Journal of Human Evolution 97 (2016) 109–122

Contents lists available at ScienceDirect

Journal of Human Evolution

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

Re-evaluation of Pleistocene and Holocene long bone robusticity trends with regards to age-at-death estimates and size standardization procedures

Lukáš Friedl [a], [*], Stanislava Eisová [b], Trenton W. Holliday [c], [d]

[a] Department of Anthropology, University of West Bohemia, 30614 Plzeň, Czech Republic
[b] CENIEH – Centro Nacional de Investigación sobre la Evolución Humana, 09002 Burgos, Spain
[c] Department of Anthropology, Tulane University, 70118 New Orleans, LA, USA
[d] Evolutionary Studies Institute, University of the Witwatersrand, 2050 Wits, South Africa

ARTICLE INFO

Article history:
Received 13 July 2015
Accepted 28 May 2016
Available online 14 July 2016

Keywords:
Postcranial robusticity
Lower limb
Femur
Tibia
Temporal trends
Aging

ABSTRACT

Long-term trends in robusticity of lower limb bones in the genus *Homo* through the Pleistocene until the present have been proposed, which have been interpreted as a consequence of decreasing levels of mobility and activity patterns, changes in lifestyle, and environmental factors. There has also long been evidence that skeletal strength increases over an individual's lifespan. This increase is caused by continuous bone remodeling that optimizes the structure of a bone to resist mechanical loadings and creates a balance between endosteal resorption and subperiosteal apposition. However, none of the previous studies of temporal trends in robusticity has considered both processes and analyzed how individual age-related robusticity might influence higher-level temporal trends. This paper therefore explores temporal trends in robusticity of lower limb long bones within the genus *Homo* and considers how individual ages-at-death can confound published evolutionary trends, given the fact that some aspects of relative bone strength tend to increase over individual lifespans. Cross-sectional diaphyseal properties of the midshaft and proximal femur and midshaft tibia of Pleistocene and early Holocene individuals, together with data on age-at-death are used to analyze changes in relative bone strength relative to individuals' ages and evolutionary time. The results show increasing bone strength in adulthood until the fourth decade and then a slight decrease, an observation that conforms to previously published results on recent human populations. However, no significant impact of age-at-death on the trends along an evolutionary trajectory has been detected. The evolutionary trends in femoral and tibial relative strength can be described as fluctuating, probably as a consequence of changing mobility patterns, environmentally and technologically influenced behaviors, and demographic processes. The differences between evolutionary trends published in several studies are explained primarily as a result of different ways of standardizing cross-sectional parameters for size, and differences in sample composition.

1. Introduction

Broadly, postcranial skeletal robusticity reflects an estimation of bone proportions relative to some other measure (Pearson, 2000a). It can thus be defined and calculated as a ratio of bone width and/or cross-sectional geometric properties and length, or relative to a mechanically relevant measure of body size (such as body mass when considering the weight-bearing bones of the lower extremities; Ruff et al., 1993). It has long been recognized that, regardless of exact definition, postcranial robusticity changes over evolutionary time (Weidenreich, 1941; Day, 1971; Kennedy, 1983, 1985; Ruff et al., 1993). For more than a century, for example, Neanderthals have been said to be robust relative to modern humans (Boule, 1911, 1912, 1913). Temporal change in postcranial robusticity throughout the Pleistocene and into the Holocene has been described both as demonstrating a gradual exponential decrease (Ruff et al., 1993) and as showing no significant trend from Early to

---

[*] Corresponding author.
E-mail addresses: lukas.friedl@gmail.com (L. Friedl), stanaeisova@gmail.com (S. Eisová), thollid@tulane.edu (T.W. Holliday).

http://dx.doi.org/10.1016/j.jhevol.2016.05.013
0047-2484/

Late Pleistocene (Trinkaus and Ruff, 2012). These differences stem primarily from different definitions of robusticity. Trends in postcranial robusticity have been studied in relation to the levels of mobility and activity patterns, changes in lifestyle, and environmental factors. Specifically, among the factors shaping hominin robusticity, mobility patterns related to subsistence strategies (Holt, 1999, 2003; Stock and Pfeiffer, 2004; Sládek et al., 2006; Sparacello and Marchi, 2008), physical properties of the landscape (Ruff, 2000a, 2005), levels of cultural development linked to encephalization (i.e., technological development; Ruff et al., 1997), and climatic factors (Pearson, 2000a,b) have been pinpointed as most prominent.

Differences in relative bone strength appear not only at the population level over evolutionary time in various environments but also at the level of individuals within their own lifespans. Bone strength tends to vary with growth and development as well as with aging (Atkinson and Weatherall, 1967; Martin and Atkinson, 1977; Ericksen, 1982; Ruff and Hayes, 1983; Feik et al., 2000; Mays, 2000; Mays, 2001; Seeman, 2001; Ahlborg et al., 2003; Russo et al., 2006; Cowgill and Hager, 2007; Cowgill, 2010; Streeter et al., 2010; Allen et al., 2012; Mantila Roosa et al., 2012; Warden et al., 2014). During childhood and adolescence, the growth trajectories of long bone shafts and articulations (lengthening and/or general increase in size) show similar progression, while shaft structural strengthening is slow at first, only catching up in early adulthood when body mass increases. Thus, body mass alone is one of the factors directly responsible for changes in appendicular bone strength as individuals get older, especially in weight-bearing limbs (lower limbs in humans; Ruff et al., 1994; Moro et al., 1996; van der Meulen et al., 1996; Ruff, 2003). Nonetheless, other factors can alter the way limb bone robustness is formed. Among these agents, diet, hormonal regulation, health status, and genetic factors are listed most often (Lieberman, 1997; Pearson, 2000a; Ruff, 2000a; Pearson and Lieberman, 2004). Bone remodeling is a process that is active throughout the life of an individual and if there are sufficient loadings, long bones tend to increase or maintain their strength to accommodate those loadings and optimize their structure (Lovejoy et al., 1976; Ruff and Hayes, 1983; Frost, 1985; Ruff et al., 1993; Trinkaus et al., 1994; Stock and Pfeiffer, 2004). Clinical studies, however, have shown that physical activity, and the resulting increase in bone rigidity during early adulthood, positively influences how this rigidity is maintained later in life when there are fewer and lower-magnitude mechanical stimuli to the skeleton (Warden et al., 2014).

Continuous remodeling during adulthood operates through subperiosteal apposition and endosteal resorption. In the earlier stages of adulthood and under the assumption of proper mechanical stimulation, subperiosteal apposition progresses roughly at the same pace or slightly faster than endosteal resorption and thus the amount of cortical bone can either slightly increase or remain constant, but the total area of a bone section and second moments of area tend to increase (Ruff and Hayes, 1983, 1988; Feik et al., 2000; Mays, 2000, 2001; Russo et al., 2006; Allen et al., 2012; Mantila Roosa et al., 2012) due to the cortical bone being placed farther from the neutral axis (Lazenby, 1990). The process of active maintenance of cortical volume slows, and eventually halts, later in life when endosteal resorption becomes increasingly more progressive, causing a reduction in cortical bone thickness. However, even in older individuals, accelerated endosteal resorption is balanced out by increased rates of periosteal apposition so that the mechanical resistance of a bone is maintained (Garn, 1970; Ruff and Hayes, 1988; Heaney et al., 1997; Ruff, 2000a; Seeman, 2001, 2003). Such periosteal apposition, however, need not operate as fast as endosteal resorption since mechanical resistance is maintained sufficiently by adding relatively small amounts of cortical bone placed farther from the neutral axis (Lazenby, 1990).

When evaluating these processes, one should also consider possible sex differences in remodeling trajectories throughout life. Ruff and Hayes (1983, 1988) showed that there are significant differences between archaic agricultural and recent populations in the way that cross-sectional geometric properties respond to aging in both sexes. While both archaic and recent males are subject to the increase in bone subperiosteal area and second moments of area, only archaic females follow the same pattern. In recent females, the appositional growth in older individuals is not detectable. It is reasonable to assume that this loss of robusticity (expressed through decreased values of polar second moment of area) in recent females is caused by insufficient mechanical stimulation with increased sedentism (Ruff and Hayes, 1988). The sex differences are even more pronounced when evaluating clinical evidence. Several studies (Seeman, 2001, 2003; Ahlborg et al., 2003; Russo et al., 2006) have demonstrated that there are significant differences between men and women in their cortical bone volume in later stages of life, primarily due to a subperiosteal appositional rate that is faster in males than in females.

Sex differences in bone remodeling during later stages of life are closely linked to circulating hormone levels and resulting menopause in females (Ahlborg et al., 2003). This would obviously put a remodeling trigger point at around 50 years of age, at least for females. This suggestion is basically confirmed by studies focusing on the amount of cortical bone (e.g., Ericksen, 1982; Feik et al., 2000). However, when one looks at other geometric properties, like total area of a section and second moments of area, there seems (with the exception of recent females; Ruff and Hayes, 1988) to be gradual increase throughout adulthood due to continual subperiosteal apposition (Ruff and Hayes, 1983, 1988; Mantila Roosa et al., 2012).

In analyzing variation in appendicular robusticity, we are left with two potentially disparate processes. One is a presumed evolutionary trend from the Pleistocene to Holocene, while the second is the trend operating over the course of individual lifespans. None of the previous studies of temporal trends in robusticity (Ruff et al., 1993; Pearson, 2000a,b; Holt, 2003; Trinkaus and Ruff, 2012) has considered both processes and analyzed how individual age-related robusticity might influence higher-level temporal trends. Additionally, Pleistocene fossil material is, and always will be, limited in quantity, especially when only lower limb long bones are considered. What if there are significant biases introduced in evolutionary trends of robusticity by having skewed demographic sampling for different temporal periods (i.e. if there are primarily young individuals in one group and primarily old individuals in other temporal groups)? This paper therefore explores temporal trends in the robusticity of lower limb long bones within the genus *Homo* in the Pleistocene and Early Holocene while accounting for both processes. The principal question tested is whether the consideration of age-at-death of Pleistocene and Holocene individuals can confound published robusticity trends, given the fact that some measures of relative bone strength tend to increase over an individual's lifespan. Since we are examining only Pleistocene and early Holocene individuals, we can assume that they all maintained relatively active lifestyles throughout adulthood and therefore expect that their age-related remodeling followed the continuing increase in parameters influenced by subperiosteal apposition, regardless of sex.

2. Materials and methods

With one exception, all the data used in this study were collected from the literature. We used femoral (Fe50%) and tibial