburg, South Africa	20th century	72	21	26°S
Indian Knoll	Green River, Kentucky	4,143–6,415 BP	88	64	37°N
Kulubnarti	Batn el Hajar, Upper Nubia	Medieval	93	24	21°N
Luis Lopes	Lisbon, Portugal	20th century	42	30	39°N
Mistihalj	Montenegro	15th century	44	30	~ 43°N
Point Hope	Point Hope, Alaska	300–2,100 BP	49	78	68°N
Jomon	Honshu & Hokkaido Islands, Japan	2,300–4,000 BP	52	83	35.7°N

Eveleth and Tanner defined each yearly age group with integers set as midpoints (e.g., “3-year-olds” are individuals 2.50 to 3.49 years old), while some of the supplemental Asian and African sources utilized non-integer midpoints (e.g., “3-year-olds” are individuals 3.0–3.99 years old). To account for this discrepancy, data from these supplemental sources were linearly interpolated so that all age group means would coincide with ranges having integer midpoints. This method is identical to that used by Eveleth and Tanner when compiling data for their global sample. Here, linear interpolation involves the assumption that a linear relationship exists between anthropometric measurements and age. Since only means are provided in the literature, this assumption cannot be adequately tested. However, a linear relationship is plausible given the small age range over which interpolation occurred. In addition, we maintain that linear interpolation is necessary for the sake of consistency in defining age groups and that other, nonlinear interpolation methods would also make assumptions about the structure of the data.

Four anthropometric measurements from Eveleth and Tanner (1976) and the more current literature were included whenever possible: stature, weight, sitting height, and bi-iliac breadth. Three additional variables were then calculated from the original data. Leg length was estimated by subtracting sitting height from total stature in cases where both measurements were given from a single population. For two other variables, relative proportions were of interest. Sitting height relative to stature was calculated by creating a ratio of population means (sitting height/stature). Body mass index (BMI) was calculated as the sample mean of body mass in kilograms divided by stature in meters squared.

Clearly, there are several methodological drawbacks to working with previously published anthropometric means. First, there is little standardization of or control over how the original data were collected; therefore, measurement error is unknown. However, the anthropometric variables used are standard body size measurements, and we believe that the methods for measurement are unlikely to vary substantially. Second, because the data set lacks a way for calculating variance within sample groups, parametric statistics are inappropriate (see Statistical Analysis below). Third, we cannot determine whether variance detected is contributed by the numerator or denominator using means. Last, some assumptions about the data must be made in the course of analyses. For example, in order to explore relative sitting height, we created a ratio of two means. A ratio of two means approximates a mean of ratios from raw data only when all original data are normally distributed.

However, Eveleth and Tanner (1976) do present some data for relative sitting height. While we chose to use the

ratio data instead to maximize sample size, cases where the original data and our ratio data overlap provide an ideal opportunity to evaluate how well the ratios of means perform. For relative sitting height at age 12, data points overlap for 27 cases. There is no significant difference between the original data and the ratio of means data (paired *t*-test, $P = 0.153$), and there is an extremely high correlation between the two types of data ($r = 0.999$). Despite obvious theoretical limitations of using mean data, it seems that the data perform well in practice.

Skeletal data. To provide a comprehensive exploration of changes in body proportions over the course of growth, ontogenetic changes in brachial and crural indices were evaluated in eight immature skeletal samples ($n = 560$). The eight samples were selected to represent a broad range of geographic locations. In order to maximize the number of samples, New World samples were included in the skeletal component of this analysis. Samples of adults were included in order to approximate the developmental endpoint for these samples in a subset of analyses ($n = 419$). While detailed descriptions of these samples are published elsewhere (Cowgill, 2010; Temple et al., 2011), Table 2 includes samples sizes, sample locations and latitudes, and general time periods for each skeletal sample.

Age was estimated whenever possible on the basis of tooth development and emergence. Crown and root development, evaluated via lateral mandibular radiographs, was compared with the standards of Liversidge and Molleson (2004) for the deciduous and Smith (1991) for the permanent dentition. When no teeth were directly associated with the postcranial remains, chronological age was predicted from within-sample Least Squares regression of femoral, tibial, or humeral length on age for each of the comparative samples in order to maximize sample size (Cowgill, 2010). Six of the eight skeletal samples are from archaeological contexts, and thus of unknown sex, due to the difficulties in determining sex in immature remains.

Maximum diaphyseal lengths were recorded from all immature humeri, radii, femora, and tibiae to the nearest millimeter. Adult limbs were also measured according to standard osteological protocols and include the following bone length measurements: femoral maximum length, tibial maximum length, humeral maximum length, and radial maximum length. In order to remain consistent with the immature data, these whole bone length measurements were converted to maximum diaphyseal lengths using equations provided by Ruff (2007; p. 702). Brachial indices were calculated as radial length/humeral length $\times 100$. Crural indices were calculated as tibial length/femoral length $\times 100$.

TABLE 3. Immature and adult Spearman's rho correlation means, number of correlations significantly different from zero (one correlation for each year of life, ages 1–18, in males and females, totaling 36), and ranges (anthropometric data)

		Stature	Weight	Sitting height	Bi-iliac	Leg	Relative weight	Relative sitting height
Latitude	Mean	0.639	0.643	0.786	0.648	0.364	0.623	0.262
	Min	0.499	0.485	0.696	0.117	-0.286	0.403	-0.260
	Max	0.786	0.750	0.877	0.937	0.845	0.741	0.578
	Sig.	36	36	36	29	11	36	0
	♂ Adult	0.493*	0.522*	0.644*	0.310	0.360	0.417*	0.172
♀ Adult	0.572*	0.485*	0.569*	0.113	0.463	0.452*	0.392	
Annual temp	Mean	-0.539	-0.551	-0.640	-0.608	-0.380	-0.537	-0.170
	Min	-0.674	-0.687	-0.736	-0.916	-0.679	-0.676	-0.826
	Max	-0.357	-0.358	-0.508	-0.133	0.717	-0.264	0.243
	Sig.	36	36	36	29	17	35	0
	♂ Adult	-0.440*	-0.564*	-0.391	-0.247	-0.244	-0.518*	-0.103
♀ Adult	-0.546*	-0.452*	-0.501	-0.224	-0.564*	-0.455*	-0.112	
Hot temp	Mean	-0.470	-0.483	-0.542	-0.364	-0.564	-0.474	0.188
	Min	-0.639	-0.672	-0.769	-0.860	-0.782	-0.633	-0.557
	Max	-0.302	-0.391	-0.386	0.070	0.481	-0.368	0.519
	Sig.	36	36	36	9	28	36	2
	♂ Adult	-0.388*	-0.589*	-0.178	-0.103	-0.330	-0.622*	0.118
♀ Adult	-0.553*	-0.507*	-0.279	-0.303	-0.432	-0.528*	0.135	
Cold temp	Mean	-0.453	-0.464	-0.694	-0.613	-0.440	-0.454	-0.189
	Min	-0.606	-0.615	-0.844	-0.893	-0.676	-0.608	-0.614
	Max	-0.125	-0.120	-0.591	-0.176	0.279	-0.035	0.425
	Sig.	33	32	33	29	20	31	2
	♂ Adult	-0.470*	-0.404*	-0.533	-0.286*	-0.252	-0.279	-0.186
♀ Adult	-0.472*	-0.313	-0.557	-0.147*	-0.348	-0.302	-0.399	
Altitude	Mean	-0.242	-0.275	-0.356	-0.231	0.069	-0.280	-0.284
	Min	-0.401	-0.450	-0.576	-0.679	-0.252	-0.467	-0.569
	Max	-0.001	-0.034	-0.051	0.567	0.444	-0.086	0.308
	Sig.	21	24	15	10	0	24	6
	♂ Adult	-0.247	-0.446*	-0.145	-0.422	-0.209	-0.390*	0.071
♀ Adult	-0.291	-0.343*	-0.049	0.070	-0.093	-0.336*	0.106	

* Significant correlations ($P < 0.05$).

METHODS

Latitude and climatic correlations

Latitude was calculated for each sample population based on the description of the location in the original publication. In addition to latitude, several temperature variables (mean annual temperature, coldest month average temperature, and warmest month average temperature) and altitude were included in the data set. Temperature variables were obtained from the Global Historical Climatology Network (GHCN) version 2 (available at: http://iridl.ldeo.columbia.edu/maproom/Global/World_Bank/Climate_Variability/). Data were taken from the weather station closest to the location where the anthropometric data was collected. Data collected after 1990 were not included in calculations of temperature variables due to the recent and unprecedented rise in global temperatures. Altitude was calculated using Google Earth (available at: <http://www.google.com/earth/index.html>).

Statistical analysis

In the analyses of the anthropometric data, sexes were considered separately, as previous research has demonstrated sexual dimorphism in some proportions among adults (Holliday, 1999). In order to evaluate changes in the pattern and the strength of the relationship between anthropometric variables and climate, Spearman's rank correlation coefficients were generated between measurement means and climatic variables for each year of age. Fisher's z-transformations were used to construct 95%

confidence intervals for the correlation coefficients. Confidence intervals that did not include zero were considered significant, and those that did not overlap between ages were considered evidence of statistically significant differences between age groups. For ease of communicating general trends across numerous correlation coefficients, correlation coefficients are categorized as “weak” (0.10–0.29), “moderate” (0.30–0.49), or “strong” (0.50–1.0), following Cohen (1988). Multiple comparison corrections were not used in favor of evaluating consistent trends across ages (see Cowgill, 2010 for a more detailed discussion of this issue).

In the skeletal data, brachial and crural indices were evaluated to determine their pattern of change during growth, age-specific differences among samples, correlations with latitude, and their similarity to or difference from adult indices. First, the pattern of change was explored by dividing the samples into three age groups: 0.0 to 2.9 years, 3.0 to 9.9 years, and 10.0 to 17.9 years. These age categories were sufficiently broad to allow statistical comparison, but narrow enough to retain biological meaning. Nonparametric Kruskal–Wallis and Mann–Whitney *U* statistics were used to determine if there were statistically significant changes within samples between age groups. Second, differences among samples were evaluated by using nonparametric comparisons of samples within the above age categories. Third, the relationship between intralimb indices and latitude was evaluated using Spearman's rank correlation coefficients, due to the violation of normal distribution assumptions associated with ratio data. The strength of the relationship between indices and latitude was compared in

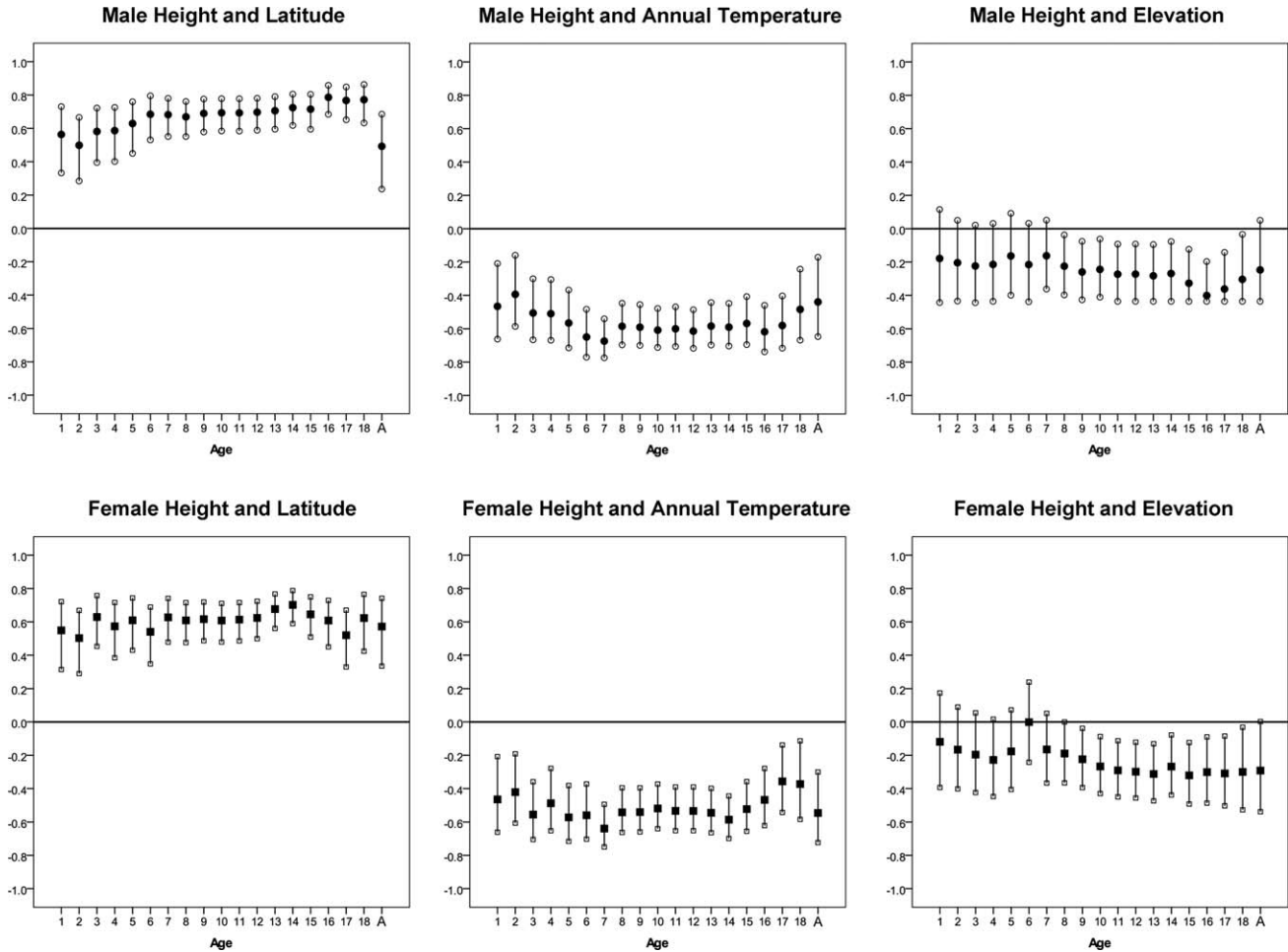


Fig. 1. Spearman's rank correlations coefficients and 95% confidence intervals for the relationship between stature and climatic variables (latitude, mean annual temperature, and elevation) using anthropometric data. Males represented by squares and females by circles.

immature individuals and adults by using Fisher's z -transformations to construct confidence intervals for the correlation coefficients.

RESULTS

Anthropometric data

Correlation coefficient means, ranges, and number of correlations that reached significance are presented for both immature and adult data in Table 3. Stature, weight, sitting height, and BMI show moderate to strong positive correlations with latitude, moderate negative correlations with temperature variables, and weak negative correlations with altitude during ontogeny (see Figs. 1 and 2 for stature and weight). The strength of these correlations fluctuates little during growth and is similar in magnitude to those of adults. In general, correlations of stature, weight, sitting height, and BMI with latitude and temperature variables were significant, while relatively fewer of the yearly correlations with altitude were significantly different from zero.

Bi-iliac breadth shows similar strong positive correlations with latitude, strong negative correlations with annual and cold temperatures, and weak negative correlations with warm temperature and altitude during ontogeny

(Fig. 3). Unlike stature, weight, and sitting height, the strength of these correlations is more variable during growth than in adulthood, and they are often strongest early in development. Yearly correlations between bi-iliac breadth and latitude, annual temperature, and cold temperature are generally significant; correlations of bi-iliac breadth with warm temperature and altitude are less likely to reach significance.

Absolute lower limb length shows weak to moderate positive correlations with latitude, weak to moderate negative correlations with temperature variables, and no correlation with altitude. Relative sitting height shows no consistent relationship with the environmental variables; however, weak negative correlations exist between altitude and relative sitting height (Fig. 4).

Skeletal data

Immature brachial and crural index means, sample sizes, and standard deviations are given in by age category in Table 4, with adult means for comparison, and graphically displayed in Figures 5 and 6. When nonparametric statistics are used to explore within-population sample differences, all age categories, including adults, show significant differences in both the brachial and crural index (Kruskal-Wallis, $P < 0.02$ in all analyses).

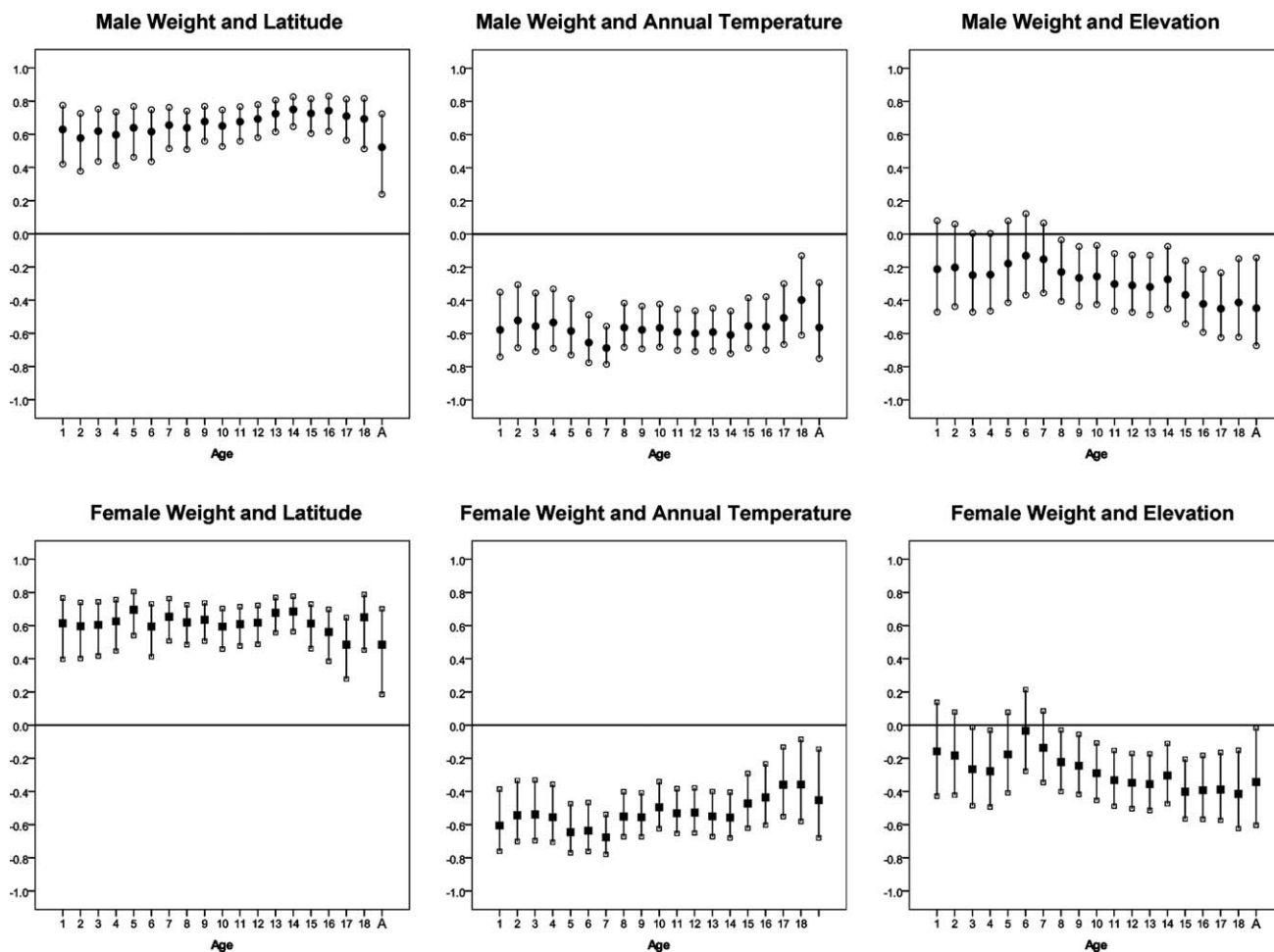


Fig. 2. Spearman's rank correlations coefficients and 95% confidence intervals for the relationship between weight and climatic variables (latitude, mean annual temperature, and elevation) using anthropometric data. Males represented by squares and females by circles.

Mann-Whitney U pairwise comparisons were used to indicate which samples were driving significant differences in each age category. Between birth and age 2.9, most significant differences are caused by low crural indices at Point Hope (which significantly differs from six out of seven samples); few pairwise differences are detected in the brachial index in this age category. Between age 3.0 and 9.9, pairwise differences highlight relatively high brachial index values among California Amerindians, Jomon, and Kulubnarti, and low brachial index values at Luis Lopes, Mistihalj, and Point Hope. Differences in crural indices in this age category show high values among California Amerindians, Dart, and Kulubnarti, with low values at Luis Lopes, Mistihalj, and Point Hope. Between 10.0 and age 17.9, most significant differences are again driven by low crural indices at Point Hope, while few differences exist in the brachial index. Analyses of adults confirm these general patterns, with Kulubnarti showing very high crural index values and Point Hope displaying relatively low values. With adult brachial indices, most of the differences among samples emphasize high versus low latitude divisions, with Point Hope, Luis Lopes, and Mistihalj being significantly different than other samples.

Analyses of changes across growth also reveal interesting patterns. Under the age of 18, three out of eight sam-

ples show statistically significant changes in brachial and crural index values during growth ($P < 0.05$; see Table 5). In all cases, this reflects high brachial and crural values in the earliest age categories (see Table 4). This trend is visually apparent in several additional samples, especially in the crural indices (Fig. 6), though it does not reach statistical significance among all of them. In addition, adult values are slightly higher than those of adolescents in the upper limb, and slightly lower in the lower limb.

Moderate negative correlations between latitude and intralimb indices exist among immature individuals throughout growth (immature brachial index: $\rho = -0.337$, CI: -0.416 to -0.253 ; immature crural index: $\rho = -0.430$, CI: -0.498 to -0.357). The strength of the relationship between intralimb indices and latitude in immature individuals differs only slightly from that of the adults (adult brachial index: $\rho = -0.578$, CI: -0.638 to -0.511 ; adult crural index: $\rho = -0.228$, CI: -0.317 to -0.135), with a stronger relationship between brachial indices and latitude in adults, and a stronger relationship between crural indices and latitude in immature individuals.

DISCUSSION

The strength and direction of the correlations between anthropometric and climatic variables remains strikingly

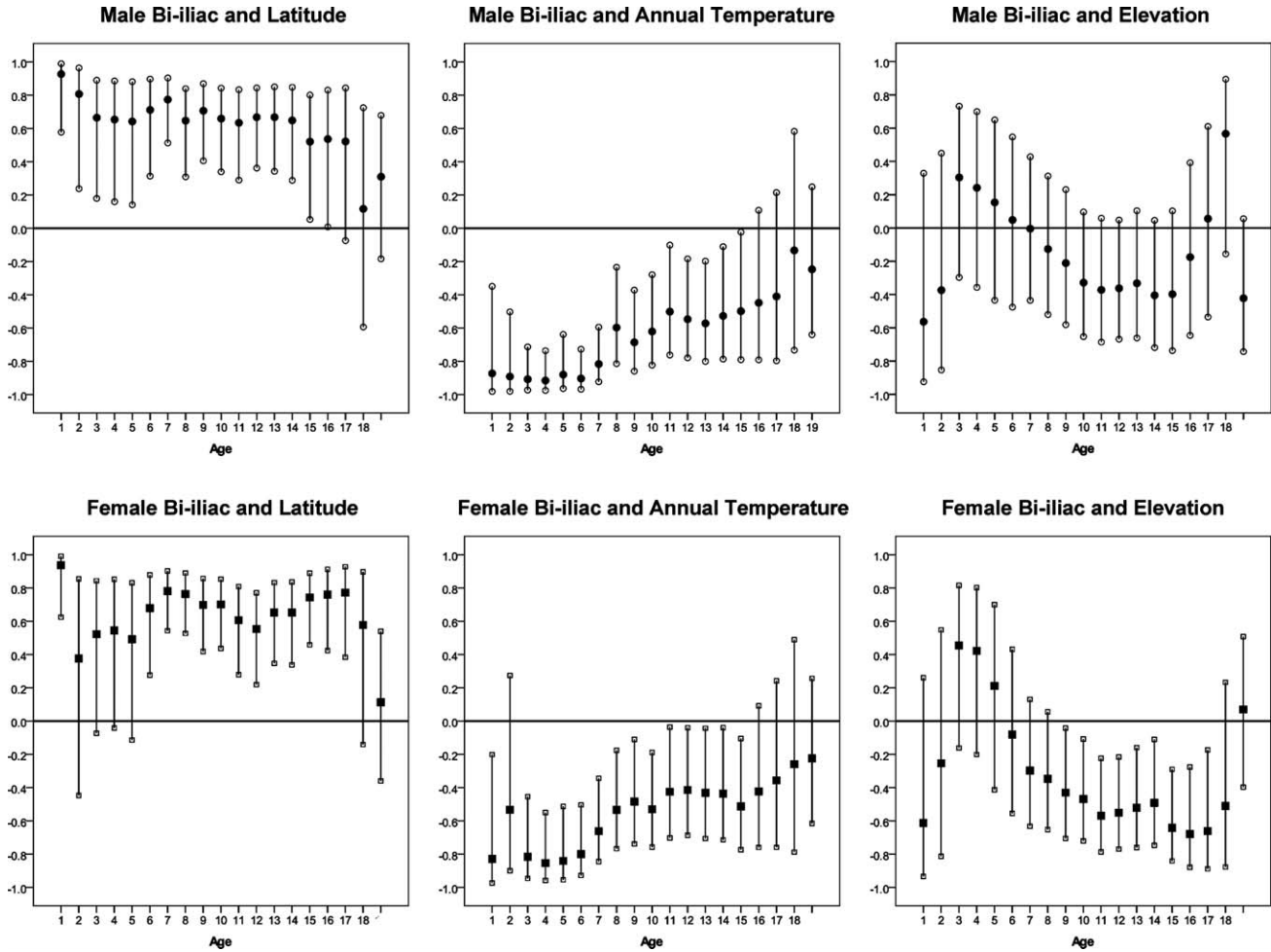


Fig. 3. Spearman's rank correlations coefficients and 95% confidence intervals for the relationship between bi-iliac breadth and climatic variables (latitude, mean annual temperature, and elevation) using anthropometric data. Males represented by squares and females by circles.

consistent across the course of growth for many measurements. Individuals at higher latitudes are taller and more massive (both absolutely and relative to stature) during the first year of life and remain that way, with little variation, into maturity. Correlations between latitude and bi-iliac breadth are actually stronger in immature individuals than in adults (although not stronger than adult correlations found in previous studies, see Ruff, 1994). Although the relationship between climatic variables and bi-iliac breadth is slightly more variable than the relationship between latitude and weight and stature, individuals at lower latitudes do consistently show relatively narrower bodies than those at higher latitudes. While correlations between relative sitting height and latitude tend to be positive, none of these correlations were significant. It is worth noting, however, that part of the reason for the lower correlations coefficients detected in the anthropometric analyses as compared with other studies may not be related to issues of age, but to issues of sample composition. Many previous studies of ecogeographic variation in adult morphology have included high latitude, arctic New World populations in their analyses. These groups display extreme morphologies that are consistent with ecogeographic predictions, and therefore, may bias

results (Harvati and Weaver, 2006; Auerbach, 2007, unpublished data; King, 2010).

In addition, correlations between latitude and brachial and crural indices are just as strong in immature individuals as they are in adults, and in some cases are actually stronger. When variation in these proportions is explored in the combined large, diverse immature sample, the overall pattern is one that does not vary substantially; while values may fluctuate over the course of growth, the relative ranking of different populations remains consistent. Overall, however, the results from the skeletal and anthropometric analyses strongly indicate genetic or developmental constraints on the dimensions that are analyzed herein, though we cannot exclude the possibility that stable developmental environments may be significantly influencing this conservation of body shape and size.

It is perhaps surprising that climatic correlations remain as consistent over growth as they do, given ontogenetic shifts in body proportions and differing physiological solutions to maintaining body temperature homeostasis among immature individuals of different ages. In this study, however, no significant correlations were detected among climatic variables and relative sitting

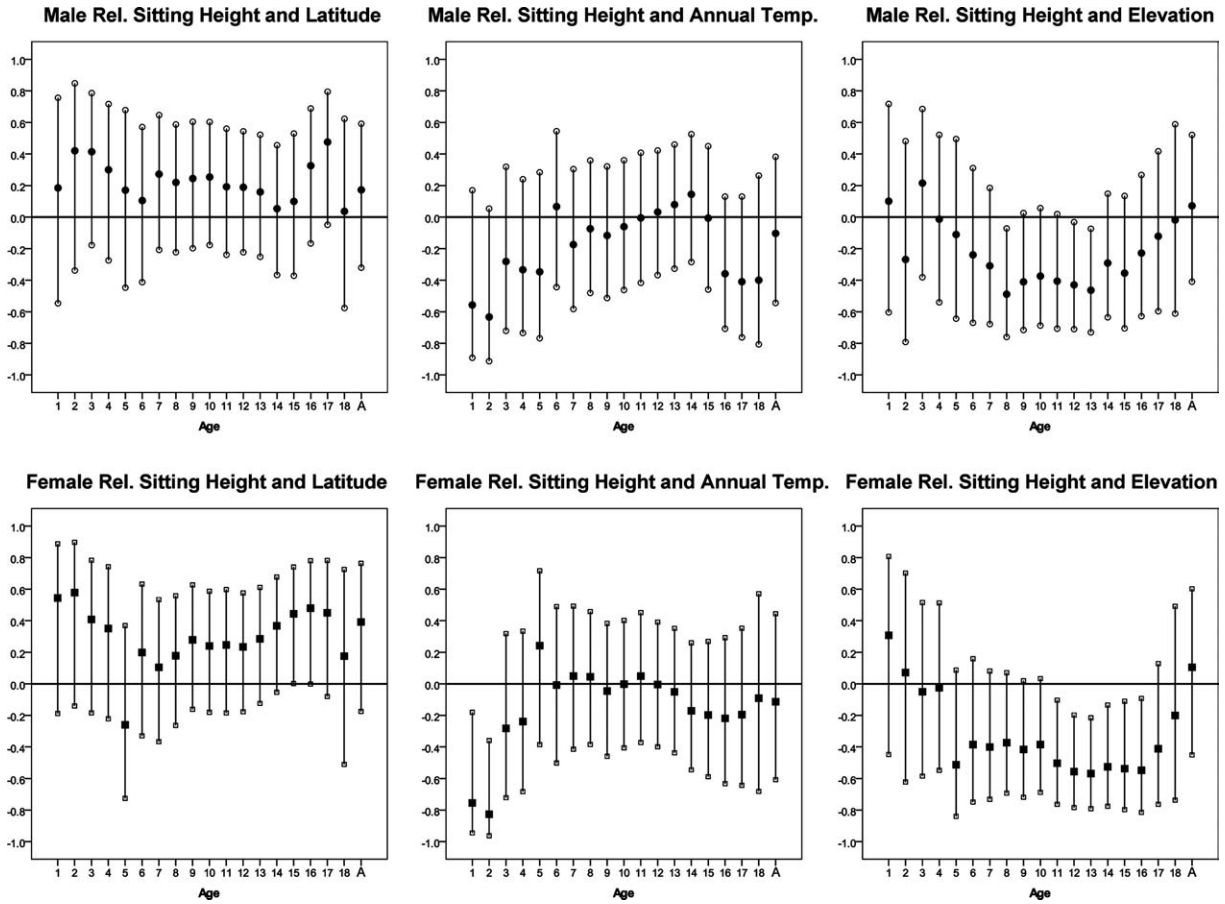


Fig. 4. Spearman's rank correlations coefficients and 95% confidence intervals for the relationship between relative sitting height and climatic variables (latitude, mean annual temperature, and elevation) using anthropometric data. Males represented by squares and females by circles.

TABLE 4. Brachial and crural index mean, standard deviation, and sample size by age category and sample

Sample		Age category							
		0.0-2.9		3.0-9.9		10.0-17.9		Adult	
		Crural	Brachial	Crural	Brachial	Crural	Brachial	Brachial	Crural
California Amerindian	<i>N</i>	22	16	21	25	26	20	90	89
	Mean	0.845	0.794	0.827	0.777	0.830	0.773	0.783	0.813
	Std. Deviation	0.024	0.026	0.015	0.027	0.025	0.021	0.027	0.021
Dart	<i>N</i>	33	33	10	10	29	29	21	20
	Mean	0.837	0.781	0.844	0.774	0.844	0.778	0.799	0.824
	Std. Deviation	0.029	0.035	0.020	0.023	0.028	0.041	0.030	0.022
Indian Knoll	<i>N</i>	27	22	36	35	25	27	64	64
	Mean	0.846	0.797	0.827	0.775	0.829	0.767	0.767	0.814
	Std. Deviation	0.020	0.032	0.021	0.023	0.022	0.030	0.028	0.019
Jomon	<i>N</i>	20	13	22	18	10	5	82	83
	Mean	0.824	0.801	0.810	0.778	0.819	0.805	0.805	0.803
	Std. Deviation	0.024	0.034	0.019	0.019	0.024	0.029	0.028	0.019
Kulubnarti	<i>N</i>	25	26	45	46	19	21	24	23
	Mean	0.845	0.781	0.850	0.778	0.841	0.789	0.800	0.831
	Std. Deviation	0.017	0.024	0.020	0.021	0.023	0.027	0.022	0.021
Luis Lopes	<i>N</i>	9	5	15	10	18	14	30	30
	Mean	0.819	0.761	0.806	0.734	0.812	0.739	0.749	0.808
	Std. Deviation	0.021	0.027	0.017	0.019	0.028	0.019	0.023	0.020
Mistihalj	<i>N</i>	16	17	19	18	9	5	30	30
	Mean	0.832	0.765	0.809	0.738	0.818	0.733	0.743	0.812
	Std. Deviation	0.029	0.035	0.018	0.022	0.018	0.010	0.030	0.021
Point Hope	<i>N</i>	10	6	15	7	24	18	78	76
	Mean	0.794	0.770	0.800	0.739	0.801	0.729	0.744	0.795
	Std. Deviation	0.030	0.043	0.027	0.026	0.018	0.021	0.027	0.020

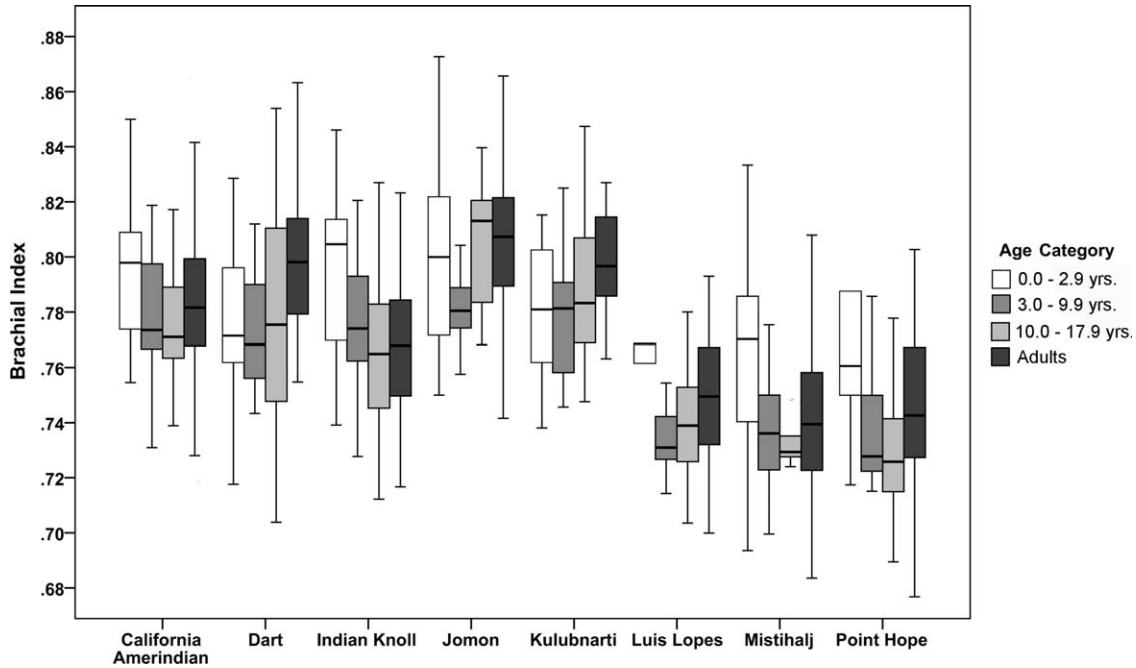


Fig. 5. Boxplots illustrating patterns of change in the brachial index across age categories in eight skeletal samples.

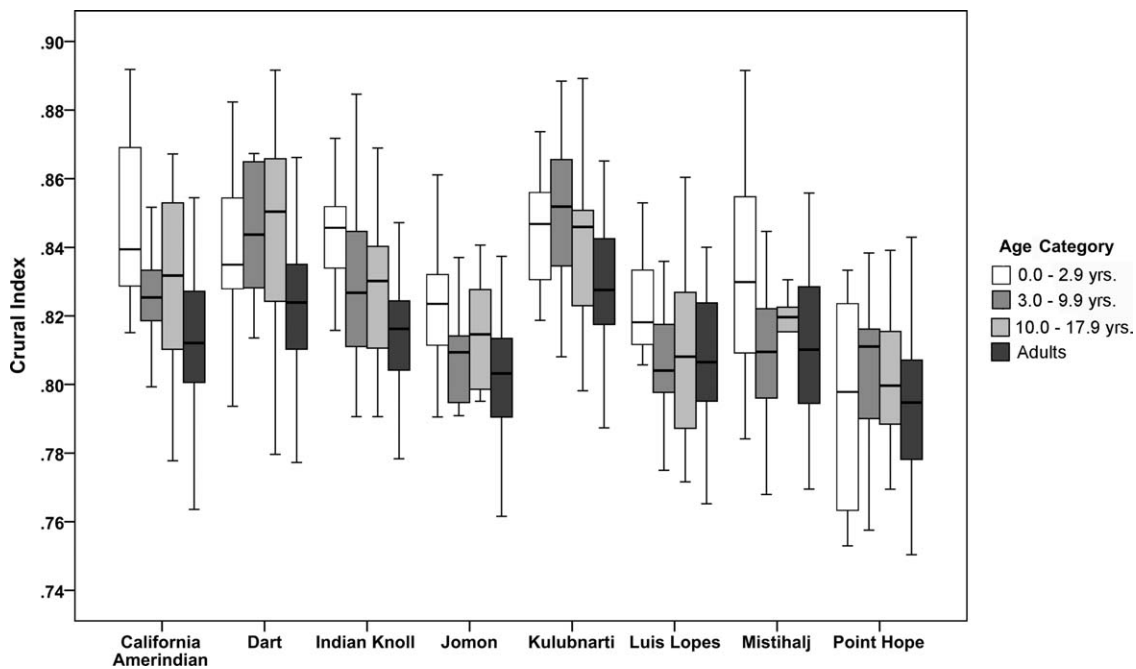


Fig. 6. Boxplots illustrating patterns of change in the crural index across age categories in eight skeletal samples.

height. In contrast, previous studies of adult populations have reported moderate but significant correlations between relative measures of lower limb length, sitting height and latitude and/or climate, which would be expected, in light of the greater ratio of surface area to volume in longer limbs (Roberts, 1978, Stinson, 1990; Holliday and Falsetti, 1995, Katzmaryk and Leonard, 1998; Leonard and Katzmaryk, 2010; but see Auerbach, 2007). In one such study, Roberts (1978) found correlations of -0.62 in adult males and -0.65 in adult females

between relative sitting height and mean annual temperature. However, the relative proportions of trunk height and lower limb length change over the course of development. For example, within the anthropometric sample, sitting height is approximately 62% of stature at age one, but 51% of stature at age 16. These natural fluctuations in human body proportions may partially account for the lack of a consistent relationship between lower limb length and climatic variables (but see discussion of additional factors below).

TABLE 5. *P* values for Kruskal Wallis test for significant differences during growth under the age of 18

Sample	Brachial	Crural
California Amerindian	0.043	0.055
Dart	0.618	0.903
Indian Knoll	0.002	0.002
Jomon	0.053	0.095
Kulubnarti	0.216	0.332
Luis Lopes	0.327	0.117
Mistihalj	0.043	0.012
Point Hope	0.891	0.041

Additional factors influencing immature body proportions

Several of the clearest and most consistent patterns detected in this analysis are likely produced by factors other than latitude and temperature. Throughout growth, immature individuals at higher latitudes and cooler annual, warmest month and coldest month temperatures are consistently taller than those at lower latitudes. In addition, they have absolutely larger sitting heights, which are probably related to their increased stature. This is surprising, given that this pattern has not been detected in adult populations, and is not expected based on widely accepted models of ecogeographic variation in human body proportions. In 1991, Ruff suggested that human body shape could be effectively modeled as a cylinder, with bi-iliac breadth as the diameter and stature as "cylinder" height. Following this, alterations in the height of the cylinder do not change the ratio of surface area to volume, provided that the diameter, or bi-iliac breadth, is held constant (Ruff, 1991, 1994). In addition, previous research has only detected nonsignificant or low correlations between stature and latitude in adults (Stinson, 1990; Ruff, 1994; Auerbach, 2007). Given this, there is no theoretical explanation based on thermoregulatory principles that explains the consistent relationship between stature and latitude found in immature individuals.

It seems more likely that this pattern is a product of subsistence and related biases within the anthropometric sample. The effects of nutritional factors, for example, on stature and stature growth rate are well established (Garn et al., 1974; Garn and Clark, 1975; Billewicz and McGregor, 1982; Bailey et al., 1984; Kimura, 1984). In general, individuals who have experienced malnutrition during growth tend to grow more slowly in stature early in ontogeny and frequently reach diminished adult statures. Within the anthropometric sample used in this analysis, differences in caloric consumption and nutritional supplementation could be patterned along latitudinal lines, and therefore, have influenced the results of this analysis. This is suggested to be the cause for latitudinal patterns in stature variation among groups analyzed by Gustafsson and Lindenfors (2009). When the anthropometric data in our sample are examined in detail, the mean distance from the equator for African samples is 12°, whereas the mean distance from the equator for Europeans is 49°. Only Australian aborigines and two of the African samples reach a comparable distance from the equator in the southern hemisphere. Given the geographic bias of the sample, and previous theoretical and quantitative research indicating that stature should not be strongly influenced by ecogeographic principles, it is likely that better nutrition among the largely industrial European samples is among

the main factors driving the patterns of stature variation detected here.

Nutritional factors may also have influenced the lack of significant correlations between temperature variables and absolute lower limb length and relative trunk length. Classic studies of secular stature changes indicate that while improved nutrition leads to increased stature, this increase is predominantly from changes in lower limb length relative to sitting height (Tanner et al., 1982; Kimura, 1984; Malina et al., 2008). For example, between 1957 and 1977, a period associated with both increased protein and caloric intake, stature of Japanese children increased by 4.3 cm for boys and 2.7 cm for girls, with virtually no increase in sitting height (Tanner et al., 1982). More recent studies have suggested a link between reduced leg growth and a variety of poor health outcomes later in life, including increased fatness, heart disease, diabetes, liver dysfunction, and certain cancers, leading some to propose reduced leg length as a marker of a suboptimal growth environment (Bogin et al., 2002; Bogin and Varela-Silva, 2010; Frisancho, 2007). Lastly, recent studies comparing trends in climate and body proportions in adults to those reported by Roberts (1978) over 30 years ago have found that correlations between relative sitting height and temperature are more modest than those previously reported, which has been attributed to secular trends in body proportions primarily related to improvements in nutrition in impoverished tropical regions (Katzmaryk and Leonard, 1998; Leonard and Katzmaryk, 2010). Therefore, it seems plausible that in addition to changes in body proportions intrinsic to basic patterns of growth, nutritional variation within the anthropometric sample may be obscuring the ecogeographic variation in relative trunk height and lower limb length.

Lastly, altitude has a modest, but clear negative correlation with some anthropometric variables, particularly stature, weight, and BMI. A wealth of previous research has indicated that high altitude environments have an influence on various biological systems during growth, and that children at high altitudes are reduced in stature and weight relative to lower altitude groups (Frisancho and Baker, 1970; Miklashevskaja et al., 1972; Hoff, 1974; Beall et al., 1977; Pawson, 1977; Mueller et al., 1978; Stinson, 1978; Frisancho, 1993; Weitz and Garruto, 2004; Weinstein, 2005; Tripathy and Gupta, 2007). In Andean children from the highlands of Peru, Chile, and Bolivia, postnatal growth in stature and weight is delayed and continues past the age of 20, and similar results have been found in both the Himalayas and the Tien Shan Mountains (Miklashevskaja et al., 1972; Hoff, 1974; Beall et al., 1977; Pawson, 1977; Mueller et al., 1978; Stinson, 1978). In addition, in a skeletal study, Weinstein (2005) found that adult highland populations had smaller body masses compared with lowland counterparts. These patterns appear to be caused by a combination of factors. While hypoxia appears to play a strong role in limiting growth prenatally via intrauterine growth retardation, much of the slow postnatal growth in height and weight among high altitude populations may be attributable to poor nutrition and persistent disease (Stinson, 1982; Greksa et al., 1985; Greksa, 1986; Leonard et al., 1990; Moore et al., 1998; Moore 2003).

Although most of the significant negative correlations detected here among immature individuals are of modest strength, it is surprising that any patterns could be detected at all, given that only approximately 9% of the

anthropometric sample is from populations living in excess of 1,500 m and only 1% over 2,500 m. While previous research has found large differences between high altitude natives and those dwelling at sea level, this study may indicate that even slight differences in altitude, through a combination of environmental factors, can affect human body proportions and patterns of growth. However, this pattern could also be a product of the data collection used in this study. As altitude for some populations was calculated as the midpoint between two or more cities, and the range of altitudes inhabited by the individuals sampled is not known, altitude estimations are likely to include error, which may have biased the results of this analysis.

Implications of variation in immature body proportions

Analyses of ecogeographic variation in adult fossil hominid body proportions have shed light on thermoregulatory adaptation in the past, as well as patterns of human migration and evolution (Trinkaus, 1981; Jacobs, 1985; Franciscus, 1989; Ruff, 1994, 2002; Holliday, 1997a,b, 1999, 2002; Pearson, 2000). Several additional studies have drawn conclusions about both adaptation and population dynamics based on immature fossil remains, using relatively small, immature modern samples as a comparative base (Ruff and Walker, 1993; Ruff et al., 2002). The results of this research indicate that while immature specimens clearly do display ecogeographic patterns similar to those of adults, caution is necessary when assuming that immature variation is identical to that detected in the mature form. Arguments about population affinity and thermoregulatory selection in immature individuals are perhaps best based on biiliac breadth and intralimb indices, which show strong correlations with putative selective factors regardless of age.

In addition, the results of this analysis have evolutionary implications beyond their application to the study of fossil hominids. Outside of research on human life history and developmental acclimatization, little attention has been paid within anthropology to the idea of immature individuals as potential targets of natural selection. In discussions of adaptive significance, some studies of human variation tend to imply that only variation in adult morphology has selective value, and by omission, ignore the fact that the units of their studies have already reached reproductive maturity and are thereby likely to be at least partially successful in an evolutionary context. Given the historically high mortality of immature individuals in many human populations, further attention should be paid to the adaptive significance of morphological variation among immature individuals. While studies such as this one are certain to be complicated by the influence of multiple biological, developmental and environmental factors, they nonetheless are developing a basis for other studies to better examine selective pressures on human populations and the adaptive pressures resulting in the adult human form.

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