Kristian J. Carlson · Damiano Marchi
Editors

Reconstructing Mobility

Environmental, Behavioral, and Morphological Determinants

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Preface

For decades, scientists have relied on the concept of mobility in describing activity patterns of past and present human populations. Population-level comparisons have traditionally sought to demonstrate differential mobility (e.g., logistical or residential) amongst Pleistocene or Holocene *Homo* groups, using this as a basis for inferring convergent or contrasting adaptive behavior. For example, shifting from a hunter-gatherer to a more sedentary agricultural subsistence strategy generally has been associated with a relative decline in mobility associated with the latter. Substantial efforts have been devoted towards inferring which musculoskeletal adaptations best reflect such a potential shift in mobility. The central role of bipedalism in human locomotion predisposes lower limb musculoskeletal anatomy to feature prominently in these inferences, although it is important to note that expressions of mobility in other areas of the postcranium (e.g., the upper limb) are gaining traction in the field when studying select populations (e.g., coastal or island groups). It is problematic that often mobility is not defined a priori in precise enough terms to facilitate comparability of results across studies. Typically, some derivation of an ethnographic definition of mobility is adopted, whether explicitly recognized or not (e.g., populations with greater mobility travel farther than populations with lesser mobility). Usually, in applying the ethnographic definition, unstated motivations for travel focus on resource acquisition or intergroup relationships (e.g., trading).

On the other hand, an excessively narrow application of the concept of mobility, such as a mechanically focused one, equally limits comparisons of results across studies. Not all studies would (nor should) integrate experimental approaches in order to quantify mobility. Resources necessary for the requisite acquisition of ground reaction force and kinematic data are not equally available to all researchers, and there are ethical and logistical constraints when studying human subjects. Rather, the optimal solution for defining mobility, or fully capturing its essence, should embrace a multidisciplinary approach in how the concept is applied. Despite such a long-standing and widespread reliance on the concept of mobility for reconstructing and comparing activity patterns and life histories of human populations, such an inclusive attempt at defining mobility has not yet been made.

To address this notable absence, in the spring of 2011, we organized a symposium on mobility at the 80th Annual Meeting of the American Association of Physical Anthropologists held in Minneapolis, MN. The symposium assembled an array of experts using different approaches for quantifying and comparing the effects of mobility on postcranial musculoskeletal anatomy. The symposium and subsequent discussions were aimed at embracing current perspectives and stimulating new ones that emphasized a holistic view of the interaction among intrinsic (i.e., skeletal) and extrinsic (i.e., environmental) factors relevant for quantifying and studying the differential expression of mobility. Moreover, the symposium highlighted the importance of disentangling environmental effects some of which transcend traditional categorical groupings, such as coastal versus inland and/or mountainous versus flat terrain environments.

This volume emanates from the original symposium. It is not intended to be the final word on the concept of mobility, but we hope that it will serve as a suitable starting point from which new discussion and future work can begin (or continue), perhaps with a renewed focus on critical issues identified herein or to be expanded laterally. We also hope that this volume represents a useful advance by articulating a consensus working definition of mobility that can be widely applied in anthropological studies in order to overcome the lack of consistency in explicitly defining the concept of mobility that currently cripples the comparisons of results across studies.

There are a number of people we would like to thank, for this volume would not have materialized without the substantial efforts of many. First, we would like to acknowledge the original participants in the 2011 symposium, not all of whom were able to contribute chapters to the volume for one reason or another. The discussions that took place leading up to, during, and following the symposium helped shape this volume considerably. Thank you for your contributions in driving this effort forward. We also would like to thank contributors to the volume who did not participate in the 2011 symposium for one reason or another. Your contributions to the collective effort have broadened its scope in new, exciting ways. Chapters were reviewed by a mix of fellow contributors, co-editors, and additional colleagues. We are indebted to everyone who assisted with reviewing the individual chapters. Thank you for your time and willingness to offer constructive suggestions. Finally, we would like to thank Janet Slobodien, Jacob Gallay, and others at Springer Press for encouraging the efforts that ultimately led to this volume. We are extremely grateful for this unwavering support throughout the entire process.

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Chapter 1
Introduction: Towards Refining the Concept of Mobility

Kristian J. Carlson and Damiano Marchi

Abstract Bone has an ability to model and remodel itself such that its distribution and material properties reflect factors occurring during the lifetime of an individual. Known factors influencing bone properties range from nonmechanical (e.g., age, sex, diet, health, and hormones) to mechanical ones (e.g., activity level and patterns). A lifetime accumulation of these inputs, therefore, should be reflected in the structure of bone diaphyses at the death of an individual. Inferring the inputs of these factors from long bone diaphyses of long dead individuals, whether Holocene agriculturalists or hunter-gatherers, or earlier human ancestors, depends in part on modern analogues being used to help identify and isolate the contributions of these factors. This chapter is both an introduction to and a synthesis of the collaborative effort that is recounted within the volume, and that is aimed at understanding the impact of human mobility as one such input to diaphyseal form.

Keywords Bone functional adaptation • Activity patterns • Hunter-gatherer • Travel distance • Terrain complexity

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Over the course of an individual's lifetime, bone, as a material, has an ability to model (deposition) or remodel (resorption followed by deposition), with this ability impacted by a number of mechanical (e.g., activity patterns) and nonmechanical factors including age, sex, diet, health, and hormonal fluctuations (Martin et al. 1998; Carter and Beaupré 2001). For example, bone modeling and remodeling processes appear to be age sensitive, in that bone responses to mechanical loading appear to be stronger during growth than during adulthood (see review in Ruff et al. 2006). Hormonal fluctuations or dietary factors may mediate these responses (e.g., Devlin and Lieberman 2007; Devlin et al. 2010). In order to prevent structural deficiency, or injury, a bone must resist deformations (strains) that occur during activities, accomplishing this through redistributive and reparative (re)modeling processes that are mediated by nonmechanical factors, such as those mentioned above, guided by the principle of material economy, and ultimately aimed at minimizing internal forces (stresses) within the bone. A lifetime's accumulation of these processes, therefore, should be reflected in the structure of a bone diaphysis preceding death.

Wolff (1892) was the first to coalesce some of these governing rules into what became known as Wolff's Law. Originally, Wolff envisaged only trabecular strut arrangements, having observed similarities between the internal structure of the proximal femur and lines of maximum internal stress in a Fairbairn crane (Roesler 1981). Corroborating work of contemporaries (e.g., Meyer 1867; Roux 1881), and subsequent studies that built upon preceding work (e.g., Kummer 1959; Pauwels 1968, 1980; Amtmann 1971), eventually extended Wolff's Law to cortical bone. More recently, the term "Bone Functional Adaptation" has been coined for the modern evolution of this concept (Ruff et al. 2006), with substantial work clearly remaining before its complexities can be fully understood (Pearson and Lieberman 2004; Judex and Carlson 2009; Robling 2009).

The concept of bone functional adaptation uses inverse dynamics to reconstruct loading profiles over the lifetime of an individual. Importantly, as bone functional adaptations during pre-adulthood and adulthood may differ, for example in response magnitude and rate (see review in Ruff et al. 2006), the sum total lifetime response to mechanical loading is probably not linear. In order to estimate how an individual may have loaded their limb bones (e.g., humerus, femur, tibia) over the course of their lifetime, where frequency (activity level) and magnitude (activity pattern) of these loads are amongst the most crucial determinants, the structure of a long bone diaphysis is modeled using engineering concepts, such as beam theory (Mott 1996). Estimating age-equivalent activity profiles in this manner (e.g., by calculating and comparing cross-sectional geometric properties) is a particularly powerful means of inferring adaptive strategies of individuals whose activities are no longer physically observable (e.g., Pleistocene and Holocene human groups characterized by different subsistence strategies). The earliest comparisons of bone functional adaptations focused on intragroup sources of structural variability (e.g., age and sex) rather than true activity profile differences between populations (see review by Ruff and Larsen, Chap. 2). The first detailed comparison of population-level activity profiles, in what would initiate a framework for subsequent attempts to interpret "mobility" differences between populations, assessed femoral cross-sectional properties from preagricultural and agricultural archeological samples of the Georgia Coast of North America (Ruff et al. 1984). Following this trailblazing approach instigated by Ruff et al. (1984), contrasting population mobility became an increasingly popular aspect of studies examining bone functional adaptations in populations characterized by different adaptive strategies (e.g., subsistence activities and life histories) (see review by Ruff and Larsen, Chap. 2).

1.1 Bone Functional Adaptation and Quantifying Mobility

Studies of bone functional adaptations incorporating mobility comparisons often utilize ethnographic accounts (e.g., Bridges 1989; Ruff and Larsen 2001; Stock and Pfeiffer 2001; Carlson et al. 2007) or archeological data (Marchi et al. 2011; Stock et al. 2011; Walker and Churchill 2014), when available, in order to corroborate the inferred activity profiles of the study populations generated from long bone diaphyseal structure. Unfortunately, behavioral resolution in such datasets rarely facilitates quantification of mobility, instead typically offering only comparative qualitative characterizations, such as high versus low distance traveled (e.g., White 1985; Williams 1988). This creates a disparity between the qualitative extent to which mobility is superficially characterized versus the subtleties that can be quantified in the structure of the postcranium. Greater refinement of the concept of mobility is needed.

Efforts to differentiate between logistical (individual) and residential (group) mobility (Kelly 1995; Binford 2001; see also Walker and Churchill, Chap. 12), and between broad substrate differences (e.g., terrestrial versus aquatic/marine: Stock and Pfeiffer 2001; Weiss 2003), have improved resolution in quantifying mobility somewhat. Additional studies (Ruff 1999; Carlson et al. 2007; Marchi 2008) have proposed that substrate complexity, particularly terrain unevenness (e.g., Sparacello et al., Chap. 6; Higgins, Chap. 13; Carlson, Chap. 14; but see Shackelford, Chap. 9), could add explanatory power (in terms of bone functional adaptations) to the concept of mobility, irrespective of distance traveled. This body of work suggests that there is a crucial need, therefore, to link substrate complexity with the behavioral complexity it evokes. Experimental studies have quantified the ground reaction forces and kinematics of gait responses resulting from perturbations created by substrate complexity (e.g., Demes et al. 2006; Daley et al. 2006; Voloshina et al. 2013). A limited number of bone strain studies describe diaphyseal surface strains during gaits where substrate complexity was introduced as well (Burr et al. 1996; Demes et al. 2001; Moreno et al. 2008). Athlete studies (e.g., Jones et al. 1977; Shaw and Stock 2009a, b; Shaw et al., Chap. 4) that document bone functional adaptations associated with varying activities also help clarify form–function relationships that are relevant to the concept of mobility. Ultimately, greater integration of experimental and comparative approaches may offer the best way to continue refining the concept of mobility. In this regard, a recent edited volume dedicated to linking field and laboratory research with respect to nonhuman primate locomotion (D’Août and Vereecke 2011) could be worth consulting.

1.2 Rationale and Organization of the Book

The primary motivation behind this edited volume is to assemble a diverse range of specialists in the study of form–function relationships manifested in the human postcranium, particularly those emphasizing approaches useful for reconstructing human mobility patterns. The goals are to (1) demonstrate the importance of the concept of mobility to understanding bone functional adaptations in the postcranium, (2) compile various factors worthy of consideration in defining the concept of mobility, and (3) provide a consensus, working definition consisting of the factors that are most integral. There are undoubtedly important contributors to the study of mobility and bone functional adaptations whose contributions have been omitted from this volume. We hope that these colleagues understand the space constraints encountered in producing this volume, and we eagerly anticipate their continued contributions in advancing issues raised herein.

This edited volume can be divided into several themes, unequal in representation by chapter counts, but which collectively fulfill the first stated goal: (1) contributions of musculoskeletal markers (MSMs) to studies of mobility (Weiss, Chap. 3); (2) comparisons of human adult morphologies from populations characterized by different activity profiles, e.g., mobility levels (Shaw et al., Chap. 4; Davies and Stock, Chap. 5; Sparacello et al., Chap. 6; Wescott, Chap. 7; Pearson et al., Chap. 8; Shackelford, Chap. 9; Wall-Scheffler, Chap. 10); (3) the role of ontogeny in differentiating lower limb morphologies of human populations characterized by different activity profiles, e.g., mobility levels (Cowgill, Chap. 11); (4) nonhuman models used to enlighten the relationship between bone functional adaptations and mobility (Walker and Churchill, Chap. 12; Higgins, Chap. 13; and Carlson, Chap. 14); and (5) a final chapter (Tamvada, Chap. 15) illustrating a promising future direction for the field.

Ruff and Larsen (Chap. 2) begin the volume with an historical account of studies that use postcranial bone functional adaptations to reconstruct mobility differences, touching on major issues such as the influence of sex-specific activities, terrain, and body shape. The authors recount how the field has responded to challenges in the past (e.g., limitations in data acquisition, scaling of cross-sectional geometric properties, and competing structural influences of activity and body proportions), and indicate future directions of critical importance (e.g., incorporating population history and genetics into evaluations and critically assessing techniques that enable larger sample sizes).

Weiss (Chap. 3), unlike other contributors, focuses on the role of muscles in reconstructing behavioral profiles. She reviews current literature on the expression of MSMs in human upper and lower limbs, and how these features are used for evaluating activity patterns (e.g., mobility) in groups characterized by differences in subsistence strategies, sexual division of labor, and home range terrain. She compares variability in MSM expression amongst upper and lower limbs, noting that the latter display as much or more variation than the former, which is opposite the expectation, since bipedalism, the author reasons, should result in more uniformity in the human lower limb. The author notes that age and body size are known confounding variables with activity levels. The author ends by suggesting that MSMs may be useful for characterizing hominin behavior, and by calling for more research into their etiology.

Two studies, Shaw and colleagues (Chap. 4) and Davies and Stock (Chap. 5), evaluate bone functional adaptations along the entire length of the human lower limb, which is seldom attempted due to constraints in acquiring such extensive datasets. Shaw and colleagues evaluate long bones in proximal and distal segments of the human lower limb in order to assess whether their strength and variability taper proximo-distally in response to tissue economy constraints and energetic trade-offs that appear to drive proximal mass concentration in the limb. Davies and Stock use a solid section model to compare diaphyseal rigidity of these long bones, including the location of minimum bending rigidity, across several human groups characterized by different mobility patterns, body sizes, and body shapes. Shaw and colleagues observe larger section moduli and cortical area in more proximal regions (e.g., proximal femoral diaphysis) and smaller values in more distal regions (e.g., distal tibial diaphysis), with exceptions around the knee joint, corroborating the notion of distal tapering. Variability in these properties, however, does not change along diaphyses, leading the authors to suggest that morphological plasticity is constant along diaphyses, and that morphological constraints (canalization) do not appear to drive the observed tapering. Davies and Stock note that Australian aborigines do not exhibit relatively high bending rigidity, or robusticity, corroborating results of earlier structural studies (e.g., Pearson 2000; Carlson et al. 2007), and contradicting the common perception that Australian aborigines are a highly mobile group. While Ruff and Larsen (Chap. 2) point out a few limitations in using the solid section model adopted by Davies and Stock (Chap. 5), it is worth noting that Davies and Stock corroborate results reported by Shaw and colleagues (Chap. 4) where both studies suggest that the tibial diaphysis may be a better indicator of group-wide mobility differences than the femoral diaphysis.

Two studies, Sparacello and colleagues (Chap. 6) and Shackelford (Chap. 9), emphasize terrain effects, specifically comparing relatively flat versus mountainous terrain. While Sparacello and colleagues examine fibular properties, including relative ratios of fibular/tibial properties, Shackelford focuses attention on femoral and tibial midshaft properties. Sparacello and colleagues report high fibular rigidity, including relative rigidity, in Late Upper Paleolithic, Neolithic, and Iron Age groups, despite the latter group being considered more sedentary than the former groups. The authors suggest that despite relative sedentism (i.e., low mobility) of the latter group, all three groups inhabited areas characterized by uneven terrain, possibly indicating similarly enhanced leg strength from frequent inversion/eversion of the foot while moving on uneven terrain. Shackelford, on the other hand, reports comparatively gracile femoral and tibial diaphyses in a Late Pleistocene Asian sample, which inhabited areas of more uneven terrain than the more robust northern African samples. Shackelford suggests that comparatively greater mechanical efficiency at the hips and knees of the Asian sample may be an alternative mechanism for counteracting elevated loading of the lower limbs associated with high mobility on uneven terrain.

Three studies, Wescott (Chap. 7), Pearson and colleagues (Chap. 8), and Cowgill (Chap. 11), examine several potential factors that influence the shape ratio ($I_{\max}/I_{\min}$)

and mobility index (I_x/I_y) at selected sites on human femoral and tibial diaphyses (i.e., midshafts). All make a case for the problem of equifinality[1] in shape ratios and mobility indices. Wescott compares femoral diaphyses of ambulatory individuals with those of impaired (disabled) individuals and also documents secular trends in femoral properties of modern North American populations. Ultimately, Wescott suggests that one potential solution for addressing the problem of equifinality in these ratios is to study mobility differences using a whole limb approach, incorporating comparisons of multiple cross-sectional properties when possible. Pearson and colleagues (Chap. 8) and Cowgill (Chap. 11), among other issues, examine confounding effects of body shape (i.e., bi-iliac breadth) and activity patterns (i.e., mobility) expressed in femoral and tibial midshaft shape and mobility indices. Pearson and colleagues find inconsistent (weak) correlations between femoral midshaft shape and bi-iliac breadth, while Cowgill observes stronger ties, though it is important to note that the two studies use different samples. Cowgill, in particular, observes evidence of mobility indices differentiating earlier (less than 6 years of age) in some populations (Point Hope) than others, which she suggests is attributable to the cold-adapted body proportions specific to the former. Pearson and colleagues observe low correlations between femoral and tibial midshaft shapes, suggesting that these two locations may record different activities (i.e., fast gaits preferentially affect the former location and slow gaits preferentially affect the latter location). Both chapters call for investigating midshaft shape ratios and mobility indices using mobility, body shape, and other determinants.

Wall-Scheffler (Chap. 10) reviews the literature on burden carrying, inclined walking, and energetics. Multiple lines of evidence support links between energetic savings or performance during specific behaviors and morphological variation expressed in populations. For example, a shorter tibia is correlated with energy efficiency during uphill walking, while a longer tibia is correlated with increased speed along flat terrain. Predominantly through her own work, Wall-Scheffler has documented that a wider pelvis for a given mass (e.g., typically a female trait) provides more energy savings during front and back burden carrying. The author also points out that during burden carrying a wider pelvis allows an individual to vary walking speed without substantially adjusting cost of transport (i.e., incurring a metabolic penalty). The evolutionary relevance to mobility could be profound, as the author points out, since women with broad pelves would be able to walk together in groups during burden carrying, but still adhere to their own individual optimal speed.

Three studies, Walker and Churchill (Chap. 12), Higgins (Chap. 13), and Carlson (Chap. 14), use nonhuman models in order to address questions relevant to linking human mobility and bone functional adaptations. Walker and Churchill use ranging data and group aggregate mass of social carnivores (grey wolves) to build a model for predicting home range areas of variably-sized Neandertal social groups. The authors suggest that even small groups of Neandertals (less than 33 individuals)

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[1] Ludwig von Bertalanffy (1956) defined equifinality as the same final state arising from different initial states. He originally used the term in helping found general systems theory. More recently, the term has been frequently applied in the study of taphonomic processes (see Lyman 2004).

would have required large territories (1,400–5,400 km^2), which they point out corroborates ranging estimates using lithic raw material procurement patterns. Agreement between the two lines of evidence suggests, according to the authors, that lithic raw material procurement was embedded in subsistence mobility during the European Mousterian. Higgins (Chap. 13) compares metacarpal structure of similarly-mobile bovid species characterized by flat terrain, mountainous terrain, and mixed terrains in order to assess the effect of sloped terrain on bone functional adaptations. The author notes that bovid species characterized by mountainous terrain routinely exhibit elevated anteroposterior (AP) and mediolateral (ML) bending rigidity, with perhaps greater relative increases in the ML direction. In contrast, human tibiae from sampled individuals occupying non-flat terrain, according to the author, usually exhibit relatively more enhanced AP bending rigidity than ML bending rigidity. Higgins suggests this is probably because of lateral buttressing by the fibula in humans, though this is not directly assessed in the study. As Sparacello and colleagues (Chap. 6) demonstrated, a structural analysis of fibulae from these human groups could prove to be enlightening. Carlson (Chap. 14) uses C57BL/6J mice to assess the effect of a specific behavior (i.e., change in direction), resulting from terrain complexity (i.e., obstacle avoidance), on bone functional adaptations in the femoral diaphysis. Structural differences in femoral diaphyses corresponding to presumed greater ML orientation of loading regimes in the experimental group engaging in more turning are observed. The author suggests that these experimental data support the notion that greater terrain complexity not only in the vertical direction, but in the horizontal direction (e.g., obstacle frequency on a landscape) would be worth evaluating when comparing bone functional adaptations of variably-mobile human groups.

Finally, Tamvada (Chap. 15) provides a glimpse of an exciting new application for finite element (FE) modeling. The author uses a finite element analysis (FEA) to explore structural integrity of the human femur. While validating an FE model presents a few logistical obstacles, the opportunity to calculate stresses and strains arising during an array of specific behaviors, or associated with specific kinematic variables (e.g., excursion angles), offers refreshing opportunities for understanding bone functional adaptations at a level that is seldom obtainable. For example, an FEA approach could permit assessment of stresses or strains associated with specific behavioral (gait) responses to elements of terrain complexity. This could offer a particularly powerful means of insight into documenting and understanding bone functional adaptations of human populations characterized by even the subtlest differences in mobility.

1.3 Conclusions and Future Directions

In summarizing the contributed chapters in this edited volume, the second and third goals stated above are fulfilled. The most commonly-adopted criteria in defining mobility are: (1) cumulative behavior over an individual's lifetime, (2) a focus on the lower limb, and (3) overall distance traveled (e.g., see Shaw et al., Chap. 4; Sparacello et al., Chap. 6; Pearson et al., Chap. 8; Cowgill, Chap. 11; and Higgins, Chap. 13). Other chapters offer definitions that include two of these three criteria, often excluding the lifetime cumulative behavior focus (e.g., see Shackelford, Chap. 9; Carlson, Chap. 14; and Tamvada, Chap. 15), or the lower limb focus (e.g., see Davies and Stock, Chap. 5). Wescott (Chap. 7) uses a logistic mobility definition, while Walker and Churchill (Chap. 12) employ both a logistic and residential mobility definition to examine different scales of mobility within their study. The concept of logistic mobility would seem to be consistent with the three most frequently adopted criteria noted above, but perhaps with the potential exclusion of the lifetime cumulative behavior criterion. It is worth noting that the chapter by Walker and Churchill stands apart from others in the volume due to its focus on both a unit of comparison at the population level (residential mobility) and at the individual level (logistic mobility). Bone functional adaptations are perhaps less useful in informing about residential mobility than in informing about logistic mobility, as individual variability in bone functional adaptations is better suited to association with individual variability in the latter. Other chapters, such as those by Shaw and colleagues (Chap. 4), Wall-Scheffler (Chap. 10), and Carlson (Chap. 14), incorporate additional criteria in defining mobility, for example, terrain complexity (e.g., elevation change and lateral movements).

Parallels between defining human mobility and defining positional behavior in observational studies of free-ranging primates offer a few intriguing points worthy of consideration. Prost (1965:1202) originally defined positional behavior as the "study of how and when an animal establishes particular spatial relations between his body mass and his physical environment" in response to existing disorder in classifications of primate locomotion. Prost argued that positional behaviors should be exhaustively categorized into dynamic (locomotor) and static (postural) states, with the former being most relevant to the concept of mobility adopted throughout this edited volume, and defined by Prost as the summary displacement of body mass. Subsequent attempts to standardize and refine classifications of positional (locomotor) behaviors into more discrete categories (i.e., Hunt et al. 1996) focused on spatial relationships between body segments, the center of body mass, and substrates/superstrates. Even this exhaustive attempt, however, has required additional fine-tuning, often due to species-specific locomotor habits (Walker 1998; Thorpe and Crompton 2006). Despite these additional efforts, there are still behavioral subcategories (e.g., turning) that remain underemphasized in classification schemes of positional behavior. Despite the continual need for adjusting its categories and subcategories, the adoption of the standardized positional behavior classificatory scheme ensured emphasis was placed on interactions between the body, its segments, and the environment, which allowed field behavioralists and morphologists to begin examining broader issues by comparing positional (locomotor) behavior profiles across groups of primates, and across different studies. It would seem that parallel benefits could come from standardizing the concept of human mobility in a similar fashion.

To this end, we suggest that standardizing an explicit definition of the concept of mobility (just as positional behavior eventually became explicitly defined) could be fruitful for strengthening behavioral inferences (e.g., activity patterns) originating from quantification of bone functional adaptations. Chapters in this edited volume converge on three primary criteria, which we suggest would be a good starting point for such a working definition of mobility: (1) cumulative behavior over a lifetime, though not necessarily implicating a life-long linear response to mechanical loading (i.e., age-equivalent samples should be compared when possible; see Cowgill, Chap. 11; Ruff et al. 2006); (2) overall distance traveled, though clearly incorporating terrain complexity is of growing importance; and (3) priority placed on use of the lower limb, which predominates as the instrument of human movement. Notably, amalgamation of the whole limb rather than consideration of discrete segments in isolation may help overcome the problem of equifinality for specific properties (e.g., diaphyseal midshaft shape and mobility indices).

While standardizing the concept of mobility going forward may benefit cross-study comparisons, just as the creation of a positional behavior classification scheme (Prost 1965; Hunt et al. 1996) enhanced opportunities to compare behavioral repertoires of different free-ranging primate species, it is important to leave open the possibility for study-specific adjustments. For example, comparisons of aquatic/marine mobility require incorporating upper limb comparisons. Also, substrate complexity clearly offers an additional, rich source of information for interpreting bone functional adaptations, particularly as separate elements of this complexity continue to be assessed. Our hope is that this edited volume stimulates further attempts to refine the concept of mobility, and of equal importance, to determine how mobility can inform on the activity patterns and substrate use visible through comparisons of bone functional adaptations. The value of experimental determinism/modeling for linking morphology and behavior (mobility), as opposed to "common sense" arguments, should not be overlooked, nor should the importance of integrating naturalistic conditions of environments occupied by the study populations be underappreciated. Unquestionably, much exciting work lies ahead!

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Chapter 2

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

Christopher B. Ruff and Clark Spencer Larsen

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

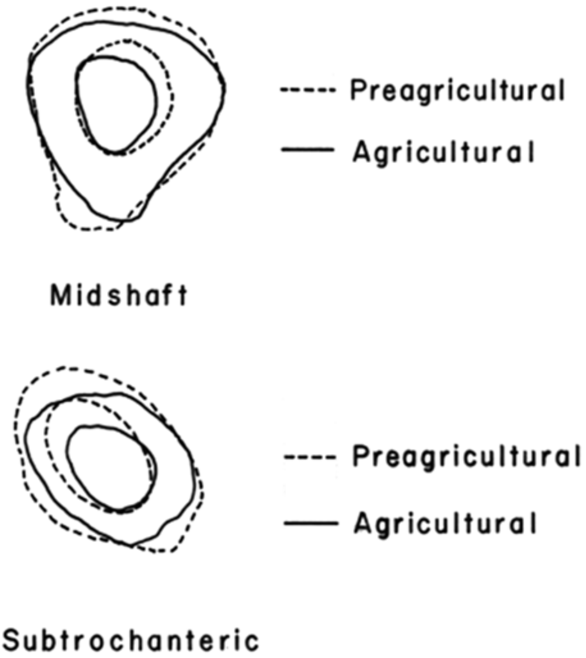
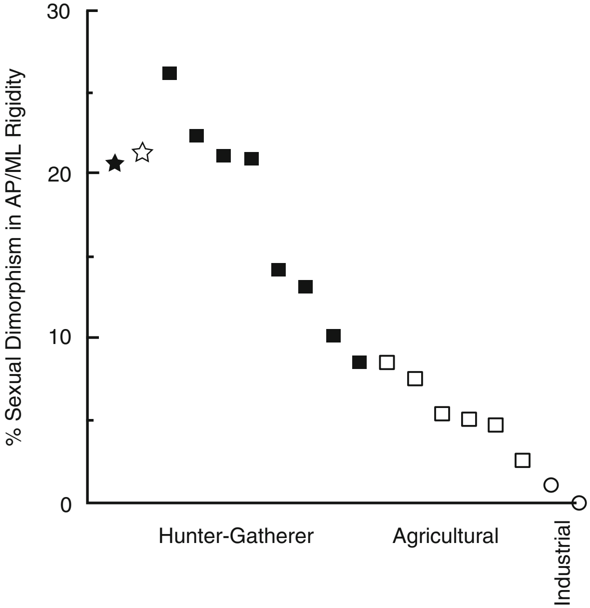


Fig. 2.1 Cross sections of femora from pre-contact preagricultural and agricultural Georgia coast samples, scaled to equal bone lengths. (Reproduced with permission from Ruff et al. 1984)

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 × 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).[1] 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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[1] 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

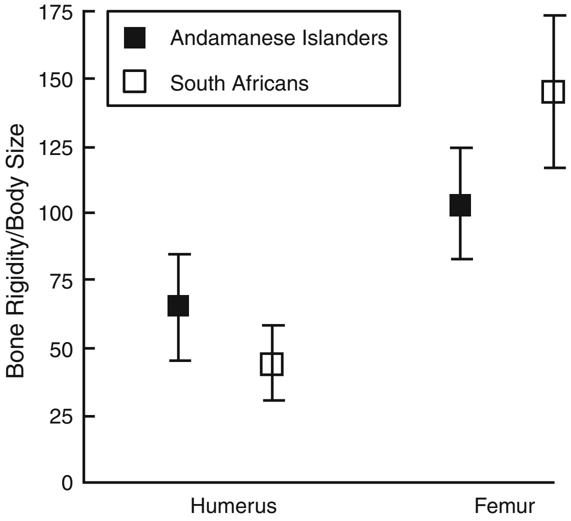

Fig. 2.3 Humeral and femoral overall rigidity (polar second moment of area) relative to body size in Andamanese Island and South African Stone Age samples (mean ± SD). (Data from Stock and Pfeiffer 2001)

(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^2 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.