Quaternary International xxx (2016) 1–13

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Evidence for genetic and behavioral adaptations in the ontogeny of prehistoric hunter-gatherer limb robusticity

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ARTICLE INFO

Article history:
Available online xxx

Keywords:
Biomechanics
Cross-sectional geometry
Functional adaptation
Growth
Hunter-gatherers

ABSTRACT

Biomechanical analyses of past populations have primarily focused on adults and interpreted variation in limb bone robusticity as indicative of differences in behavior. However, prior to skeletal maturity large changes occur in limb bone robusticity and shape. During ontogeny, the accrual of bone is regulated by differences in genetics and nutrition as well as mechanical loading. We consider how long bone robusticity changes from birth to young adulthood in order to understand when population differences appear during development and why this occurs.

We analyzed the femoral and humeral midshafts of four prehistoric hunter-gatherer skeletal samples from four regions: Cis-Baikal, Siberia, Point Hope, Alaska, the central Japanese coast, and the South African Cape. Some statistically significant differences between populations manifest at birth or soon after. Some of this systemic patterning likely reflects adaptation of body shape to climate. Later Stone Age South Africans also appear to demonstrate low limb rigidity residuals as a result of growth towards a unique body type. Differentiation between populations also increases with age, pointing to functional adaptation as a result of behavioral differences. This proves largely concordant with other lines of evidence for differing levels of terrestrial and aquatic mobility in these populations.

1. Introduction

1.1. Bone robusticity and studies of behavioral variation in past populations

Skeletal robusticity refers to the “strengthening or structural buttressing” of skeletal elements (Ruff et al., 1993, 21–22). The study of bone robusticity can assist in reconstructing the behavior of past populations. *In-vivo* mechanical loading stimulates changes in cortical thickness and diaphyseal shape in order to keep the strains experienced by skeletal elements during the performance of activities within an optimum customary level, a process referred to as bone functional adaptation (Ruff et al., 2006a). Comparisons of robusticity are made possible by the calculation of the cross-sectional geometric properties (CSG) of bone diaphyses. A plethora of animal experiments as well as studies of humans demonstrate that increased strain levels trigger cortical bone deposition, changes in diaphyseal shape, and increases in CSG. Conversely, reductions in mechanical strain lead to cortical bone resorption and decreases in CSG.

Biomechanical investigations of skeletal robusticity have been especially important for the study of mobility, here defined as the total distance traveled during an individual's lifetime (Stock, 2006; Ruff and Larsen, 2014). Two types of mobility are often recognized, terrestrial and aquatic. Terrestrial mobility refers to walking or running, and primarily affects lower limb robusticity (Carlson and Marchi, 2014). Greater amounts of terrestrial locomotion have been linked to elevated lower limb robusticity and anteroposterior reinforcement of lower limb diaphyses (Carlson and Marchi, 2014). Studies of lower limb robusticity and shape indicate considerable geographic and chronological diversity in the terrestrial mobility of past hominin populations (Ruff et al., 1993; Stock and Pfeiffer, 2001, 2004; Holt, 2003; Ruff, 2005; Shackelford, 2005; Marchi et al., 2006; Sladek et al., 2006; Wescott, 2006; Shackelford, 2007;

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http://dx.doi.org/10.1016/j.quaint.2015.09.093

Marchi et al., 2011; Shaw and Stock, 2013; Macintosh et al., 2014; Ruff and Larsen, 2014; Shackelford, 2014).

Investigations of hunter-gatherer terrestrial mobility are of particular interest to our study. These demonstrate diachronic change and regional variability in lower limb robusticity. For instance, from the Early Upper Paleolithic to the Mesolithic, Old World forager populations show decreasing anteroposterior reinforcement of the femur (Holt, 2003; Shackelford, 2005, 2007; Ruff et al., 2006b). This has been considered indicative of a decrease in terrestrial mobility, perhaps due to increased territoriality and changes in technology. Holocene forager populations from different regions also show considerable diversity in lower limb CSG (Stock and Pfeiffer, 2001, 2004; Stock, 2006; Wescott, 2006; Stock et al., 2010; Lieverse et al., 2011; Shackelford, 2014). This diversity in lower limb robusticity can, in large part, be attributed to variation in foraging strategies necessitated by environmental differences.

Aquatic mobility refers to the use of watercraft or swimming for traversing landscapes, and it has been associated with higher levels of upper limb robusticity (Stock and Pfeiffer, 2001; Weiss, 2003; Stock, 2006; Stock et al., 2010; Lieverse et al., 2011; Shackelford, 2014). However, upper limb rigidity also reflects differences in foraging technology and the amount or intensity of resource processing. For instance Weiss (2003) noted that although female Aleutian islanders probably did not use boats, they had higher levels of humeral robusticity than other populations that inhabited aquatic environments. This was attributed to the processing of large marine mammals by these individuals. Similarly the use of fishing gear such as stone weighted nets can also engender high humeral strains (Watanabe, 1972; Weiss, 2003; Ruff, 2005).

1.2. *The ontogeny of bone robusticity*

While studies of robusticity in past populations have focused on adults, a growing body of experimental research indicates that adult patterns of skeletal robusticity primarily reflect functional adaptation during development. Steinberg and Trueta (1981) and Lieberman et al. (2001) subjected juvenile and adult animals to equivalent amounts of exercise, but only juvenile animals demonstrated increases in skeletal robusticity. Clinical studies have also linked increased levels of physical activity to increases in bone mass and CSG during childhood. Children preserve these gains in diaphyseal robusticity into adulthood (Nordstrom et al., 1996; Bradney et al., 1998; Khan et al., 1998; Bass et al., 2002; Kontulainen et al., 2002; Burrows, 2007). The greater response of juveniles to loading has been attributed to the greater number and sensitivity of cells involved in bone modeling and remodeling (Ruff et al., 1994; Pearson and Lieberman, 2004).

Genetic factors and body shape also contribute to the development of long bone robusticity. Human body shape varies as an adaptation to climate, emphasizing either heat retention at high latitudes or radiation at low latitudes (Pearson, 2000; Ruff, 2008). Ecogeographic differences in body breadth likely alter the relative intensity of mediolateral and anteroposterior strains and can contribute to variation in femoral form, particularly at the subtrochanteric level (Weaver, 2003). Furthermore, genetic influences play a large role in determining population and individual-level mechanosensitivity to loading stimuli and overall long bone size. Studies of mouse lineages have demonstrated that genes can code for a higher base level of bone robusticity or increased sensitivity to mechanical loading (Akhter et al., 1998; Kodama et al., 2000; Robling and Turner, 2002; Lovejoy et al., 2003; Ruff et al., 2006a; Wallace et al., 2010). It has been theorized that genetic differences should prove most visible early in ontogeny after which adaptation to mechanical loading becomes the main driver of changes in CSG (Carter and Beaupre, 2001; Ruff, 2008; Cowgill, 2014a).

In addition, overall health and nutrition-related factors may also influence bone growth. It has long been noted that malnourished individuals have less robust limb bones than well-nourished juveniles of the same age (Garn et al., 1969; Himes et al., 1975; Van Gerven et al., 1985; Agarwal, 2008). However, malnutrition does not in and of itself produce cortical bone wastage; increases in bone mass and CSG during development prove closely tied to variations in body mass (Ruff, 2003a,b; Lambert et al., 2005; Galusca et al., 2008). An experiment conducted on juvenile rats showed that the limbs of individuals placed on a restricted diet appeared gracile relative to those of controls (Lambert et al., 2005). However, differences in bone robusticity disappeared when measurements were standardized for body mass. Likewise, a study of anorexics and women with naturally low body mass found a strong correlation between bone density and BMI (Galusca et al., 2008). Such research strongly suggests that the gracile bones of less well-nourished individuals may result from a low skeletal load being applied throughout life. Precisely how malnutrition mediates bone loss, either via reduced body mass or a more direct mechanism, remains unclear. Temple et al. (2013) also proposed that reductions in bone formation associated with malnutrition may be overwritten by elevated levels of mechanical loading. This emphasizes the need to account for the multiple factors influencing bone accrual when analyzing skeletal robusticity.

Few studies have considered what the ontogeny of bone robusticity indicates about the mobility and activity levels of immature individuals from past populations. Cowgill et al. (2010) study of the femoral shape of several Holocene populations detected the same general developmental pattern regardless of mode of subsistence. The femoral midshaft became reinforced along the anteroposterior axis throughout ontogeny. This reflected maturation of the hip joint and increasing terrestrial mobility. Significant population level differences in femoral shape as well as lower and upper limb robusticity emerge by the end of the first year of life or shortly thereafter (Cowgill and Hager, 2007; Cowgill, 2010, 2014a,b). This indicates that systemic factors, genetics and body mass, are important determinants of population level variation in robusticity. However, different levels of mechanical loading in these groups likely maintained differences between populations later in ontogeny (Cowgill, 2010). To date no study has explicitly considered the effect of aquatic mobility on the accrual of bone robusticity during growth.

1.3. *Study goals*

While other studies have analyzed populations that practiced different modes of subsistence (hunter-gatherer, pastoralist, urban) (Cowgill and Hager, 2007; Cowgill, 2010, 2014a,b), we focus here on hunter-gatherer populations. We evaluate two research questions. Firstly, how do the populations studied differ from each other in terms of robusticity and when during development do these differences appear? Secondly, what factors account for variation or homogeneity in bone robusticity? The discussion will consider systemic and behavioral influences on bone accrual and shape changes.

We predict that differences can be detected before maturity. The existence of differences between populations early in development would suggest genetically encoded differences in robusticity or body size. Alternatively it may reflect health related variation in body mass. Variation later in ontogeny would be more parsimoniously interpreted as indicative of behavioral differences. In hunter-gatherer groups, children commonly begin foraging early in life and start practicing adult behaviors prior to the end of adolescence (Jones et al., 1994; Bliege-Bird and Bird, 2002; Hewlett and Lamb, 2005; Stock, 2006). Children also begin using boats early in life, so

Please cite this article in press as: Osipov, B., et al., Evidence for genetic and behavioral adaptations in the ontogeny of prehistoric hunter-gatherer limb robusticity, Quaternary International (2016), http://dx.doi.org/10.1016/j.quaint.2015.09.093