

## Chapter 2

# Long Bone Structural Analyses and the Reconstruction of Past Mobility: A Historical Review

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**Abstract** The use of long bone structural analysis to reconstruct past human behavior had its origins in the 1970s, although it was only in the last 30 years that true population-level comparisons began to be carried out. Since then, several dozen studies of archaeological and paleontological samples have been completed, illustrating the complexity as well as some consistencies in the relationship between bone morphology and mobility. Bone cross-sectional shape rather than relative size appears to be more clearly related to mobility differences. This is particularly true in comparisons between males and females within the same population. Terrain has a strong effect on relative strength of the lower limb bones. Body shape differences also have an effect on structural properties, and must be factored into comparisons. New methods of noninvasively acquiring structural properties promise even greater accessibility of information and larger samples in the future, although caution must be applied when extrapolating from approximations to true section properties.

**Keywords** Biomechanics • Long bone • Mobility • Sexual dimorphism • Body size • Body shape

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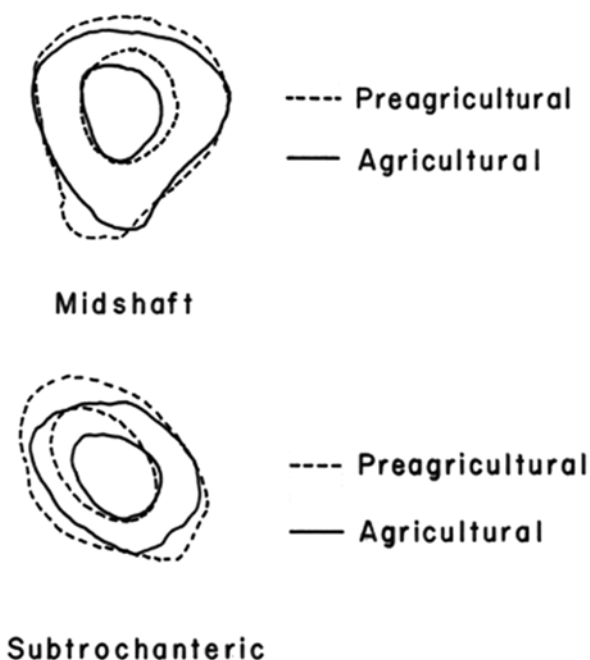
## 2.1 Earlier Studies

Assessing long bone strength through the analysis of diaphyseal cross-sectional geometry can be traced back as far as Galileo (Galilei 1638). The first full-scale analysis of an actual human long bone (a femur) is probably that of Koch (1917), almost 100 years ago. Endo and Kimura first applied this technique in a human paleoanthropological or archaeological context in 1970, in their comparative analysis of the Amud 1 Neandertal tibia. Several mechanically oriented analyses of human samples rather than individuals soon followed (Amtmann 1971; Kimura 1971; Minns et al. 1975; Lovejoy et al. 1976; Martin and Atkinson 1977; Miller and Piotrowski 1977; Lovejoy and Trinkaus 1980). With the exception of Lovejoy and coworker's studies of modern and Neandertal tibias, none of these were explicitly comparative, being mainly concerned with general mechanical modeling and/or age and sex differences within samples. A number of other investigations of archaeological samples were carried out during the same general time period (Dewey et al. 1969; Van Gerven et al. 1969; Van Gerven and Armelagos 1970; Van Gerven 1973; Carlson et al. 1976) but with a focus on cortical thickness and areal measurements and systemic age-related bone loss (osteoporosis) rather than mechanical effects.

Most of these early studies were limited in size and scope by two factors: the need to destructively sample (i.e., section) specimens in order to obtain cross sections, and the use of manual point-counting methods to input bone distribution information. The development and wider availability of computed tomography (CT) for anthropological research (e.g., Jungers and Minns 1979; Tate and Cann 1982; Sumner et al. 1985; Ruff and Leo 1986) helped to alleviate the first problem. Other new noninvasive techniques, including external molding combined with multiplane radiography (Trinkaus and Ruff 1989; O'Neill and Ruff 2004), provided additional ways to accurately reconstruct cross sections without physical sectioning of specimens. Biplanar radiographs alone are not adequate for reconstructing human lower limb long bone cross sections (O'Neill and Ruff 2004), even when corrected for eccentricity of the endosteal and periosteal contours (Ohman 1993). At the same time, new automated and semi-automated methods for deriving section properties from images were developed (Nagurka and Hayes 1980; Sumner et al. 1985). These made possible, for the first time, truly demographic studies of large samples (Ruff and Hayes 1983a, b; Sumner 1984).

The first controlled population-level comparison of long bone structural properties was carried out by the present authors on archaeological samples from the Georgia coast (Ruff et al. 1984). Cross-sectional properties of femora from preagricultural (2200 B.C.–A.D. 1150) and agricultural (A.D. 1150–1550) groups were compared. The agricultural group showed a decline in all properties (see Fig. 2.1), with many of the declines remaining significant even after adjustment for different body sizes (bone lengths). The agricultural group also showed an increase in circularity (Fig. 2.1). Both results were attributed to a decline in activity levels in the agricultural group. Interestingly, when compared to similar data from the Pecos Pueblo, New Mexico sample (Ruff and Hayes 1983a, b), the Georgia coast preagricultural

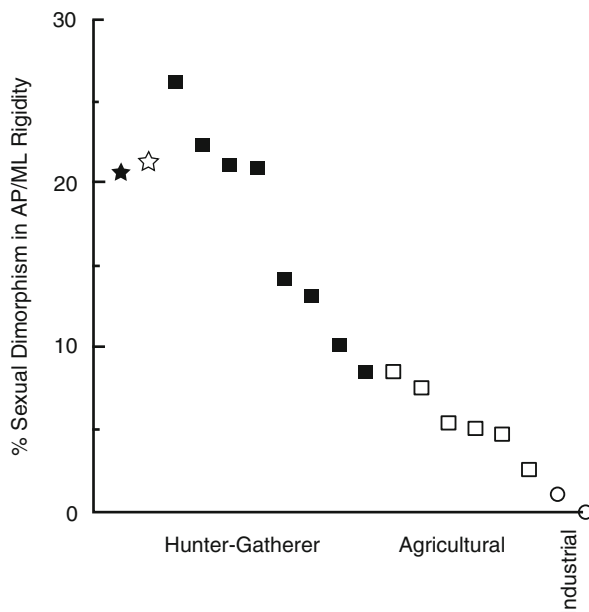
**Fig. 2.1** Cross sections of femora from pre-contact preagricultural and agricultural Georgia coast samples, scaled to equal bone lengths. (Reproduced with permission from Ruff et al. 1984)



group was more similar in overall robusticity, or relative size, to Pecos (which was agricultural), while the Georgia coast agricultural group was more similar to Pecos in bone shape, i.e., relative bending rigidity in different planes. This was interpreted to reflect relatively high overall mechanical loadings at Pecos, due to the rugged terrain (a hypothesis later confirmed by broader comparisons: Ruff 1999), but more similarity in *types* of activities between the two agricultural samples, specifically, lower levels of overall mobility. There was also some evidence for more diachronic change in bone shape among Georgia coast males than among females, suggesting greater effects of subsistence strategy on activities among males. Sex differences in femoral and tibial structure had also been noted within the Pecos sample (Ruff and Hayes 1983b), and tentatively attributed to a combination of sexual dimorphism in body shape (wider hips in females) and activity differences between the sexes (males more mobile).

This theme was taken up again in broader comparisons between the Pecos sample and a modern US autopsy sample, as well as a number of other femoral and tibial archaeological samples (Ruff 1987). Males were shown to have relatively greater anteroposterior (AP) strength in the region about the knee, and females to have relatively greater mediolateral (ML) strength in the region near the hip. The AP/ML strength difference near the knee declined from hunter-gatherers to agriculturalists to modern industrial samples, while sexual dimorphism near the hip showed no trend. External breadth measurements, available for a wider sampling of populations, exhibited similar patterns. The decline in sexual dimorphism near the knee (including the femoral and tibial midshafts) was due to a decrease in male AP/ML

**Fig. 2.2** Sexual dimorphism in femoral midshaft AP/ML bending rigidity in relation to subsistence strategy [(male–female)/female  $\times$  100]. *Filled and open squares*: Native North American hunter-gatherers and agriculturalists, respectively; *open circles*: industrial samples; *filled and open stars*: Neandertals and Upper Paleolithic humans, respectively. Each point represents a population (or in the case of the two earliest groups, sample). (Reproduced with permission from Ruff 2005)



strength, with no change in females. AP bending rigidity or strength in this region is probably related to the degree of flexion of the knee and applied force of the knee flexors and extensors during locomotion, all of which should increase with more rapid locomotion over longer distances, i.e., increased mobility (Ruff 1987, 2005). These results were thus consistent with ethnographic data indicating a decline in sexual division of labor through the same subsistence changes, specifically, a decline in male mobility. Later comparisons incorporating a larger number of population samples further supported this conclusion (Ruff 1999, 2005) (see Fig. 2.2). Interestingly, Neandertal and early anatomically modern (Upper Paleolithic) humans showed similar levels of sexual dimorphism in bone shape to modern hunter-gatherers (Fig. 2.2), suggesting a similar division of labor. The relatively constant sexual dimorphism in bone shape near the hip is consistent with observed sexual dimorphism in pelvic shape and predictions based on biomechanical models of this region (Ruff 1995).

The Georgia coast study was later extended to include more population samples in the region, including several living during the Spanish contact period, and the humerus as well as the femur, with a total sample size of 168 femora and 189 humeri (Fresia et al. 1990; Ruff and Larsen 1990, 2001). This broader sampling revealed several interesting patterns and trends, with implications for reconstructing mobility and other behavioral characteristics. First, the reduction in overall femoral robusticity (strength relative to body size) and midshaft AP/ML bending rigidity observed earlier between preagricultural and agricultural samples did not continue in a uniform manner in the contact period. Both sexes actually increased slightly in overall femoral rigidity in missionized Guale samples, and in humeral rigidity among males,

although not among females. This was interpreted to reflect an overall increase in workload as well as possible increases in relative body mass under mission conditions. However, AP/ML bending rigidity of the midshaft femur continued to decline in contact period females, while showing a slight initial increase in males followed by a decrease. The early missionized males also showed a large increase in variability in this index suggestive of a bimodal distribution. Together this evidence suggested that some males from the early mission period became less mobile and some increased in mobility, while females as a whole became less mobile. These observations are consistent with historical evidence for enforced long-distance travel by some male Guale as part of the Spanish *repartimiento* labor system, with other males (and all females) not involved. Thus, sexual dimorphism in bone shape was quite high on average among mission period Guale, similar to that of many hunter-gatherer populations, possibly because sexual “division of labor” (in this case, forced labor) also increased (on average). Interestingly, a contemporary, geographically adjacent but less acculturated sample of Timucua did not show this same increase in male diversity or sexual dimorphism, as would be predicted given the less drastic effects of missionization in this population (they also had relatively lower overall robusticity).<sup>1</sup> The somewhat disparate temporal patterns for the upper and lower limbs in male and female Guale also suggests different behaviors, i.e., work requirements, during the mission period, with males engaging in heavier or more frequent lifting activities. Again, the less acculturated Timucua did not show this pattern.

Several other comparative studies of Native North American archaeological samples were carried out during this time period, from geographic regions ranging from the Delaware coast (Robbins et al. 1989) to the Tennessee River Valley (Bridges 1989), Great Plains (Ruff 1994a), New Mexico (Brock and Ruff 1988), and the Great Basin (Ruff 1999). The effect of subsistence strategy and relative mobility on long bone cross-sectional geometry was a major theme of each of these studies. One of the most consistent patterns observed was a decline in sexual dimorphism in midshaft femoral shape with increased sedentism, supporting the general model presented above (Fig. 2.2). Wescott (2006) reported similar findings for a number of other North American archaeological and modern samples. In some other respects, these various studies showed a fair degree of heterogeneity in results. For example, Bridges (1989) found an increase in relative strength at some skeletal locations in the femur and humerus between preagricultural and agricultural samples in the Tennessee River Valley, unlike the temporal decline found in the Georgia coast samples (and see Larsen and Ruff 2011). However, she did find that circularity of sections increased with the adoption of agriculture, which is similar to the Georgia coast findings. As with the original comparisons with the Pecos sample

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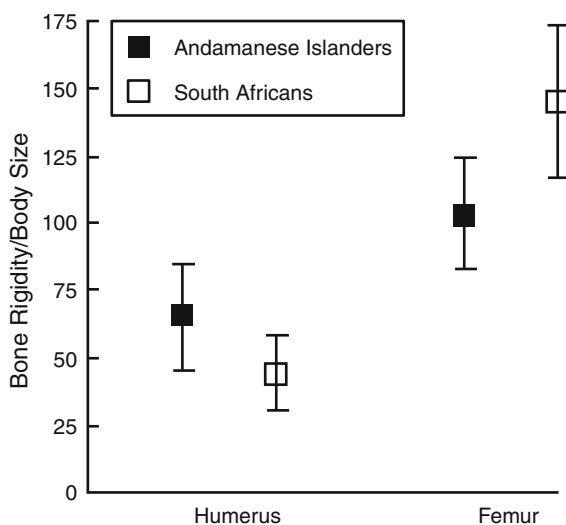
<sup>1</sup> Our earlier study (Ruff and Larsen 2001) assumed that the “Yamassee” sample represented a group who had emigrated to Amelia Island, Florida, from South Carolina. New biodistance and mortuary evidence indicates the likelihood that the series is from an early Timucua population, the descendants of a native tribe indigenous to Amelia Island (see Stojanowski 2013).

(Ruff et al. 1984), then, bone shape appeared to be a better indicator of types of activity (including mobility) than overall cross-sectional size. The combined effects of nutrition and behavior on cross-sectional morphology were emphasized in a study of three Great Basin samples (Ruff 1999). These samples had relatively thin, but expanded long bone cortices, leading to high levels of bending rigidity. This morphology may reflect the combination of a relatively poor diet, leading to endosteal resorption of bone (Garn et al. 1969), combined with a very vigorous lifestyle, which would favor periosteal expansion (Ruff and Hayes 1988). In broader comparisons with other Native North American samples, this study also demonstrated a marked effect of terrain on relative rigidity of the femur, with femora from mountainous regions (including the Pecos as well as Great Basin samples) exhibiting greater rigidity relative to body size than those from plains or coastal regions.

## 2.2 Other Factors: Terrain and Body Shape

The effects of different types of “terrain” on long bone robusticity were also addressed in two later studies (Stock and Pfeiffer 2001; Weiss 2003). Stock and Pfeiffer (2001) compared relative rigidity of the femur and humerus in Andamanese Islanders and Later Stone Age South Africans. Both groups were highly “mobile,” but in different ways: via marine transport (canoeing) in the Andamanese and via long-distance terrestrial travel in the South Africans. Consistent with these behavioral differences, the Andamanese showed greater relative rigidity in the humerus and clavicle, and the South Africans in the femur, tibia, and metatarsal (see Fig. 2.3). AP/ML rigidity was not assessed directly, but the Andamanese did show increased circularity

**Fig. 2.3** Humeral and femoral overall rigidity (polar second moment of area) relative to body size in Andamanese Island and South African Stone Age samples (mean  $\pm$  SD). (Data from Stock and Pfeiffer 2001)



(reduced maximum/minimum bending rigidity) in the midshaft femur compared to the South African sample, with a much more marked difference among males.

Weiss (2003) compared a combined measure of humeral diaphyseal robusticity in five different Native North American samples with varying degrees of dependence on water transport, including ocean-rowing Aleut and British Columbian samples, river-rowing Georgia coast samples, and the non-rowing Pecos Pueblo sample. Males were responsible for rowing in those samples that practiced this form of transport. Consistent with expectations, males showed a progressive increase in humeral robusticity with increased dependence on water transport, while females showed no similar trend, except that Aleut females were the most robust. The author speculated that this latter result may be attributable to the other vigorous tasks performed by Aleut females, such as butchering whales, although factors such as overall body build related to climatic effects were considered possible contributors.

How to standardize long bone structural properties for body size and shape differences is a long-standing issue that has important implications for comparative studies (Ruff 1984, 2000b; Ruff et al. 1993; Trinkaus et al. 1999a; Polk et al. 2000; Shaw and Stock 2011). It is actually part of a more general issue regarding allometry, or size-shape relationships, within long bones, again first broached centuries ago (Galilei 1638; also see, e.g., Schultz 1953; McMahon 1973; Alexander et al. 1979). In earlier studies, bone length or powers of bone length were often used to size-standardize cross-sectional diaphyseal dimensions (Ruff et al. 1984, 1993; Bridges 1989; Ruff 1999; Pearson 2000). This was based in part on the strong allometric scaling relationships between bone length and cross-sectional size observed within human samples (Ruff 1984; Ruff et al. 1993). However, it was also realized that this procedure carries an implicit assumption that body proportions, i.e., bone or limb length relative to body size, are invariant. When this was manifestly not true, for example, in comparisons between Neandertals and modern humans, a correction factor was applied (Ruff et al. 1993). Even in comparisons between different modern (Holocene) samples, indiscriminant use of bone length alone to standardize properties can lead to misleading results (Ruff 2000a). For mechanically oriented studies, and based on a beam model of the diaphysis (Lovejoy et al. 1976; Ruff and Hayes 1983a; Gere and Goodno 2013), the best measure of body size is body mass, together with some measure of beam length for bending and torsional rigidity/strength parameters. For strength measures (i.e., section moduli), body mass \* beam length is appropriate; for rigidity measures (i.e., second moments of area), body mass \* beam length<sup>2</sup> should be used (see Ruff 2008 for description of properties). These factors apply to the upper as well as lower limb (Ruff 2000b). For most long bone diaphyseal locations, “beam length” here can be taken as bone length; however, for the proximal femur, body (maximum pelvic, or bi-iliac) breadth is a better measure of beam length (Ruff 2000b).

The importance of accounting for body shape variation in reconstructing mobility patterns was illustrated in a study of the “Ice Man,” the late Neolithic body discovered in the Tyrolean Alps (Ruff et al. 2006b). The Ice Man’s femoral strength relative to body size was about average for European Neolithic males, but his tibial relative strength was very high. In terms of cross-sectional shape, his femur was

slightly rounder, i.e., ML reinforced, than average for Neolithic males, but his tibia had a high AP/ML bending strength ratio. Together these results imply relatively higher mechanical loads on his tibia, particularly AP bending loads, and relatively higher ML bending loads on his femur. This overall morphology is consistent with a combination of high mobility, increasing the AP loadings on his tibia, with his relatively “stocky” body shape, i.e., high body (bi-iliac) breadth to stature ratio, which increases ML bending of the more proximal lower limb (Ruff 1995). This illustrates that body shape must be factored into interpretations of mobility based on structural analyses. Similar conclusions were reached in a broader comparison involving a wide range of archaeological samples (Shaw and Stock 2011), and an even broader analysis of Pleistocene *Homo* specimens (Trinkaus and Ruff 2012). In fact, the relationship between long bone robusticity and body shape can be used to work backwards from cross-sectional geometry to reconstruction of body shape in more incomplete specimens (Trinkaus et al. 1999a, b).

Because climate has strong effects on body shape, in humans and other animals (Mayr 1963; Roberts 1978; Ruff 1994b), this is related to another potentially significant issue: how the effects of climate might modulate the relationship between long bone diaphyseal structure and activity patterns. Studies that have explicitly examined this issue (Pearson 2000; Stock 2006) have found, not surprisingly, that climate and various indices of relative long bone strength or rigidity are in fact correlated. However, these findings can largely be explained as indirect effects of climate on body shape, which then affects mechanical loadings (particularly of the lower limbs). In one study (Pearson 2000), diaphyseal breadths were divided by bone length to size-standardize them. As noted above, this systematically biases results for populations with different body proportions, i.e., it will systematically underestimate body mass in relatively stocky, short-limbed (e.g., arctic) populations, which have more mass per unit length compared to equatorial populations, and vice versa. Therefore, it was inevitable that “climate” would be strongly correlated with “robusticity” in this analysis, but this does not indicate any direct effect of climate on mechanical loadings per se. Incorporation of body mass is necessary in order to appropriately size-standardize structural properties. This was done in the other study (Stock 2006), which found some strong partial correlations between lower limb bone shape indices and degree of terrestrial mobility when controlling for average (“effective”) temperature, especially among males. Significant partial correlations between temperature and lower limb bone shape and relative strength mainly occurred in the proximal femur. However, as noted above, the most appropriate measure of “beam” length in this region is body (bi-iliac) breadth (Ruff 2000b), and in this study bone lengths were used exclusively as beam lengths. Therefore, this result also likely simply reflects a climatic effect on relative body breadth, which shows very strong ecogeographic clines among humans (Roberts 1978; Ruff 1994b). There is, in fact, no plausible physiological mechanism that would directly link climatic variation with variation in long bone mechanical parameters. Thus, climate per se should not be a confounding factor in mobility reconstructions.



## 2.3 Recent Studies

The past decade has witnessed an explosion of interest in using long bone structural analyses to address issues concerning mobility and other activity patterns among past populations (Holt 2003; Stock and Pfeiffer 2004; Kimura 2006; Marchi et al. 2006, 2011; Sládek et al. 2006a, b; Wescott 2006; Wescott and Cunningham 2006; Carlson et al. 2007; Shackelford 2007; Maggiano et al. 2008; Marchi 2008; Sparacello and Marchi 2008; Nikita et al. 2011; Ogilvie and Hilton 2011; Sparacello et al. 2011; Stock et al. 2011). The geographic range represented in these studies has also spread beyond an earlier, largely North American focus to include many regions of the Old World. (A number of studies of modern and archaeological samples from Japan had also been carried out earlier (Kimura and Takahashi 1982, 1984; Nakatsukasa 1990)). With expansion into many different environments—both physical and cultural—has come a greater appreciation of the complexities involved in the relationship between behavior and cross-sectional morphology. In many respects—for example, sexual dimorphism in lower limb bone cross-sectional shape in relation to varying mobility levels—earlier observations have been largely confirmed and extended. The variety of ways in which “mobility” itself can be defined, and the different effects this can have on bone morphology and sexual dimorphism, have been addressed in a number of studies (e.g., Ogilvie 2000; Marchi et al. 2006, 2011; Sládek et al. 2006b, 2007; Carlson et al. 2007; Marchi 2008; Sparacello and Marchi 2008; Ogilvie and Hilton 2011; Stock et al. 2011). For example, in a series of investigations, Marchi and coworkers have shown that males in a Neolithic sample from Liguria, Italy, conform more closely in morphology to Upper Paleolithic and Mesolithic European samples, consistent with their highly seasonably mobile (transhumant) subsistence economy combined with a very rugged terrain (Marchi et al. 2006, 2011; Marchi 2008). Thus, the simple dichotomy between foraging and food production is actually much more complex, with actual degrees and kinds of mobility varying with local circumstances. Overall, however, there is a tendency for foragers to be more robust and more mobile than farmers.

Several studies have reported stronger associations between mobility levels and cross-sectional shape of lower limb bones (i.e., AP/ML or maximum/minimum bending rigidity) than with overall robusticity (average rigidity or strength) (Wescott 2006; Carlson et al. 2007; Maggiano et al. 2008; Sparacello and Marchi 2008), paralleling earlier findings (Ruff et al. 1984; Bridges 1989). This may be attributable in part to the difficulty of adequately standardizing for body size differences in robusticity analyses—a variety of techniques have been used, although the general approach advocated above (Ruff 2000b) has been employed in many of the most recent studies. Examining cross-sectional shape ratios avoids this problem, although the issue of possible body shape effects should still be considered, especially in analyses that include geographically disparate populations. Inclusion of upper limb bones in many of the more recent studies is useful in distinguishing between general activity levels and changes in mobility per se (since the upper limb should be much

less affected by locomotor demands). Again, this approach was presaged in some earlier studies (Ruff and Larsen 1990, 2001; Ruff 1999). The addition of other less commonly studied long bones, such as the fibula, can also provide information on types of mechanical loadings of the lower limb, and thus mobility and terrain effects (Marchi and Shaw 2011; Marchi et al. 2011).

Recent experimental studies of humans and other animals have provided further context for interpreting bone shape differences in archaeological remains. Shaw and Stock (2009) compared midshaft tibial cross-sectional geometry in young adult male cross-country runners, field hockey players, and controls. Both groups of athletes had increased robusticity, or bone rigidity relative to body size, but only the runners had increased maximum/minimum bending rigidity, i.e., increased AP bending rigidity, compared to controls. Thus, field hockey players had robust, but more rounded cross sections, which the authors interpreted as a response to more varied mechanical loading (ML as well as AP) of the lower limb, due to frequent turning and change of direction, compared to the more straight-line movements of the runners. Similar findings were reported by Carlson and Judex (2007) in their study of the femora of young mice subjected to increased turning versus linear locomotion. Macdonald et al. (2009) found that a jumping activity (which would primarily load the tibia in AP bending) preferentially increased AP bending rigidity in the midshaft tibia in school children. Cowgill et al. (2010) reported age-related increases in AP/ML rigidity of the midshaft femur that corresponded to ontogenetic changes in lower limb loading, with relatively higher ML loadings in very young children learning to walk. Thus, there is experimental support for a relationship between AP/ML shape of the lower limb bones and the degree and kinds of mobility practiced. Preferential loading in the sagittal (AP) plane, which would be expected in long-distance travel in a relatively straight line, leads to relatively increased AP bending strength. Conversely, more irregular movements, such as those involved in negotiating steep and rough slopes, may produce relatively higher ML (as well as AP) loadings, and thus a rounder cross section (see Higgins 2014). Therefore, as with overall robusticity, terrain is a consideration in interpreting bone shape responses to increased mobility.

Results of some recent experimental and observational studies have also led to calls for caution in overly simplistic interpretations of bone structural responses to exercise (e.g., Lieberman et al. 2004; Cowgill 2010; Wallace et al. 2012). For example, genetic adaptation as well as developmental plasticity is likely involved in producing differences in bone form between and within populations and species. However, this in itself does not negate the effects of mechanical loadings applied during life (Ruff et al. 2006a). Population history as well environment should be considered when interpreting bone structural variation, but, as with all physical characteristics, within a functional and physiological framework (Ruff et al. 2013).

Finally, another very recent development in this field has been to derive bone cross-sectional properties from periosteal contours only, obtained using external molding or laser scanning (Stock and Shaw 2007; Sparacello and Pearson 2010; Marchi et al. 2011; Sparacello et al. 2011; Davies et al. 2012; Macintosh et al. 2013), a technique that has been used to help reconstruct mobility differences

between populations (Marchi et al. 2011; Sparacello et al. 2011). In methodological tests, very high correlations between properties determined in this way and true cross-sectional properties were obtained in several of these studies. This follows from the fact that the most critical structural properties—second moments of area and section moduli—are highly dependent on the distribution of bone around a central axis or point; thus, the position of the outer contour of a section is much more important than that of the inner contour (see Ruff 2008). The use of only outer contours in analyses has several advantages, including more rapid acquisition of data (i.e., without the need for radiographing or CT scanning) and some simplification of reconstruction techniques (e.g., see Biknevičius and Ruff 1992; O'Neill and Ruff 2004; Sylvester et al. 2010). However, there are several important caveats that must be kept in mind when applying such methods: (1) While average errors in estimation of properties between samples may be relatively small, *individual* errors may be much larger (Sparacello and Pearson 2010; Macintosh et al. 2013). This has particular relevance for analyses that involve individual paleontological specimens, pathological specimens, or special subgroups of samples. (2) Error varies depending on the location of the sections, with rounder sections near midshaft showing smaller errors than those nearer bone ends (O'Neill and Ruff 2004; Macintosh et al. 2013); some of the above methodological tests examined only mid-diaphyseal regions. Thus, the approach is less applicable to regions such as the proximal tibia or femur. (3) Changes at the endosteal surface are critical in many kinds of analyses, including evaluation of nutritional effects (Garn et al. 1969), bone growth and development (Ruff et al. 1994), and aging (Ruff and Hayes 1983b). The endosteal surface also appears to be the most sensitive to mechanical influences after mid-adolescence (Ruff et al. 1991, 1994; Bass et al. 2002; Kontulainen et al. 2002), which may explain why earlier humans have relatively thick long bone cortices (Kennedy 1985; Ruff et al. 1993). (4) Related to this last point, not factoring in systematic differences in endosteal dimensions may lead to biased comparisons in broader studies. For example, chimpanzees and humans have systematically different relative cortical thicknesses of their femora and humeri; thus, consideration of external dimensions alone results in overlapping inter-limb proportions, while comparison of true cross-sectional properties yields complete separation between the species (Ruff 2009).

Therefore, as Sparacello and Pearson (2010: 620) noted in advocating the external approximation method: “Our conclusions apply best for researchers comparing estimates of population means drawn from fairly similar skeletal samples to make inferences about the behaviorally determined mechanical environment of past populations.” Even in that situation, however, caution is advised: one of the most striking differences between the preagricultural and agricultural samples from the Georgia coast (Ruff et al. 1984) was the relatively inwardly “contracted” external and internal contours of the agricultural sample, which resulted in elevated relative cortical thickness combined with reduced rigidity (see Fig. 2.1). Reductions in cortical area in the agricultural group were thus very small compared to those in second moments of area. This had important implications regarding interpretations of dietary versus mechanical effects on morphology (diet might be expected to have

more effect on amount of cortical bone, and behavior on distribution of bone), an observation that would have been missed had endosteal dimensions not been assessed. This also emphasizes the importance of considering non-mechanical as well as mechanical influences when interpreting bone structural variation (Ruff 1999; Ruff et al. 2006a).

Of course, even simpler linear external breadths or circumferences of long bone diaphyses have long been used to assess morphological and in some cases behavioral differences between populations (see references in Lovejoy et al. 1976; Ruff 1987). This may be most justifiable when applied in the form of “shape” indices, e.g., AP/ML breadth, in broader comparisons (Jungers and Minns 1979; Ruff 1987). However, in more fine-grained comparisons, linear dimensions, including shape ratios, do not accurately reflect variation in true cross-sectional properties (Stock and Shaw 2007).

## 2.4 Conclusions

The application of long bone structural analyses in archaeology and human paleontology had its beginnings in the 1970s. The development of more automated and noninvasive techniques in the next decade allowed larger-scale demographic studies and the first true population-level comparisons to be carried out. Methods for standardizing for body size and shape differences were developed, and the effects of terrain as well as behavior were factored into comparisons. Recent studies have emphasized the complexity of influences on bone structure, including local environmental variation, different forms of “mobility” and sex-related economic roles, and effects on the upper as well as lower limb. Despite this complexity, though, a number of general observations can be drawn: (1) The degree of sexual dimorphism in bone shape (AP/ML rigidity or strength) in the middle region of the lower limb (midshaft femur through midshaft tibia) parallels the degree of sexual division of labor, in particular, the relative mobility of males versus females. (2) Bone shape in general is a better indicator of mobility differences than relative bone size. This may be in part due to difficulties in adequately standardizing for body size differences, as well as the relative behavioral non-specificity of overall bone robusticity. (3) It is important to consider body shape (relative limb length, relative body breadth) when interpreting differences in structural properties. Climate per se does not have a direct influence on bone mechanical properties, but does affect them through its influence on body proportions.

Given the tremendous increase in interest in this field in recent years and the increasing availability of rapid data acquisition techniques, we look forward to many new advances in the coming decades. As noted elsewhere (Ruff et al. 2006a: 484): “While physical context and material culture give clues to past behavior, analysis of the skeletons themselves is the most direct way to reconstruct individual behavior, and to explore intra- and inter-populational differences in behavior.” The continued application of engineering techniques to skeletal remains will yield insights into mobility patterns and other forms of past behavior that would not otherwise be achievable.

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