

Variation in the Development of Postcranial Robusticity: An Example from Çatalhöyük, Turkey

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ABSTRACT While the study of variation in adult postcranial robusticity has a long history, few analyses have examined the acquisition of postcranial robusticity within an ontogenetic context. This research evaluates differences in the ontogenetic trajectories of immature femora from three samples, in order to assess the point at which differences in levels of adult postcranial robusticity arise during development. Femoral midshaft cross-sectional properties were compared between three diverse samples: Neolithic agriculturalists from Çatalhöyük, Turkey ($n = 42$); Byzantine agriculturalists from Çatalhöyük, Turkey ($n = 24$); and urban Americans from the Denver Growth Study ($n = 151$). While the two adult samples from Çatalhöyük do not differ statistically, both Neolithic and Byzantine adults have relatively larger cortical and total areas than the American urban adults, and these differences are clearly established by the age of six. In addition, by the age of three, individuals from the Denver Growth Study have already attained a greater percentage of their adult length, total area, and cortical area relative to those in both the Neolithic and Byzantine samples. These results indicate that the differing levels of postcranial robusticity characterising adult populations appear relatively early during development, and that populations vary in the rate and pattern through which adult levels of postcranial robusticity are achieved. Copyright © 2007 John Wiley & Sons, Ltd.

Key words: growth; ontogeny; Neolithic; femur

Introduction

A wide variety of evidence has accrued in support of the idea that variation in mechanical loading affects diaphyseal morphology (Chamay & Tschantz, 1972; Jones *et al.*, 1977; Uhthoff & Jaworski, 1978; Goodship *et al.*, 1979; Jaworski *et al.*, 1980; Woo *et al.*, 1981; Lanyon *et al.*, 1982; Lanyon & Rubin, 1984; Carter & Beaupré, 2001; Martin, 2003). In light of the influence of

mechanical environment on long bone remodeling, the application of engineering principles to bone has been used extensively to analyse behavioural patterns and mobility levels in past populations (Lovejoy & Trinkaus, 1980; Bridges, 1989; Larsen *et al.*, 1990; Kimura & Takahashi, 1992; Ruff *et al.*, 1993; Larsen & Kelly, 1995; Churchill & Formicola, 1997; Weiss, 2003). Cross-sectional geometry applies these principles by modelling long bone diaphyses as beams (Ruff & Hayes, 1983), and has been used frequently to explore variation in adult activity patterns in bioarchaeological populations. This technique has been used to examine such diverse topics as humeral bilateral asymmetry (Fresia *et al.*, 1990;

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Trinkaus *et al.*, 1994; Churchill & Formicola, 1997; Sakaue, 1997), behavioural differences between Neandertals and early modern humans (Ruff *et al.*, 1993; Trinkaus, 1997; Trinkaus *et al.*, 1998; Trinkaus & Ruff, 1999a,b), and osteological changes associated with shifts to different means of subsistence, particularly agriculture (Ruff *et al.*, 1984; Bridges, 1985, 1989, 1991; Brock & Ruff, 1988; Ruff & Larsen, 1990; Ruff, 1999). This research has documented wide variation in degrees of adult postcranial robusticity, and has provided insight into how levels of physical activity, mobility and mechanical loading varied among past populations.

In contrast, little research has focused on potential population differences in the developmental trajectories that result in varying degrees of skeletal robusticity in the adult form. Additional research on variation in the developmental acquisition of postcranial robusticity in both recent and archaeological populations is necessary in order to provide more information about the resulting adult morphology. While a few studies have utilised cross-sectional geometry as a tool to explore cortical bone growth within a single sample (Van Gerven *et al.*, 1985; Ruff *et al.*, 1994; Sumner & Andriacchi, 1996; Ruff, 2003a,b), the inclusion of immature remains from multiple bioarchaeological samples is necessary to detect broader patterns of developmental variation in cross-sectional strength.

Hypotheses to be tested

This study will use cross-sectional geometry to evaluate the variation in femoral robusticity during human growth among three populations. Through the comparison of immature individuals from two samples from Çatalhöyük, Turkey, with a sample of urban American children, differences in the developmental acquisition of postcranial robusticity during growth will be assessed. We test the hypothesis that populations of immature humans vary in the pattern and rate with which they attain postcranial robusticity. Although drawing conclusions regarding causal mechanisms of biological variation is often difficult, several possible explanations for developmental

variation and similarity among the three samples will be discussed.

Materials and methods

Samples

The first two samples represent different temporal components of the same site, Çatalhöyük, which is located in central Anatolia in south central Turkey. Situated on a wide alluvial fan at the southern edge of the Konya Plains, Çatalhöyük is a sizeable tell of Neolithic origin dating to ~7400 cal. BC to ~6200 cal. BC (Cressford, 2001). James Mellaart first excavated Çatalhöyük from 1961–1965 (Mellaart, 1962, 1963, 1964, 1966, 1967), followed by Ian Hodder and colleagues beginning in 1993 and continuing to the present (Hodder, 1996, 2000, 2005).

The first bioarchaeological sample from Çatalhöyük consists of 42 Neolithic adults and children. The numerous and closely packed mud-brick houses indicate that Çatalhöyük was a large Neolithic settlement, which faunal evidence suggests was occupied year-round (Cressford, 2005; Russell & McGowan, 2005). Surrounded by wetlands with good alluvial soils, the Neolithic inhabitants of Çatalhöyük cultivated cereals and legumes but also relied on wild plants. Sheep and goat were the dominant domesticated animals; cattle remained in the wild form. There is evidence to suggest that at least some of the agricultural fields and fuel sources were located in the upland areas some distance away from the mound (~10 km), and long-distance travel may also be indicated from the trade items found at the site (Asouti, 2005; Rosen, 2005).

The second sample from Çatalhöyük represents a Late Roman/Early Byzantine population ($n = 24$). These later agriculturalists may have lived in a settlement to the south of the Neolithic mound. During this time period, the original Neolithic mound was used as a cemetery, resulting in a large number of Late Roman/Early Byzantine burials being excavated at Çatalhöyük. The second sample comes from one part of the cemetery excavated near the top of the mound.

The third sample of immature femoral cross-sectional properties is derived from the Denver

Growth Study, a longitudinal study composed of data collected by the Denver Child Research Council between 1927 and 1967 (McCammon, 1970). This sample is comprised of data from middle to upper-middle class children of European ancestry from the Denver area. Children were radiographed at four and six months of age, and then again at six-month intervals until mid-adolescence (McCammon, 1970; Ruff, 2003a,b). Measurements taken on 20 children over the course of the study produced the 151 data points used in this analysis. The cross-sectional properties of the individuals included in this analysis were processed and calculated by Dr Christopher Ruff (Ruff, 2003a,b).

These three samples have been collapsed into six age categories in order to test for statistical differences between the samples (0–3 years, 3.5–6 years, 6.5–9 years, 9.5–12 years, 12.5–15 years, and adults or individuals over the age of 18). It is necessary that these categories be narrow enough to have biological relevance, but broad enough to account for ageing errors or variations among the samples. Ages for the two bioarchaeological samples were estimated based on dental eruption when dentition was available (Ubelaker, 1989); when dentition was absent, assessment of epiphyseal union or within-sample comparisons of metaphyseal length permitted the assignment of the femur to a given age category. A sample of mixed-sex, prime-age adults from each population was used to approximate the average population end-point for each growth trajectory. For the Denver Growth Study sample, individuals over the age of 18 were used; for both bioarchaeological samples, adults between the approximate ages of 18 and 30 were selected.

Reconstruction of cross-sectional geometric properties

The primary data for this analysis consists of the midshaft cross-sectional properties of immature femora. By modelling long bones as hollow beams, relative levels of robusticity, which is defined here as the strength or rigidity of a structure relative to some mechanically relevant measure of body size, can be quantified (Ruff *et al.*, 1993). For this analysis, cross-sections of adult

femoral diaphyses were reconstructed at 50% of biomechanical length (Ruff & Hayes, 1983). In immature femora, however, intermetaphyseal biomechanical length was used prior to epiphyseal fusion, and the 50% level was calculated as 45.5% of femoral intermetaphyseal length, since this measurement best corresponds to the location of the 50% level in individuals with fused distal femoral epiphyses (Trinkaus *et al.*, 2002a,b; Ruff, 2003b).

Two methods were used to reconstruct the immature femoral cross-sectional morphology. Cross-sectional properties for the Neolithic and Byzantine samples from Çatalhöyük were calculated using the 'latex cast method' (LCM), which relies on anteroposterior and mediolateral radiographs and silicone moulding putty (O'Neill & Ruff, 2004). Using the LCM, the external surface of the diaphysis was moulded with Cuttersil Putty PlusTM silicone moulding putty to determine the subperiosteal contour of the section. Measurements of cortical thickness were taken through biplanar radiography, corrected for parallax, and endosteal contours were interpolated using the subperiosteal outline as a guide. The sections were enlarged on a digitising tablet, and the endosteal and periosteal contours digitised. Cross-sectional properties were computed from the resulting sections in a PC-DOS version of SLICE (Nagurka & Hayes, 1980; Eschman, 1992).

For the Denver Growth Study sample, however, cross-sectional properties were calculated using anteroposterior radiographs alone (Ruff, 2003a,b). Cross-sectional parameters for the Denver Growth Sample were calculated with standard geometric formulae assuming circularity of the cross-section (Ruff, 2003a,b). While this method may cause high levels of error when the long bone cross-sections deviate from circularity, prior comparisons of femoral section moduli measured in both mediolateral and anteroposterior planes indicate that the average A-P/M-L ratios of immature femora do not differ significantly from 1.00, indicating that immature femora are likely to approximate a circle (Ruff, 2003a).

Cross-sectional areas and polar moments of area for the midshaft femur were then compared between immature individuals in the three samples. Cortical area is proportional to strength

under tension and compression, when forces are applied non-eccentrically during axial loading. Polar moments of area provide a general measure of the element's overall bending and torsional strength and are calculated from the sum of I_{\max} and I_{\min} (Ruff & Hayes, 1983; Daegling, 2002). Percentages of adult values attained at each age were also calculated in order to assess differences in the developmental timing of the acquisition of robusticity among the three samples.

Size standardisation

In order to study skeletal robusticity, cross-sectional properties must be standardised by a mechanically relevant measurement of body size (Ruff *et al.*, 1993). Since body mass is not directly available for bioarchaeological samples, a variety of measurements, including powers of long bone length, bi-iliac breadth, and measurements of articular surfaces, have previously been used to approximate it (Ruff *et al.*, 1991, 1993, 1994; McHenry, 1992; Grine *et al.*, 1995; Ruff, 2000b; Auerbach & Ruff, 2004). However, calculating body mass from skeletal remains becomes more complicated when attempting to produce estimates for immature remains. Lack of epiphyseal fusion within the immature skeleton and the shifting relationship between long bone length and stature during growth makes the already complex issue of body mass estimation even more problematic (Feldesman, 1992). Due to the degree of error involved in reconstructing an unfused pelvis, calculation of body mass from bi-iliac breadth is not ideal for estimating body mass in immature remains (Trinkaus *et al.*, 2002a,b). In addition, while it is possible to standardise cross-sectional properties of juvenile specimens by measures of metaphyseal surface size (Trinkaus *et al.*, 2002a,b), the fragmentary state of much of the Neolithic postcrania from Çatalhöyük made this option impractical as well.

Due to the limitations in estimating body mass caused by the unfused and fragmentary nature of the immature bioarchaeological samples, cross-sectional properties were standardised by powers of biomechanical length (Ruff *et al.*, 1993). Cross-sectional areas were standardised by biomechanical femoral length,³ and polar moments of area

standardised by biomechanical femoral length^{5.33} (Ruff *et al.*, 1993). When metaphyseal length alone was available in the two bioarchaeological samples, total biomechanical length was calculated from least squares regression formulae based on measurements from the Denver Growth Study. While using long bone length to standardise cross-sectional properties is problematic when modern human samples differ in ecogeographical body proportions (Ruff, 2000c), the three samples used here are unlikely to deviate substantially from temperate climate body proportions. Relative limb length compared with trunk height also varies during growth, and this may affect the pattern of standardised cross-sectional properties within a sample (Feldesman, 1992; Ruff *et al.*, 1994). However, this should not affect comparisons among the samples substantially, as the general pattern of limb growth has remained relatively constant over the time period examined here (Ruff *et al.*, 1994).

Statistical analysis

Growth differences between the three samples were evaluated in two separate steps. First, statistical differences within each age category in the Neolithic and Byzantine samples from Çatalhöyük were explored through the use of non-parametric Mann–Whitney U tests. Once the patterns of variation between the two populations from Çatalhöyük were assessed, the bioarchaeological samples were compared with the growth trajectory of the children in the Denver Growth Study.

The Denver Growth Study, however, is a longitudinal sample, making direct statistical comparison with the two cross-sectional samples difficult. The problem lies in the fact that Denver Growth Study measurements taken from the same individual at different ages are likely to be correlated, and therefore violate the assumption of independence required by most statistical tests (Armitage & Colton, 1998; Diggle *et al.*, 2002). As such, the Denver Growth Study sample was used in this analysis to create a model of immature femoral growth in the assumed absence of extensive mechanical loading or large amounts of physical activity. This assumption is justified

both by the large body of literature documenting the comparatively more active lifestyle of non-urban children, and by studies of cross-sectional geometric trends through time in adults, illustrating a decline in relative postcranial robusticity in urban populations (Ruff *et al.*, 1993; Hawkes *et al.*, 1995; Walton *et al.*, 1999; Trost *et al.*, 2002; Hewlett & Lamb, 2005). Both bioarchaeological samples were compared with the age-specific means of the Denver Growth Study sample through the use of one-sample *t*-tests, as an equivalent non-parametric statistical test is not available. Sequentially reductive Bonferroni multiple comparison tests, which increase the power of detection of more than one false null hypothesis relative to the standard Bonferroni technique, were used to adjust the alpha level in these analyses (Holms, 1979; Rice, 1989; Proschan & Waclawiw, 2000). All statistical procedures were performed using either SPSS 11.0 or STAT-XACT.

Results

Çatalhöyük Neolithic and Byzantine comparisons

The cross-sectional properties of the two bioarchaeological samples reveal that there is little difference in the femoral growth patterns between the Neolithic and Byzantine samples from Çatalhöyük (Table 1). Since the length, cross-sectional areas and polar moments of area did not differ in the Neolithic and Byzantine

adults, it is not surprising that their patterns of femoral growth are quite similar. While two categories display *P* values that exceed an alpha level of 0.05, all comparisons between these two samples are not statistically significant when corrected for multiple comparisons.

Çatalhöyük and Denver Growth Study sample comparisons

The results of single sample *t*-test comparisons between the Çatalhöyük bioarchaeological samples and the age-specific means of the Denver Growth Study are shown in Table 2. As minimal differences were found between the two samples from Turkey, the bioarchaeological samples were combined for this analysis in order to maximise sample size.

The combined Çatalhöyük and Denver Growth Study adults differ from one another in length and all cross-sectional properties except the polar moment of area. Denver Growth Study adults have relatively longer femora with smaller total and cortical areas. During skeletal ontogeny, these differences appear at a relatively early age. While the differences in length are present prior to age three, most differences in cross-sectional properties generally arise within the second age category, ages 3.5 to six years. Analyses of the percentage of adult values illustrate that the children from the Denver Growth Study appear to be achieving a greater percentage of their growth at an earlier age. In Figure 1, a robust locally weighted regression technique, LOWESS,

Table 1. Results from Mann-Whitney U tests (values of *P*) of the Byzantine and Neolithic femoral samples from Turkey

	Category 1 (0–3 years)	Category 2 (3.5–6 years)	Category 3 (6.5–9 years)	Category 4 (9.5–12 years)	Category 5 (12.5–15 years)	Adults
Biomechanical Length (mm)	0.234	0.857	0.048	0.800	0.400	0.229
TA (mm ²)	0.628	0.143	0.262	0.267	0.800	0.452
CA (mm ²)	0.366	0.071	0.095	0.533	1.000	0.934
MA (mm ²)	0.945	0.643	0.905	0.800	0.800	0.187
J (mm ²)	0.628	0.143	0.262	0.267	0.2000	0.559
% of Adult TA	0.628	0.429	0.167	1.00	0.4000	NA
% of Adult CA	0.836	0.429	0.548	0.800	0.800	NA
% of Adult MA	0.945	0.857	0.095	0.800	0.800	NA
% of Adult J	0.836	0.857	0.095	1.00	0.2000	NA
% of Adult Bio. Length	0.534	1.00	0.024	0.800	0.4000	NA

Table 2. Results from single sample *t*-test of Çatalhöyük archaeological samples against expected Denver Growth Study age-specific means

	Category 1 (0–3 years)	Category 2 (3.5–6 years)	Category 3 (6.5–9 years)	Category 4 (9.5–12 years)	Category 5 (12.5–15 years)	Adults
Biomechanical length (mm)	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	170.1 (8) 232.6 (111) <0.001*	240.6 (9) 291.9 (114) <0.001*	295.8 (6) 344.6 (107) 0.008*	362.2 (5) 407.7 (108) 0.007*	393.5 (25) 440.5 (14) <0.001*
Standardised total area (m ²)	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	4230.7 (13) 3534 (151) 0.027*	1295.1 (9) 903.7 (114) 0.002*	865.0 (6) 716.6 (111) 0.016*	809.6 (5) 622.0 (108) 0.004*	868.8 (25) 624.4 (14) <0.001*
Standardised cortical area (mm ²)	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	3079.1 (13) 2563.8 (149) 0.066	872.0 (9) 663.0 (114) 0.013*	632.4 (6) 527.2 (111) 0.039	653.9 (5) 474.0 (108) 0.020	664.2 (25) 499.8 (14) <0.001*
Standardised medullary area (mm ²)	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	1151.7 (13) 950.4 (149) 0.092	423.1 (9) 240.8 (114) 0.001*	232.6 (6) 189.3 (111) 0.017*	155.7 (5) 148.0 (108) 0.747	204.6 (25) 124.6 (14) <0.001*
Standardised J (mm ⁴)	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	6800.1 (13) 5280.6 (149) 0.097	987.5 (9) 558.6 (114) 0.007*	521.2 (6) 393.4 (111) 0.034*	306.5 (5) 328.4 (108) 0.471	325.9 (25) 353.5 (14) 0.226
Percentage of adult total area	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	14.9% (13) 18.2% (151) 0.006*	36.9% (9) 45.0% (114) 0.010*	46.5% (6) 59.7% (111) 0.017*	73.9% (5) 78.5% (108) 0.586	NA
Percentage of adult cortical area	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	14.0% (13) 16.4% (149) 0.019*	32.3% (9) 41.3% (114) 0.001*	44.3% (6) 55.0% (111) 0.031	78.0% (5) 75.2% (108) 0.774	NA
Percentage adult medullary area	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	17.7% (13) 25.4% (149) 0.005*	52.3% (9) 59.9% (114) 0.287	53.6% (6) 78.6% (111) 0.005*	60.6% (5) 92.0% (108) 0.039*	NA
Percentage of adult J	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	4.3% (13) 3.6% (149) 0.0216	25.6% (9) 19.6% (114) 0.115	42.7% (6) 34.6% (111) 0.292	64.6% (5) 60.9% (108) 0.776	NA
Percentage of adult length	Çatalhöyük \bar{X} Denver \bar{X} <i>P</i>	31.5% (13) 33.0% (151) 0.228	63.0% (9) 68.1% (114) 0.042*	77.4% (6) 80.7% (111) 0.302	92.0% (5) 92.5% (108) 0.845	NA

* Indicates results that were significant with sequentially reductive multiple comparison corrections.

^a Sample sizes for each analysis shown in parentheses.

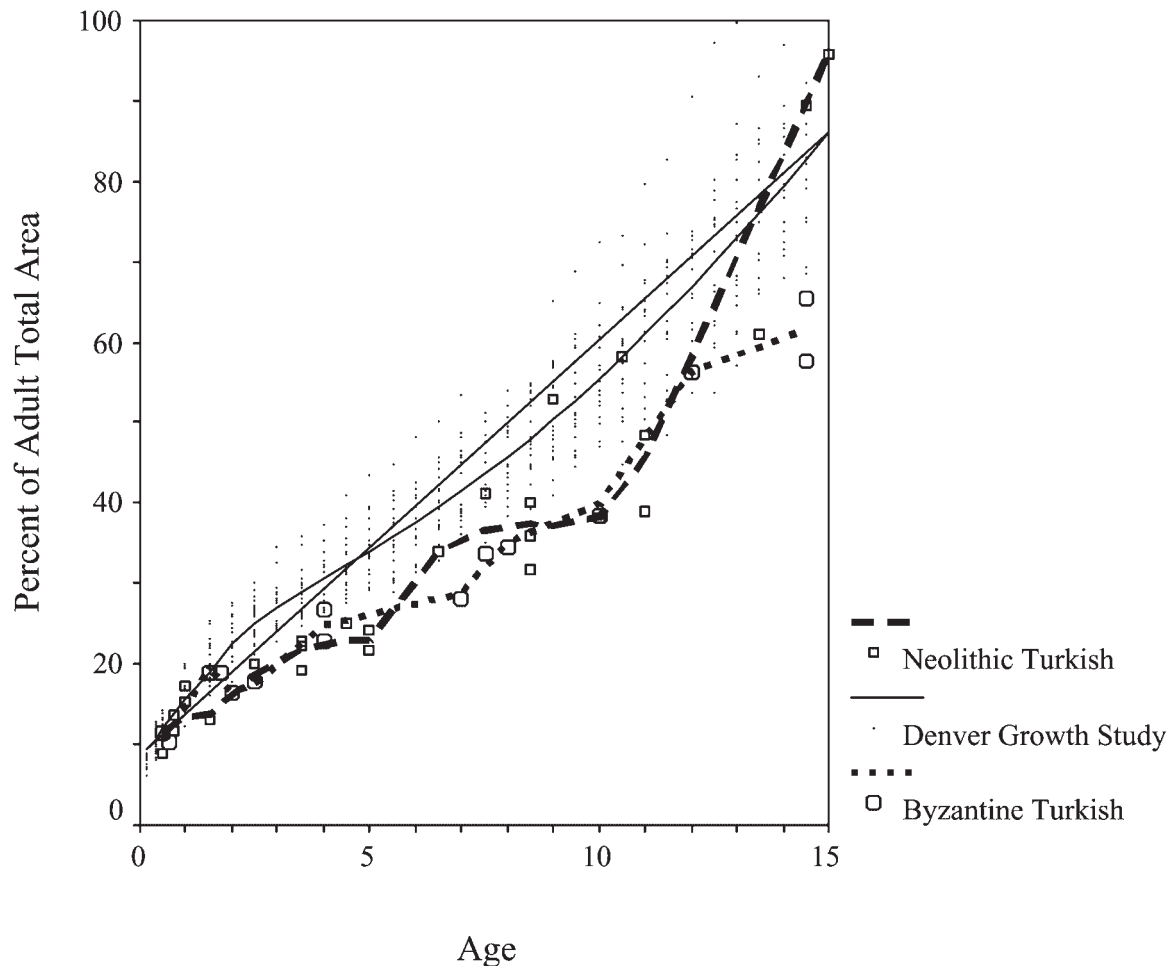


Figure 1. Smoothed growth curves to compare the three study samples

has been used to smooth growth curves to assist in comparing the three growth trajectories (Cleveland, 1979, 1994). The individuals from the Denver Growth Study display relatively accelerated growth prior to the age of 12 when compared with individuals from Çatalhöyük.

Discussion

Limitations of study

Prior to discussing the significance of the results of this research, it is necessary to address several of its limitations and assumptions. Firstly, the

sample sizes for the archaeological samples (particularly those within age categories) are small, due to the fragmentary condition and age of the available materials. The very small size of several of the age category samples alone demands that the results be interpreted with caution. Future research with both a larger sample size and a wider range of populations will help to clarify the developmental patterns suggested here.

Secondly, this study compares dentally-aged individuals with the known-age individuals in the Denver Growth study. Therefore, this analysis implicitly assumes equivalent dental formation and eruption schedules between Neolithic and Byzantine individuals, when in actuality dental

development varies across populations (Garn *et al.*, 1973; de Melo e Freitas & Salzano, 1975; Brown, 1978; Loevy, 1983; Blankenstein *et al.*, 1990; Eveleth & Tanner, 1990; Harris & McKee, 1990; Davies & Hägg, 1994). While studies of variation in dental development have found that populations differ in the timing of both dental formation and eruption, population differences in the timing of eruption are likely to be small, with eruption times generally varying by as little as three to six months between populations (Liversidge, 2003).

Thirdly, this study compares patterns of postcranial development in a cross-sectional, archaeological population with a longitudinal, recent population. While the statistical problems associated with this comparison have been addressed above, there may be additional difficulties associated with the comparison of a recent sample of living children with an archaeological sample of deceased children. It has long been recognised that studies of growth in the past using archaeological skeletal samples cannot be assumed to represent the growth patterns of healthy, living populations, as selective mortality is operating to create a biased sample of all the children that were alive at a given time (Johnston, 1962; Buikstra & Cook, 1980; Cook, 1981; Wood *et al.*, 1992). However, it remains debatable how much this actually affects skeletal analysis of immature remains. It has been argued that most deaths of individuals prior to maturity are the result of acute conditions unlikely to affect patterns of growth and skeletal maturation greatly (Lovejoy *et al.*, 1990). An analysis by Saunders & Hoppa (1993) specifically addressed the effect of mortality bias on the study of long bone growth by examining statistical differences in femoral lengths in populations of survivors and non-survivors. While statistically significant differences in femoral length were found between survivor and non-survivor populations, the actual differences in femoral length remained under 3 mm. These authors concluded that, while the possibility of bias does exist, the overall effect of selective mortality is likely to be minor (Saunders & Hoppa, 1993). For the samples analysed here, mortality bias does not seem to have had a strong effect on the majority of the results, as the immature individuals in the archaeological

samples from Çatalhöyük generally display larger total and cortical areas than the living children from the Denver Growth Study.

Possible explanations for variation in the development of postcranial robusticity

Given the inherent difficulties in assigning causal mechanisms in any study of growth, it is clearly not possible to reach concrete conclusions regarding which specific factors are responsible for ontogenetic variation in cross-sectional robusticity in this study. However, it is possible to undertake a brief consideration of several factors known to affect bone growth and to evaluate the relative magnitude of their influence on the specific patterns observed in this analysis.

Genetic influences on bone growth

The use of both twin and multigenerational familial studies to examine genetic influence on bone growth and morphology has a long history within the discipline of anthropology, and various components of bone shape and other anthropomorphic variables have been shown to have a high degree of heritability (Shields, 1962; Vandenberg & Falkner, 1965; Wilson, 1979; Bergman *et al.*, 1981; Mueller, 1986; Livshits, 1986; Fischbein & Pedersen, 1987). Stature has long been known to possess a large genetic component, and heritability estimates for stature across populations generally range from 60–90% in healthy individuals (Roberts *et al.*, 1978; Phillips & Matheny, 1990; Carmichael & McGue, 1995; Preece, 1996; Silventoinen *et al.*, 2000; Li *et al.*, 2004). Studies of bone mineral density and bone mineral mass have also revealed that a significant portion of the variation in these features is of genetic origin, and heritability estimates for bone mineral density and mass can be as high as 80% (Smith *et al.*, 1973; Pocock *et al.*, 1987; Seeman *et al.*, 1989; Krall & Dawson-Hughes, 1993; Howard *et al.*, 1998; Prentice, 2001).

Long bone cross-sectional properties, however, appear to have less of a genetic component than either stature or bone mineral density. In a recent study, Volkman *et al.* (2004) examined genetic effects on long bone geometry and other mechanical properties of the mouse femur. This study found that only 2.9% to 15.4% of the variance in the mechanical traits included in the study could be linked to genetic effects (Volkman *et al.*, 2004). While few other analyses have directly measured genetic influence on cross-sectional properties, additional studies indirectly support the conclusion that environmental factors have a relatively greater effect on long bone cross-sectional size and strength. Studies of bilateral humeral asymmetry have illustrated that cross-sectional properties can vary widely within a single individual in response to environmental stimuli. The differences between cross-sectional geometric properties of dominant and non-dominant arms range from 5–14% in normal, non-pathological individuals, and can reach levels of 57% in athletes engaging in pronounced unilateral activity (Jones *et al.*, 1977; Trinkaus *et al.*, 1994; Sakaue, 1998).

While the results of the present analysis certainly do not negate the possibility of strong genetic influence on cross-sectional properties of the human femur, they do appear to indicate that environmental factors play a more important role. Adults from Çatalhöyük and the Denver Growth Study differ in femoral length, and these differences are already present in the first age category, indicating that either genetic factors or pre-natal environment strongly influences variation in long bone length. Differences in the majority of the cross-sectional geometric properties, however, do not appear until slightly later in ontogeny. These results are consistent with research indicating that differences in relative limb lengths emerge early in development, while differences in limb strength do not assume adult proportions until mid-adolescence (Ruff, 2003b). The later appearance of differences in cross-sectional properties of the femur may imply that they are not as strongly genetically canalised as long bone length. While this certainly does not eliminate the possibility that some populations may be genetically predisposed to develop relatively greater degrees of postcranial robusti-

city, the results of this analysis combined with evidence from previous studies points to environmental factors as the predominant influence on cross-sectional properties during growth.

Nutritional influences on bone growth

Malnutrition has a strong negative impact on bone growth, and studies focusing specifically on diaphyseal measurements have pointed to reduced levels of cortical bone and diminished shaft diameters as evidence of poor nutrition during development (McFie & Welbourn, 1962; Widdowson & McCance, 1963; Allen & Zeman, 1971; Blanco *et al.*, 1972; Shrader & Zeman, 1973; Himes *et al.*, 1975). Malnourished monkeys exhibit slower growth in midshaft femoral diameter than well-fed controls (Fleagle *et al.*, 1975), and several studies have shown reduced long bone periosteal deposition in protein-deficient experimental animals (Jha & Ramalingaseami, 1968; Shrader & Zeman, 1973). Experimental studies inducing severe starvation in pigs have found that in addition to stunting long bone length, starvation results in a reduction of cortical bone and numerous Harris lines (Dickerson & McCance, 1961; Pratt & McCance, 1964; Adams, 1969).

Studies of cortical bone growth in human children have noted periodic declines in percentage cortical area, and suggested that the reduction in relative levels of cortical bone may be indicative of nutritional stress (Garn *et al.*, 1964, 1969; Garn, 1970; Huss-Ashmore, 1981; Hummert, 1983; Van Gerven *et al.*, 1985). The decline in percentage of cortical area is usually accompanied by continued growth in total area, cortical area, and/or polar moment of area (Huss-Ashmore, 1981; Hummert, 1983; Van Gerven *et al.*, 1985). Contrary to being an indication of poor health, it seems likely that this reduction in relative cortical area is an artifact of normal bone growth and modelling (Van Gerven *et al.*, 1985; Ruff *et al.*, 1994). Ruff *et al.* (1994) found that there are age-related changes in relative sensitivity of the periosteal and endosteal diaphyseal envelopes during growth. Prior to mid-adolescence, the periosteal diaphyseal surface is more responsive to increased mechanical loading, resulting in a

relatively large medullary cavity and low percentages of cortical area during this time period. From mid-adolescence to early adulthood, the primary bone forming surface is endosteal, leading to endosteal contraction and a reduction of the medullary cavity (Ruff *et al.*, 1994).

While it remains possible that differences in nutritional factors have influenced the present study, it is an unlikely explanation given the pattern of variation observed among the three samples used in this analysis. Both archaeological samples had higher measures of standardised total and cortical area than the children in the Denver Growth Sample, which is comprised of upper-middle class American children. If large measures of total and cortical area are interpreted as indicators of adequate nutrition during growth, both samples from Çatalhöyük appear well-nourished, and it is hard to argue that children from Denver in the 1950s were experiencing high levels of nutritional stress, based on what is known about the socioeconomic background and dietary intake of children in this particular sample (Beal, 1970). This conclusion is supported by general bioarchaeological analysis conducted on the samples from Çatalhöyük. Other than their relatively short stature, immature remains from Çatalhöyük show relatively few classic osteological signs of elevated levels of non-specific nutritional stress, such as Harris lines, dental enamel hypoplasias, cribra orbitalia, or porotic hyperostosis.

Although dietary differences between the three samples used in this study are likely to have existed, it is unlikely that they were responsible for the absolute differences in cross-sectional geometric properties detected among the three populations. While minor dietary deficiencies may have been a factor for any of the populations in this analysis, evidence from experimental studies of animals and clinical research on growing children indicates that the effects of nutritional deficits on the quantity of growing cortical bone can be modulated by the introduction of physical activity (Lanyon *et al.*, 1986; Welten *et al.*, 1994). However, nutritional differences may have influenced the apparent growth rate differences among the samples. The Denver Growth Study individuals attained a greater proportion of their total and cortical area

during early skeletal ontogeny, whereas the two bioarchaeological samples initially grew more slowly and then accelerated as they neared adulthood. This pattern may be related to differences in nutrition prior to maturity, as it is well known that nutritional intake impacts the rate of longitudinal and cortical growth before skeletal growth is completed (Adams, 1969; Garn *et al.*, 1969). In addition, juvenile skeletal development prior to the adolescent growth spurt may be less genetically canalised and more susceptible to environmental disruptions, which may explain the differences between these three samples before the age of 12 (Johnston *et al.*, 1976; Stinson, 2000).

Mechanical loading and bone growth

It remains likely that the factors producing variation in adult postcranial robusticity also play a major role in developmental variation prior to skeletal maturity. While growth has seldom been examined from a purely biomechanical standpoint, recent research indicates that biomechanical forces acting upon the immature skeleton represent a significant external influence during human skeletal ontogeny (Carter & Beaupré, 2001). The production of normal long bone morphology is highly dependent on mechanical loading during both pre- and postnatal growth (Carter *et al.*, 1987; Carter & Beaupré, 2001). Studies of mechanical loading during postnatal development have generally shown that immature bone responds to habitual physical activity with elevated levels of strength, bone mass and bone mineral density (Woo *et al.*, 1981; Biewener & Bertram, 1994; Kannus *et al.*, 1995; Bradney *et al.*, 1998; Schönau, 1998; McKay *et al.*, 2000). It has also been suggested that immature bone may respond differently than mature bone to mechanical stimuli; bone may actually be more sensitive to loading prior to adulthood, becoming particularly responsive around adolescence (Steinberg & Trueta, 1981; Raab *et al.*, 1990; Slemenda & Johnston, 1993; Kannus *et al.*, 1995; Haapasalo, 1998; Lieberman & Crompton, 1998; Heinonen *et al.*, 2000; Lieberman *et al.*, 2001; MacKelvie *et al.*, 2001, 2002; Bass *et al.*, 2002; Kontulainen *et al.*, 2003;

Pearson & Lieberman, 2004). In fact, before skeletal maturity, even moderate levels of exercise are sufficient to elicit an osteogenic response (Saville & Whyte, 1969; Woo *et al.*, 1981; Forwood & Burr, 1993; Bradney *et al.*, 1998). While the results of this analysis generally support the idea that mechanical loading prior to maturity plays a critical role in the production of adult morphology, several important issues remain unresolved.

No major differences were detected between either the adults or the juveniles in the two bioarchaeological populations. Although both populations are perhaps best categorised as non-mechanised agriculturalists, they probably differed substantially in technology, culture and behaviour. Both archaeological populations did, however, occupy the same geographical area, and therefore probably utilised the same types of landscapes and terrain during life. Terrain has been found to have a significant impact on cross-sectional morphology in several analyses (Ruff, 1999, 2000a; Weiss, 2003; Marchi *et al.*, 2005). In a three-way analysis of variance including subsistence strategy, sex and terrain, Ruff (1999, 2000a) found that while variation in subsistence strategy had no significant effect on all the cross-sectional properties examined, variation in terrain had a significant effect on both standardised cortical area and polar moment of area. The common terrain occupied by the two Çatalhöyük populations may have overwhelmed potential postcranial growth differences caused by activity patterns, making terrain a more critical feature in the local mechanical environment than subsistence strategy in this analysis. It also remains possible, however, that the biomechanical signal generated by two variants of non-mechanised agriculture in the small samples from Çatalhöyük is not sufficiently distinct to be differentiated.

In contrast to the developmental trajectories of the two Çatalhöyük samples, the patterns of growth of the two bioarchaeological samples and the Denver Growth Study differ strongly. Contrasting femoral lengths and cross-sectional areas characterise adults from these two samples, and these differences in adult femoral robusticity appear during growth at a developmentally early age. This supports the idea that immature bone

may be particularly responsive to even the low levels of mechanical loading associated with childhood activity, and the early developmental appearance in immature individuals of the cross-sectional attributes that characterise adult populations indicates that at least some of the biomechanical signal being detected in studies of adult cross-sectional geometry is a product of activity patterns prior to skeletal maturity (Bradney *et al.*, 1998; Lieberman & Crompton, 1998; Lieberman *et al.*, 2001; Pearson & Lieberman, 2004). However, most research seems to indicate that while immature bone does respond strongly to mechanical loading, the effects of physical activity under the age of 18 are not maintained throughout the entire life course without the continued maintenance of the loading regime during the adult years (Karlsson *et al.*, 1995, 2000; Bass *et al.*, 1998; Valdimarsson *et al.*, 2005).

Ethnographic studies of children's activities in non-mechanised societies indicate that children assume adult patterns of labour at an early age (Moberg, 1985; Bradley, 1993), which may partially explain why adult patterns of variation in postcranial robusticity emerge so early in ontogeny. Children in non-urban societies engage in a wide variety of subsistence related tasks that impact their levels of postcranial mechanical loading, not limited to but including hunting small game, gathering, childcare, food preparation, burden carrying, and other domestic work (Bradley, 1993). In a large proportion of non-mechanised subsistence groups, children begin to contribute to subsistence between the ages of six and 10, and after the age of 10, the labor patterns of children are similar to those of same-sex adults (Moberg, 1985; Bradley, 1993). When young children are functionally behaving as adults from such an early age, it is perhaps less surprising that immature cross-sectional properties resemble so closely those of the adults in their respective populations. Nonetheless, differences between these three populations in most cross-sectional properties appear between the ages of 3.5 and six, which is a surprisingly young age even if an earlier onset of subsistence-related behaviours is taken into account. While biomechanical factors clearly influence the developmental acquisition of postcranial robusticity,

additional research is necessary to clarify fully the intrinsic and extrinsic factors influencing variation in cross-sectional geometry during growth.

Conclusion

This study illustrates the potential utility of cross-sectional geometry as a technique to examine differences between samples in both the pattern and rate of postcranial growth, as well as demonstrating that this technique is sufficiently sensitive to detect variation in developmental trajectories between populations. The strong differences detected between the samples from Çatalhöyük and the Denver Growth Study confirm the importance of both ontogenetic history and mechanical environment in the production of adult postcranial robusticity. This analysis illustrates that the differing levels of postcranial robusticity that characterise adult populations appear relatively early during development, and that populations vary in the rate and pattern through which adult levels of postcranial robusticity are achieved.

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