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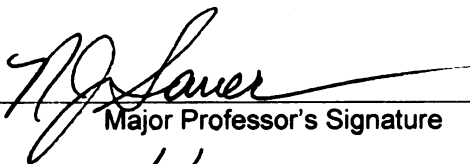
RECONSTRUCTING BEHAVIOR FROM ARCHAEOLOGICAL
SKELETAL REMAINS: A CRITICAL ANALYSIS OF THE
BIOMECHANICAL MODEL

presented by

GILLIAN BICE

has been accepted towards fulfillment
of the requirements for the

Ph.D. degree in Anthropology


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**RECONSTRUCTING BEHAVIOR FROM ARCHAEOLOGICAL SKELETAL
REMAINS: A CRITICAL ANALYSIS OF THE BIOMECHANICAL MODEL**

By

Gillian Bice

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Anthropology

2003

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ABSTRACT

RECONSTRUCTING BEHAVIOR FROM ARCHAEOLOGICAL SKELETAL REMAINS: A CRITICAL ANALYSIS OF THE BIOMECHANICAL MODEL

By

Gillian Bice

A biomechanical model for reconstructing behavior from archaeological skeletal remains was developed in the early 1980s. The model makes three predictions: 1) Group variation in cross-sectional geometry reflects group differences in levels and types of physical activity. 2) Group variation in sexual dimorphism of cross-sectional geometry reflects differences in sexual division of labor. 3) Group variation in upper limb bilateral asymmetry of cross-sectional geometric properties reflects differential usage of the upper limb. These predictions have become unquestioned tenets of bioarchaeological research. This dissertation utilized principles borrowed from informal logic to reconstruct and critically evaluate the argument presented by anthropologists for their ability to infer behavior from long bone cross-sectional geometry.

A core construct of the biomechanical model is the premise that bones functionally adapt to their mechanical environment. This late 19th century construct, known as Wolff's Law, proposes a causal relationship between the mechanical forces generated by physical activity and bone architecture. It is proffered as the principal theoretical foundation for inferring behavior from long bone diaphyseal cross-sectional geometry.

Since the mid-1980s, the study of long bone structural variation has become a virtual subspecialty in the field of biological anthropology, yet the biomechanical model

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has not changed since its conception twenty years ago, and does not reflect on-going, non-anthropological theoretical, experimental, and clinical research on the adaptation of bone to mechanical loading. Based on a review of this literature, it is shown that:

1) Although treated as axiomatic, Wolff's Law is fundamentally flawed, and not universally accepted, 2) The argument fails to make use of all available relevant evidence regarding the relationship of physical activity to bone structure, and 3) The conclusions of bioarchaeological research are confounded by variables (e.g., genetics, diet) that provide alternative explanations for the data. Furthermore, behavioral inferences are frequently based on statistically non-significant group differences in the cross-sectional geometric properties analyzed. Therefore, behavior-based conclusions resulting from the study of cross-sectional geometry are not borne out by scientific evidence, and must be rejected as conjecture.

This dissertation concludes by suggesting that bioarchaeological studies of past human behavior are based on simplistic and generally unsupported assumptions about the relative contribution of physical activity, age, genetics, and nutrition to cross-sectional geometric variation. Because of its complex etiology, long bone cross-sectional geometry cannot be used to make inferences, or test hypotheses regarding past human behavior. Furthermore, while specific "causes" cannot be identified, long bone cross-sectional geometric variation among archaeological populations can potentially be explained without resorting to behavior-based interpretations.

This dissertation is de

This dissertation is dedicated to my best friends ---my husband John and my sister Sigrid

The complete
unwavering support and
you Norm for never g
thank all of my comm
and Bill Lewis, and pa
and patience is deeply

I also gratefully
beseeched at the last m

In addition, I v
and colleagues who ha
good advice, assistance
back in the rear: Holly
Groch, Judy James, V
Jim Rechten, and Jo

I also wish to
Radiology Department

Most importa
unconditional love and
Dad and Celeste! I a
was Yvonne and Joh
you goes to my sister
being loving cheerlea

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is helped with in

this dissertation.

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LIST OF FIGURES

CHAPTER 1
INTRODUCTION

Statement of the problem
Overview of the book
Chapter summary

CHAPTER 2
BACKGROUND IN
BIOMECHANICS

Introduction
Skeletal biology
Basic biomechanics
Ontogeny of bone
Mechanics of bone
Conclusions
Technical overview
Terminology

CHAPTER 3
LITERATURE REVIEW
RECONSTRUCTION

Introduction
Literature review
Methodology
Biomechanics
A critique of the literature
Summary

CHAPTER 4
METHOD OF ANALYSIS

Application of the method
Inductive and deductive
Analytical techniques
Background

TABLE OF CONTENTS

LIST OF FIGURES	ix
CHAPTER 1	
INTRODUCTION	1
Statement of the problem	2
Overview of the method of analysis	5
Chapter summaries	6
CHAPTER 2	
BACKGROUND INFORMATION: SKELETAL BIOLOGY AND BIOMECHANICS	8
Introduction	8
Skeletal biology and mechanics	8
Basic bone biology	8
Ontogenetic processes in skeletal growth and development	15
Mechanical behavior of bones	19
Concepts in skeletal mechanobiology	27
Technical overview of cross-sectional geometry	37
Terminology and definitions	38
CHAPTER 3	
LITERATURE REVIEW: BIOMECHANICAL ANALYSES AND BEHAVIORAL RECONSTRUCTION IN BIOARCHAEOLOGY	45
Introduction	45
Literature review	45
Methodological and theoretical literature	45
Bioarchaeological studies of cross-sectional geometry	55
A critique of bioarchaeological studies of behavior	82
Summary	85
CHAPTER 4	
METHOD OF ANALYSIS	87
Application of critical reasoning	87
Inductive arguments	87
Analytical procedure	91
Techniques for criticizing inductive arguments	93
Begging the question	95

CHAPTER 5	
RECONSTRUCTION	
Introduction	
Reconstruction	
Critical analysis	
Analysis	
Analysis	
The process	
Summary	

CHAPTER 6	
WOLFF'S LAW, FUNCTIONAL ADAPTATION	
VARIABLES	
Introduction	
The "Law" of Wolff	
The origin of Wolff's Law	
Functional adaptation	
Problems	
Function	
Age effects	
Non-mechanical factors	
Genetics	
Nutrition	
Summary	

CHAPTER 7	
CONCLUSION	
Review of findings	
Determining the future	
Conclusion	
Suggestions	

BIBLIOGRAPHY	
--------------	--

CHAPTER 5	
RECONSTRUCTION AND EVALUATION OF THE ARGUMENT	96
Introduction	96
Reconstruction of the argument	96
Critical analysis of the argument	97
Analysis of the 'theoretical argument'	100
Analysis of the 'empirical argument'	111
The problems with premises 5a through 5e	116
Summary	120
 CHAPTER 6	
WOLFF'S LAW, FUNCTIONAL ADAPTATION, AND CONFOUNDING VARIABLES	122
Introduction	122
The "Law" that is not a law	122
The origin of Wolff's Law	126
Wolff's Errors	129
Functional adaptation	133
Problems linking physical activity to cross-sectional geometry	134
Functional adaptation: an "umbrella term" for a plurality of effects	141
Age effects on functional adaptation	144
Non-mechanical confounding variables	154
Genetic effects on cross-sectional geometry	156
Nutrition effects on cross-sectional geometry	171
Summary	177
 CHAPTER 7	
CONCLUSION	179
Review of functional adaptation: a summary	180
Determining physical activity from cross-sectional geometry: an analogy	184
Conclusion	186
Suggestions for future bioarchaeological research	189
 BIBLIOGRAPHY	193

Figure 2-1. Effects of

Figure 2-2. External

Figure 2-3. Axial load

Figure 2-4. Loads that

Figure 2-5. Structural

Figure 2-6. The "mech

Figure 2-7. Second m

Figure 3-1. Reconstro

Figure 3-2. Reconstro

Figure 3-3. Reconstro

Figure 3-4. Argumen

LIST OF FIGURES

Figure 2-1. Effects of modeling drifts on bone size and shape	18
Figure 2-2. External forces and modes of loading	21
Figure 2-3. Axial loading	22
Figure 2-4. Loads that produce bending of long bones	23
Figure 2-5. Structural and material properties	25
Figure 2-6. The “mechanostat” model	32
Figure 2-7. Second moments of area	42
Figure 5-1. Reconstruction of the overall argument	98
Figure 5-2. Reconstruction of the ‘theoretical argument’	100
Figure 5-3. Reconstruction of the ‘empirical argument’	101
Figure 5-4. Argument for I_x/I_y as an indicator of sex differences in mobility	118

Thus it often happens that
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Skeletal variation
to determine sex and
Similarly, a bioarchaeologist
physical activity is one
pathological skeletal variation
differences in bone mineral
different physical activities

Inferring behaviour from
human skeletal remains
Kennedy 1989; Larsen 1997
diaphyseal structure is
indirect means of predicting
under specified loading conditions
properties is hypothesised
loadings produced by
biomechanical concepts
efforts of Ruff and co-workers
1990; Ruff et al. 1993; 1994
biomechanical model
populations. The most

CHAPTER 1—INTRODUCTION

Thus it often happens that every step in the scientific method is carried out correctly except the last, but this can be sufficient to nullify all the previous efforts.

James K. Feibleman (1972)

Skeletal variation provides the empirical foundation for a skeletal biologist's ability to determine sex and ancestry or estimate age and stature from human skeletal remains. Similarly, a bioarchaeologist's "reconstruction" of past human lifeways, of which habitual physical activity is one component, is also predicated on the existence of normal or pathological skeletal variation. The underlying assumption is that certain observable differences in bone morphology among individuals are the direct result of performing different physical activities.

Inferring behavior (e.g., habitual physical activity patterns, occupation, etc.) from human skeletal remains has become a standard component of bioarchaeological research (Kennedy 1989; Larsen 2000). Cross-sectional geometric analysis of long bone diaphyseal structure is a common approach. This biomechanical method provides an indirect means of predicting the mechanical behavior (e.g., strength, rigidity) of bones under specified loading conditions. Group variation in cross-sectional geometric properties is hypothesized to result primarily from differences in localized mechanical loadings produced by differing patterns of physical activity. The application of biomechanical concepts to archaeological populations is largely due to the pioneering efforts of Ruff and colleagues (Ruff 1987; Ruff and Hayes 1983a, 1983b; Ruff and Larsen 1990; Ruff et al. 1984, 1993, 1994; Trinkaus et al. 1994). Their research has generated a biomechanical model that is the basis for "reconstructing" the behavior of past populations. The model makes three predictions: 1) Group variation in cross-sectional

geometry reflects growth
variation in degree of
differences in sexual
asymmetry of cross-sections
unilateral and bilateral
bioarchaeological research
evaluation of the applicability of
behavioral reconstruction

Statement of the problem

Bioarchaeological research has
variation in long bone diaphyseal
behavioral changes associated with
In the United States, the majority of
gathering to maize agriculture
Southeast Bridges 1994, Bridges
1994, Northeast Bridges 1994,
Plains Ruff 1994, Vash 1994,
structure between prehistoric
Georgia and northern Georgia
1998.

A core consists of
units mechanical energy
relationship between

geometry reflects group differences in levels and types of physical activity. 2) Group variation in degree of sexual dimorphism of cross-sectional geometry is attributable to differences in sexual division of labor. 3) Group variation in degree of bilateral asymmetry of cross-sectional geometry reflects behavioral differences related to specific unilateral and bilateral activities. These predictions have become unquestioned tenets of bioarchaeological research. This dissertation presents the results of a qualitative critical evaluation of the application of long bone diaphyseal cross-sectional geometry to behavioral reconstruction.

Statement of the problem

Bioarchaeological studies are often undertaken to detect temporal or geographic variation in long bone cross-sectional geometric properties, inferred to result from behavioral changes associated with adaptive shifts in subsistence and mobility strategies. In the United States, many studies have focused on the transition from hunting and gathering to maize agriculture in the Midwest (Barondess 1998; Bridges et al. 2000), Southeast (Bridges 1989, 1991; Larsen et al. 1996; Ruff and Larsen 1990; Ruff et al. 1984), Northeast (Barondess 1998), Southwest (Brock and Ruff 1988), and the Great Plains (Ruff 1994; Wescott 2000). Studies have also investigated differences in bone structure between pre- and post-European contact Native American populations on the Georgia and northern Florida coast (Ruff and Larsen 1990), and in Michigan (Barondess 1998).

A core construct of this research is the premise that bone has the ability to adapt to its mechanical environment. This construct, known as Wolff's Law, proposes a direct relationship between bone architecture and mechanical forces; bone is added where it is

needed to maintain s
proffered as the prime
diaphyseal structure
Although virtually as
Wolff's Law is not w
Curry 1997, 2002: 1

The notion th
from dried skeletal re
others have question
Lovejoy et al. 2002:
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of anthropology the c
fields regarding Wolf
loading. This disserta

needed to maintain structural integrity, and removed from where it is not needed. It is proffered as the principal theoretical foundation for inferring behavior from long bone diaphyseal structure (e.g., Barondess 1998; Bridges 1989; Ruff and Hayes 1983a). Although virtually axiomatic, and often cited by skeletal biologists and biomechanists, Wolff's Law is not without its detractors (Bertram and Swartz 1991; Cowin 2001b; Currey 1997, 2002; Dobbins 1992; Roesler 1982, 1987).

The notion that biological anthropologists are capable of reconstructing behavior from dried skeletal remains has been recently discredited (Jurmain 1999). In addition, others have questioned the fruitfulness of the biomechanical approach specifically (Lovejoy et al. 2002; Ohman and Lovejoy 2001; Wescott 2001). While there can be little doubt that bone can and does respond to its mechanical environment under certain circumstances (Martin et al. 1998), the relationship of habitual physical activity to non-evolutionary bone modification, particularly with regard to cross-sectional geometry, and especially in adults, is not fully understood (Bertram and Swartz 1991; Cowin 2001a; Currey 2002). Without a thorough reexamination of the most fundamental principles upon which the study of human behavioral adaptation is based, biological anthropologists run the risk of failing to adequately consider alternative explanations for their data.

This dissertation project was undertaken because of an apparent discordance between the theoretical underpinnings of the bioarchaeological research and the hypotheses emerging from non-anthropological research on the response of bone to its mechanical environment. An important goal of this dissertation is to bring into the forum of anthropology the ongoing debate among skeletal biologists in non-anthropological fields regarding Wolff's Law and the relationship of bone architecture to mechanical loading. This dissertation demonstrates that Wolff's Law has been the subject of much

criticism by skeletal
theoretical framework
Hayes 1983a, whose
model suggest a limit
Hayes' interpretation
explanation for bone
theory does not provide
features probably result
factors..." p. 371.

Subsequent to
in the early-1980s, the
bone adaptation in response
have appeared in numerous
International Journal of
Bone and Mineral Research,
Physiology, Osteoporosis
Cowan 1981a, 2001a,
1995.

While the biological
virtual subspecialty,
non-anthropological
skeletal biology research
biomechanical models
late-1970s to early-1980s.

criticism by skeletal biologists, and suggests that it does not provide an adequate theoretical framework for inferring behavior from bone structure. Interestingly, Ruff and Hayes (1983a), whose pioneering studies led to the development of the biomechanical model, suggest a limitation of Wolff's Law in a footnote, "Note that while [Ruff and Hayes' interpretation of] Wolff's Law may appear to invoke a purely environmental explanation for bone form (i.e., response to in-vivo mechanical stresses and strains), the theory does not preclude heritable genetic effects. In fact, most bone morphological features probably result from a combination of both genetic and environmental factors..." (p. 371).

Subsequent to the first bioarchaeological application of cross-sectional geometry in the early-1980s, there has been a tremendous amount of research on the biology of bone adaptation in response to mechanical stimuli (mechanobiology). Published studies have appeared in numerous preeminent journals including *Bone*, *Calcified Tissue International*, *Journal of Biomechanics*, *Journal of Bone and Joint Surgery*, *Journal of Bone and Mineral Research*, *Journal of Experimental Biology*, *Journal of Applied Physiology*, *Osteoporosis International*, and in many books (e.g., Currey 1984, 2002; Cowin 1981a, 2001a; Martin and Burr 1989; Martin et al. 1998; Odgaard and Weinans 1995).

While the bioarchaeological study of cross-sectional geometry has grown into a virtual subspecialty, anthropologists have for the most part remained uninformed by the non-anthropological literature. This is inferred from the relative lack of citations for skeletal biology research conducted since the mid-1980s, and the fact that the basic biomechanical model has not changed. A handful of experiments conducted from the late-1970s to early-1980s (e.g., Goodship et al. 1979; Lanyon and Rubin 1984; Woo et al.

1981 are repeatedly
Bioarchaeologists have
processes that produce
the non-anthropological
the anthropological
presented by Ruff, 1981

Overview of the model

The analysis
borrowed from information
presented for interpretation
modeled as a series of
support of the conclusions
premises, and 2 will be
evaluated in this discussion
argument, the truth of the
premises. Because the model
to support its claim that
i.e., premises can be used

Based on the model
that 1 Wolff's Law
follow from the model
for the data, and the
regarding the model

1981) are repeatedly cited as providing empirical support for Wolff's Law.

Bioarchaeologists have focused on skeletal mechanics while all but ignoring the biological processes that produce, maintain, and adjust the mechanical properties of bone. Much of the non-anthropological research on skeletal biology suggests alternative explanations for the anthropological findings, and casts doubt on the premises, inferences, and conclusions presented by Ruff, Larsen, Bridges, and others.

Overview of the method of analysis

The analysis presented in this dissertation was accomplished utilizing principles borrowed from informal logic to reconstruct and evaluate the strength of the argument presented for inferring behavior from cross-sectional geometry. In logic, an argument is modeled as a series of propositions; one is a conclusion, the rest are premises offered in support of the conclusion. The success of an argument is dependent on 1) the truth of the premises, and 2) whether the conclusion follows from the premises. The argument evaluated in this dissertation is inductive, rather than deductive. Unlike a valid deductive argument, the truth of an inductive conclusion is not guaranteed by the truth of the premises. Because of this, an inductive argument must use all available relevant evidence to support its claims. If it does not, it can be shown that the introduction of new evidence (i.e., premises) can change the conclusion.

Based on a review of non-anthropological literature on skeletal biology, it is shown that: 1) Wolff's Law is not strongly supported, 2) The conclusions do not necessarily follow from the premises because confounding variables provide alternative explanations for the data, and 3) The argument fails to make use of all available relevant evidence regarding the relationship of physical activity to bone structure. In addition, many

conclusions are based
behavior-based con-
clusions are not based

Chapter summary

Chapter 2 provides an overview of the
presented in this discussion
fields of skeletal biology

Chapter 3 provides an overview of
geometric variation in
contexts. Through the
bioarchaeological

Chapter 4 provides an overview of
involves applying
arguments. This
outlines the process of
inductive argument

Chapter 5 provides an overview of
bioarchaeological
and evaluates the

Chapter 6 provides an overview of
flaws. This is followed by
review of evidence
structure. The

conclusion**s** are based on statistically non-significant group differences. Therefore, behavior**-**based conclusions resulting from bioarchaeological studies of cross-sectional geometry are not borne out by scientific evidence, and must be rejected as conjecture.

Chapter summaries

Chapter 2 provides the requisite background information for the critical analysis presented in this dissertation, and introduces relevant concepts and terminology from the fields of skeletal biology and biomechanics.

Chapter 3 presents a review of the anthropological literature on cross-sectional geometric variation, and its application to behavioral reconstruction in archaeological contexts. Throughout the dissertation this body of literature is referred to as “bioarchaeological.”

Chapter 4 describes the method of critical analysis used in this dissertation, which involves applying concepts borrowed from informal logic to critically evaluate inductive arguments. This chapter provides an operational definition of an inductive argument, outlines the process of reconstructing an argument, and discusses the ways in which an inductive argument can be critiqued.

Chapter 5 reconstructs and critically analyzes the argument contained in the bioarchaeological literature reviewed in chapter 3. This chapter identifies the premises, and evaluates the strength of the argument.

Chapter 6 provides a brief history of Wolff’s Law and presents a summary of its flaws. This is followed by a discussion of the concept of functional adaptation, as well as a review of evidence for the effects of genetics and nutrition on long bone diaphyseal structure. The information presented in this chapter was obtained from non-

anthropological the
functional adaptatio

Chapter 7 p

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potentially complex
inferences, or test b
cannot be identified
populations can pose
explanations.

anthropological theoretical, experimental, and clinical literature on skeletal biology and functional adaptation.

Chapter 7 presents the conclusion of the critical analysis. This dissertation concludes by suggesting that the bioarchaeological studies are based on poorly defined and generally unsupported assumptions about the relative importance of physical activity, age, genetics, and nutrition to cross-sectional geometric variation. Because of its potentially complex etiology, long bone cross-sectional geometry cannot be used to make inferences, or test hypotheses regarding behavior. Furthermore, while specific “causes” cannot be identified, cross-sectional geometric variation among archaeological populations can potentially be explained without resorting to behavior-based explanations.

CHAPTER 2—BA

The learning and know
we are ignorant.

Introduction

This chapter
in this dissertation, a
overview of key topics
the relationship between
mechanobiology, and
diaphyses, and intro

Skeletal biology

This section
concepts relating to
skeletal growth and
mechanobiology, and
of basic skeletal biology
biology contains i

Basic bone bio

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dynamic tissue, v

CHAPTER 2—BACKGROUND INFORMATION: SKELETAL BIOLOGY AND BIOMECHANICS

The learning and knowledge that we have, is, at the most, but little compared with that of which we are ignorant.

Plato

Introduction

This chapter presents background information for the critical analysis presented in this dissertation, and is divided into two main sections. The first section provides an overview of key topics in skeletal biology and establishes a foundation for understanding the relationship between skeletal structure and the biology of mechanical adaptation (mechanobiology). The second section focuses on cross-sectional geometry of long bone diaphyses, and introduces and defines the terminology used throughout the dissertation.

Skeletal biology and mechanics

This section of the chapter presents important terminology and qualitative concepts relating to four subjects: 1) basic bone biology, 2) ontogenetic processes in skeletal growth and development 3) the mechanical behavior of bones, and 4) skeletal mechanobiology. Jee (2001) and Martin et al. (1998) provide excellent up-to-date reviews of basic skeletal biology. Unless otherwise indicated, the following primer of skeletal biology contains information drawn from these sources.

Basic bone biology

The enduring quality of dried skeletal remains belies the fact that living bone is a dynamic tissue, which undergoes dramatic transformations throughout the life of an

individual. An understanding of the relationship between

Functions of bone

The skeletal system has several functions. The primary function of some bones is to support the body. However, as components of the musculoskeletal system, bones also serve as levers, providing attachment points for muscles that produce movement. Bones are also hard, rigid, and strong (i.e., able to withstand stress). In addition, bones have several other vital functions. For example, the bone marrow produces blood cells, and bones store calcium, which are essential for many body functions. The complementary field of bone physiology studies bone physiology. (Curry 2002; Martin 2002)

Composition of bone

Bone is a type of connective tissue. It is composed of organic and inorganic mineral components. At the molecular level, bone is composed of collagen and hydroxyapatite. This distinguishes it from cartilage, and characterizes it as a hard tissue.

individual. An understanding of basic bone biology is a prerequisite to any discussion of the **relationship** between cross-sectional geometry and physical activity.

Functions of bone

The skeletal system is important biomechanically and metabolically. A critical **function** of some bones is to enclose and protect the visceral organs of the body. **However,** as components of the musculoskeletal system, most bones serve as struts and levers, **providing** attachments for the skeletal muscles that maintain body posture and produce **movement.** For this, bones need to be both rigid (i.e., able to resist deformation) and **strong** (i.e., able to withstand loads without breaking). Physiologically, bones have **additional** vital functions. The marrow that resides within most bones of the body produces **blood** cells, and the bone tissue itself serves as a reservoir for minerals, such as **calcium,** which are critical in muscle contraction and nerve conduction. In the **complementary** fields of biomechanics and skeletal mechanobiology the mechanical **function** of bone is emphasized. Indeed, in the view of most contemporary skeletal **biologists** bone physiology is primarily regulated by mechanical usage (Cowin 2001a; **Currey** 2002; Martin et al. 1998; Rubinacci et al. 2002).

Composition of bone

Bone is a type of connective tissue in which the extracellular matter consists of **inorganic** mineral deposited into an organic protein and water matrix. Thus, at a **molecular** level, bone is a composite material. The mineral component of bone **distinguishes** it from the other structural connective tissues (e.g., tendons, ligaments, and **cartilage**), and characterizes it as a “hard” tissue. Sixty-five to 70% of bone is inorganic,

consisting of hydroxyl groups, which is responsible for its solubility. The remaining 30-35% of the matrix is composed of bone cells. The matrix is called type I collagen. It consists of numerous molecules of osteonectin, the function of which is to perform important roles in bone. For example, osteopontin (Nomura et al. 2000) is involved in bone turnover. The osteonectin is functioning, particularly in the bony matrix.

Cell types

Four types of cells are found in bone and bone-lining cells. The first is the hemopoietic bone marrow. The primary function of the bone-lining cells is to border adjacent to the bone. They are mineral and collagen. The second type of osteoclasts, called Haversian cells, are the activity of osteoclasts. The third type of osteoclasts is the signal for osteoclasts.

consisting of hydroxyapatite crystals ($\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$). The mineral component of bone is responsible for its rigidity and material stiffness, and its strength in compression. The remaining 30-35% of bone is made up of proteins and water (the organic matrix), and bone cells. The majority of protein in bone, roughly 90%, is the fibrous structural protein called type 1 collagen, which provides bone with tensile strength. The remaining 10% consists of numerous non-collagenous proteins, including osteocalcin, osteopontin, and osteonectin, the function of which is the subject of speculation. These proteins may perform important roles in the regulation of skeletal adaptation to mechanical usage. For example, osteopontin is thought to mediate osteoclast attachment to bone surfaces (Nomura et al. 2000). The presence of some of these proteins in urine is used to assess bone turnover. The water component of bone is also essential to its mechanical functioning, particularly with regard to the flow of extracellular (interstitial) fluid through the bony matrix.

Cell types

Four types of bone cells have been identified: osteoclasts, osteoblasts, osteocytes, and bone-lining cells. Osteoclasts are large, multinucleated cells derived from hemopoietic bone marrow and formed by fused cells of the monocyte/phagocytic lineage. The primary function of osteoclasts is to resorb bone. An active osteoclast has a ruffled border adjacent to the bone surface, which secretes acids and enzymes to dissolve the mineral and collagen components of bone, respectively. The resorption spaces created by osteoclasts, called Howship's lacunae, represent transient porosity in bone tissue. The activity of osteoclasts is regulated by many factors including numerous hormones. The signal for osteoclasts to begin resorption at a specific site likely involves the activity of

bone-lining cells. M

(Osteoblasts

near bone surfaces

mesenchymal cells

of osteoblasts is both

participate in the m

agents known to aff

metabolites, steroid

Osteocytes

that became trap

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Osteoblasts are cuboidal cells derived from multipotent mesenchymal cells located near bone surfaces and in marrow stromal tissue. Differentiation of osteoblasts from mesenchymal cells is thought to be dependent on mechanical stimulation. The function of osteoblasts is bone formation; they secrete osteoid (the unmineralized bone matrix) and participate in the mineralization process. Active osteoblasts possess receptors for many agents known to affect bone metabolism, e.g., parathyroid hormone, vitamin D metabolites, steroid hormones, and growth factors.

Osteocytes, the most abundant cell type in mature bone, are inactive osteoblasts that became trapped within the bony matrix during bone formation. The spaces they occupy are called lacunae. Osteocytes are stellate-shaped cells with numerous slender cellular processes housed within tiny canals called canaliculi, which extend from and interconnect the lacunae. Gap junctions between the cellular processes provide a means for osteocytes to communicate and exchange substances with other osteocytes, bone-lining cells, and osteoblasts in an extensive “connected cell network” (Cowin and Moss 2001). Although not thoroughly understood, the functions of osteocytes likely include: 1) maintenance of the local ionic environment, 2) detection of microdamage, and 3) detection of alterations in their local strain environment and transmission of the signal to initiate bone adaptation processes.

Bone-lining cells are flattened, elongated cells, which cover all quiescent bone surfaces, e.g., periosteal, endosteal, trabecular, and vascular canals. Like osteocytes, bone-lining cells are inactive osteoblasts, which maintain cellular connections with osteocytes and osteoblasts via the lacunocanalicular network. The functions of bone-lining cells are still poorly understood (Jee 2001), but are thought to include bone

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Classification of

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formation and mineral homeostasis. In addition, bone-lining cells likely play an important role in initiating mechanical adaptation.

Classification of bone tissue

At the macroscopic level, bone tissue is categorized as either compact or cancellous, distinguished primarily by its porosity. Porosity refers to the fraction of a volume of bone tissue consisting of voids in the bony matrix, e.g., trabecular spaces filled with bone marrow, vascular canals (Haversian and Volkmann's canals), and the temporary resorption spaces formed by osteoclasts.

Compared to cancellous bone, healthy compact bone is dense and appears solid—its porosity is very low (5-10%). Approximately 80% of the mass of the skeleton is compact bone, the majority of which is contained in the cortices (or outer shells) of the shafts of long bones; hence, compact bone is often referred to as cortical bone.

Cancellous bone is often referred to as spongy bone because it is very porous (75-95%). It is also known as trabecular bone because it consists of a lattice of bony struts and plates called trabeculae. The majority of cancellous bone is located in the ends of long bones, within the vertebral bodies, and sandwiched between the cortices of flat bones (skull, sternum, hip bones). Compact and cancellous bone differ with regard to function, development, architecture, material properties, rate of turnover, and age-related changes.

Bone tissue is also categorized based on its microstructure. Woven and lamellar bone tissue differ with regard to collagen fiber organization. In woven bone, the collagen fibers are oriented somewhat randomly making it mechanically inferior to lamellar bone. The primary biological advantage of woven bone is that it can be formed rapidly. In humans, woven bone forms early in development, and later as part of the normal

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response in fracture repair and adaptation to extreme mechanical overloading. Woven bone is subsequently replaced by lamellar bone. A special type of woven bone, called parallel-fibered (or fine-fibered) bone, has more organized collagen fibers, and is found in small animals such as mice and rats.

Lamellar bone, as the name implies, is organized in layers, i.e., lamellae. Its structure is often described as being analogous to plywood, with alternating collagen fiber orientation in adjacent layers; however, the microstructural organization and variation of lamellar bone is complex, and still largely unresolved (Currey 2002). Lamellar bone is laid down much more slowly, and is ultimately less mineralized than woven bone. This is the predominant type of bone found in the human adult skeleton.

Plexiform bone, also called fibrolamellar or laminar bone, is a combination of woven and lamellar bone. It is formed when an initial scaffolding of woven bone is laid down and the gaps are filled in with lamellar bone. Plexiform bone can be formed much more rapidly than lamellar bone, and is common in large, fast-growing animals like cattle and deer; it is not characteristic of adult human bone.

Cortical bone tissue may be further classified as either primary or secondary bone. Primary bone is either plexiform or circumferential lamellar bone. The lamellae of circumferential lamellar bone are oriented around the circumference of the bone parallel to the bone surface. Blood vessels within a region of circumferential lamellae are contained within primary osteons, which consist of a central vascular canal surrounded by several concentric lamellae. In adult human long bones, circumferential lamellae are generally restricted to several layers immediately subjacent to the periosteum.

In humans and many other vertebrates, primary bone is gradually replaced by secondary bone via remodeling, a process whereby existing bone is removed by

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osteoclasts, and the resorption space filled in with new lamellar bone by osteoblasts. The secondary osteon or Haversian system is one outcome of remodeling. Secondary osteons consist of concentric lamellae surrounding a central neurovascular canal (Haversian canal). Unlike primary osteons, a distinct boundary called the cement line separates each secondary osteon from the surrounding bone tissue. In skeletally mature humans, most cortical bone has been remodeled and is composed of numerous complete and fragmentary secondary osteons. Haversian bone is mechanically weaker than primary bone. The trabecular bone of adults is also secondary bone; however, individual trabeculae are typically too small to contain whole secondary osteons, and may instead contain crescent shaped osteons called hemiosteons.

Between the early-1960s and mid-1980s Harold M. Frost developed the concept of the “intermediary organization” (IO) of bone (i.e., tissue level organization) (Frost 1973a, 1973b, 1986). As part of the skeletal IO, Frost (1986: 150) conceptualized four “functionally independent bone surfaces” which he called bone envelopes: periosteal, intracortical (Haversian), endosteal (endocortical), and trabecular. According to Frost, the net bone balance (the difference between the amount of bone resorbed and the amount formed), and the biological processes that affect bone balance, differ among the envelopes. Over a lifetime, the periosteal envelope exhibits a net positive bone balance, i.e., formation is greater than resorption. The intracortical envelope shows close to a zero, or slightly negative, balance resulting from increased porosity due to reduced formation relative to resorption. In contrast, the endosteal and trabecular envelopes show a fairly substantial net negative bone balance resulting from increased resorption relative to formation on bone surfaces adjacent to bone marrow.

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Ontogenetic processes in skeletal growth and development

Most of the skeleton is preformed in cartilage that develops from condensations of **me**senchymal cells during early embryonic life. Endochondral ossification involves **repl**acing the cartilaginous anlage with osseous tissue. This process produces most of the **bone**s of the appendicular skeleton, as well as the cranial base. In contrast, most bones of **the** cranial vault and facial skeleton, as well as portions of the mandible and clavicle **develo**p from membrane-like sheets of mesenchymal tissue. Ossification in the absence of **an** initial cartilaginous model is termed intramembranous. Most bones ultimately **undergo** both types of ossification during the course of their development. For example, **long** bones grow in length through a process of endochondral ossification involving the **repl**acement of existing cartilage by osseous tissue at the epiphyscal plate (physis). **G**rowth in diameter occurs through an intramembranous ossification process involving **bone** apposition by cells located in the osteogenic layer of the periosteum.

Following the initial development and ossification of the skeleton *in utero*, bones **undergo** an extended period of postnatal growth and shape modification, which ceases at **ske**letal maturity. Thereafter, bones experience less dramatic modifications from **mai**ntenance and repair functions, as well as age-related degenerative processes, such as osteopenia. Frost (1986: 111) succinctly describes the processes involved, “Growth determines the size. Modeling molds the growing shape. Remodeling then maintains functional competence.”

Growth involves an increase in size resulting from a proliferation of cells and an increase in extracellular matter. Unlike many tissues in the body, bones cannot grow by expansion (interstitial growth), only by apposition of osseous tissue onto an existing surface (cartilage or bone). Simply growing larger would ultimately result in grossly

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dysfunctional bone shapes and altered anatomical relationships with surrounding organs, **such** as muscles and other bones. Modeling guides the growth process “by locally **ret**arding growth in some locations and directions, and potentiating it in others” (Frost 1985: 213). Modeling (sometimes called macromodeling) involves the independent **ac**tions of osteoblasts and osteoclasts resulting in formation and resorption “drifts” that “**m**ove periosteal and cortical-endosteal [envelopes] in tissue space” (Frost 1985: 2). For **ex**ample, formation and resorption drifts are responsible for changes in cortical thickness **and** diaphyseal curvature in growing long bones (Figure 2-1). One purpose of modeling is **to** match a growing bone to changing functional demands incurred by increasing body **mass**, muscle strength, and mechanical usage. The dramatic shape altering potential of **mo**deling virtually ceases following skeletal maturity (Frost 1985, 1990; Martin et al. 1998; Jee 2001).

In contrast to modeling, remodeling continues throughout the life of an **i**ndividual. In 1964, Frost (1997) redefined the term remodeling to mean the removal and **sub**sequent replacement of “quantized” packets of bone through the “coupled” actions of **os**teoclasts and osteoblasts. Frost (1986) named the group of cells that replace a “**q**uantum” of bone the basic multicellular unit (BMU). BMUs replace bone in an activation-resorption-formation (ARF) sequence that takes roughly four months to complete. Remodeling of cortical bone produces secondary osteons, the basic structural units (BSU) of bone.

Remodeling typically results in a net loss (disuse mode remodeling) or no change (conservation mode remodeling) in bone quantity, depending on the bone envelope (Frost 1990). The decrease in bone mass that results from remodeling is often referred to as “bone remodeling-dependent bone loss” (Jee 2001: 1-31). Remodeling has both positive

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and negative consequences for the skeletal system. The beneficial effects include: 1) the **removal** of microscopic fatigue damage (microdamage) and necrotic bone, and 2) **adaptation** of the microarchitecture to local mechanical stresses or strains. Deleterious **effects** include: 1) the thinning and eventual loss of trabeculae resulting from the negative **bone** balance on the trabecular envelope, 2) an increase in intracortical porosity through **the** creation of resorption spaces, 3) decreased cortical thickness with aging, and 4) the **production** of mechanically inferior bone (i.e., Haversian bone).

In the literature, use of the term remodeling often interjects ambiguity. While, **skeletal** biologists use the term remodeling to refer specifically to the BMU—ARF **sequence**, biomechanists often use the pre-1964 definition of “remodeling,” which is **synonymous** with “adaptation” (Martin et al. 1998; Odgaard and Weinans 1995). This **difference** in meaning can be problematic because, depending on the circumstances, bone **adaptation** to mechanical usage may involve the processes of modeling, BMU **remodeling**, or both. Mechanical loading differentially activates these processes; they **produce** different effects in terms of bone macromorphology (including cross-sectional **geometry**), and they are dominant at different points during the life of an individual. **Unfortunately**, it is not always clear from the context in what sense bioarchaeologists are using the term remodeling when discussing long bone structural variation.

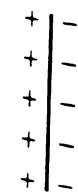
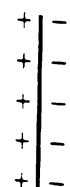
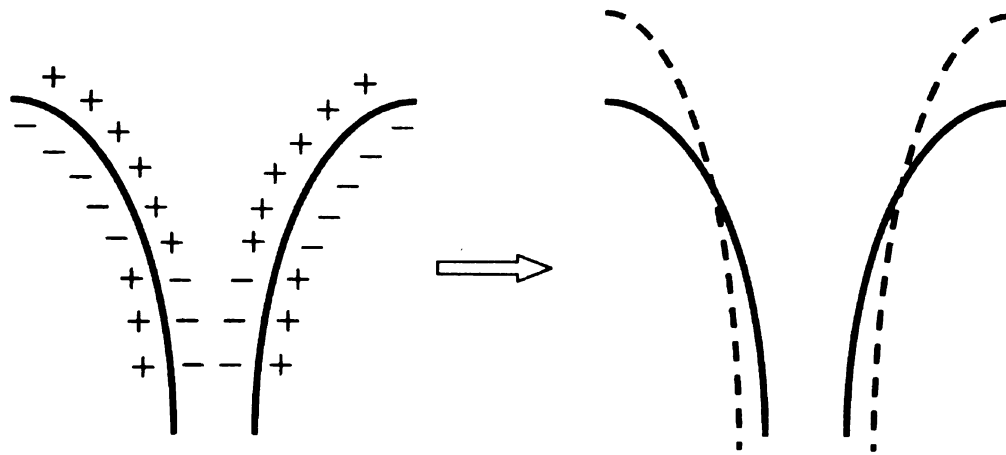
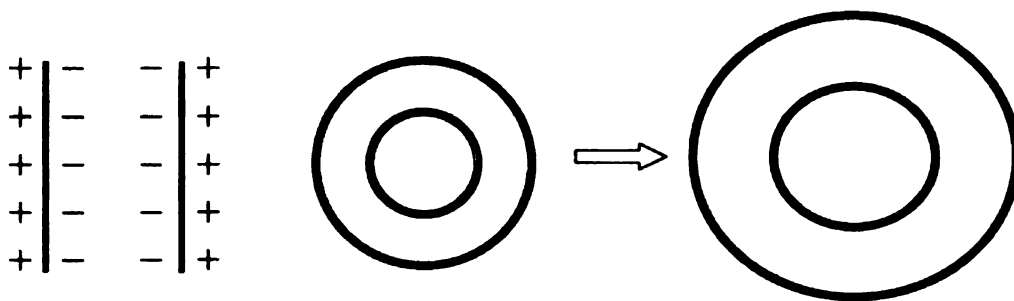


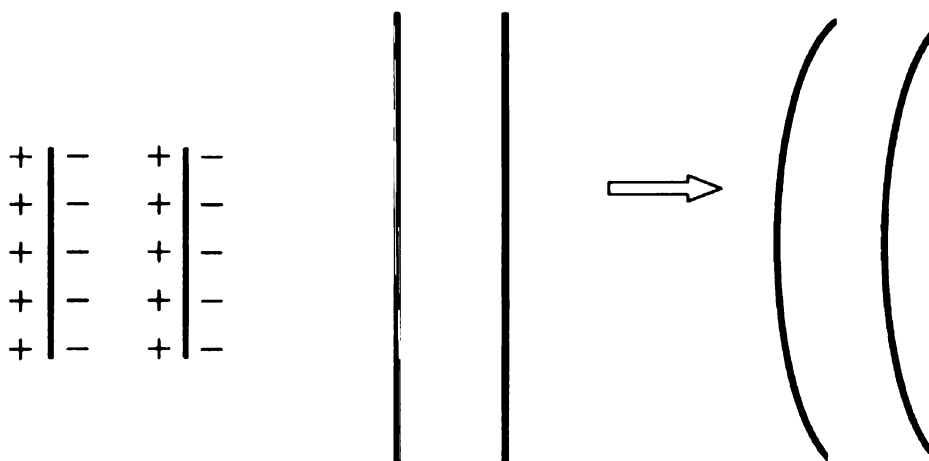
Figure 2-1. Effects
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(b)



(c)

Figure 2-1. Effects of modeling drifts on bone size and shape. (a) Metaphyseal cutback. (b) Changes in cortical thickness, external (periosteal) diameter, and internal (endosteal) diameter. (c) Changes in bone curvature. (+) indicates bone formation; (-) indicates bone resorption.

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Mechanical behavior of bones

Unless otherwise indicated, most of the information contained in the following discussion of the mechanical behavior of bones was derived from Martin et al. (1998) and, especially, Cochran (1982).

Force is defined as the action of one body on another; its units are the Newton (N) or the pound (lb). Mathematically, forces are represented as vectors, which are characterized by magnitude, direction, and point of application. The application of external forces (i.e., a mechanical load) to a structure, such as a bone or a portion thereof, changes its original dimensions (i.e., causes deformation) and produces internal forces that resist the deformation. Strain refers to a relative change in some dimension, such as length (i.e., $\Delta L/L$), of a structure due to an external load, and is therefore unit-less. In the literature strain is represented by the symbol ϵ . The strains in bone are very small and are generally reported as microstrain ($\mu\epsilon$; $1\mu\epsilon = 10^{-6}\epsilon$). As an example, a 10cm piece of bone stretched to 10.00001cm represents a change in length of 0.00001cm ($\Delta L = 10^{-5}\text{cm}$); therefore, the strain is 0.000001ϵ , and the microstrain is $1.0\mu\epsilon$ ($\Delta L/L = 10^{-5}\text{cm}/10\text{cm} = 10^{-6}\epsilon = 1\mu\epsilon$). The internal forces that develop within a structure to resist deformation are called stress. Stress is defined as a force per unit area (F/A), and is represented by the symbol σ . The unit of stress is the Pascal (Pa), which is equal to one Newton per square meter ($1\text{Pa} = 1\text{ N/m}^2$). Stress levels in bone are typically reported in megapascals (Mpa; $1\text{ Mpa} = 10^6\text{Pa}$). Stress and strain are directly related to one another ($\sigma = E\epsilon$; E is a material property known as the elastic modulus). Stress is not measurable phenomenon; however, strain is.

Externally applied forces are classified as either normal or shear, depending on

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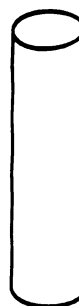
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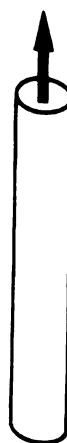
their point of application relative to the surfaces of a structure (Figure 2-2a). Normal forces are applied perpendicular to a surface, and produce tension if the object is stretched, or compression if the object is shortened. Shear forces, on the other hand, tend to cause one plane of the material to slide relative to an adjacent parallel plane. Compressive, tensile, and shear forces produce corresponding strains and stresses. By convention, compressive strains are reported as negative values, and tensile strains as positive values. Bone is strongest in compression, weakest in shear, and of intermediate strength in tension.

In the science of mechanics, a distinction is made between a structure and the material of which it is composed. In biomechanics therefore, one must distinguish the structural properties of a bone, such as a femur, from the material properties of the bone *tissue*. The mechanical behavior of a bone (i.e., how it responds to a specific loading regime) depends on a combination of its geometry (size and shape), its material properties, and the mode of loading (e.g., axial, bending, and torsion; see Figure 2-2b). The typical loads experienced by bone are primarily produced by muscle contraction (Frost 1997a) and, to a much lesser extent, by gravity. “[D]uring normal function bone is subjected to continuously variable modes of loading” (Cochran 1982: 172), resulting in complex distributions of stresses and strains.

With reference to an idealized vertical cylinder, axial loads are applied either off-center (eccentrically) or aligned with the center axis (Figure 2-3). Because bones are not idealized cylinders, but rather have anatomically complex shapes and joint configurations, axial loading in the skeleton is typically eccentric. Weight-bearing bones such as the femur commonly experience a type of loading called eccentric column loading (Cochran 1982) in which a longitudinally oriented force applied eccentrically produces

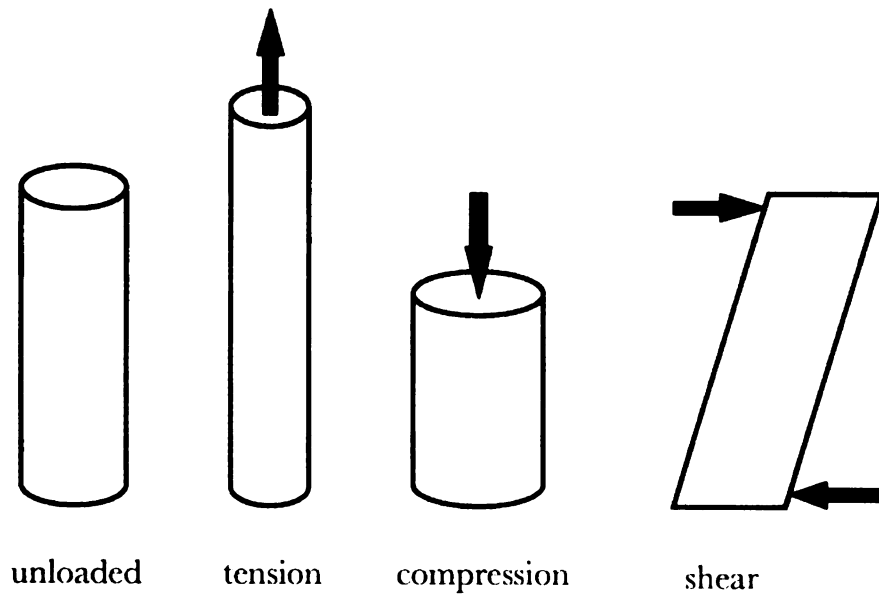


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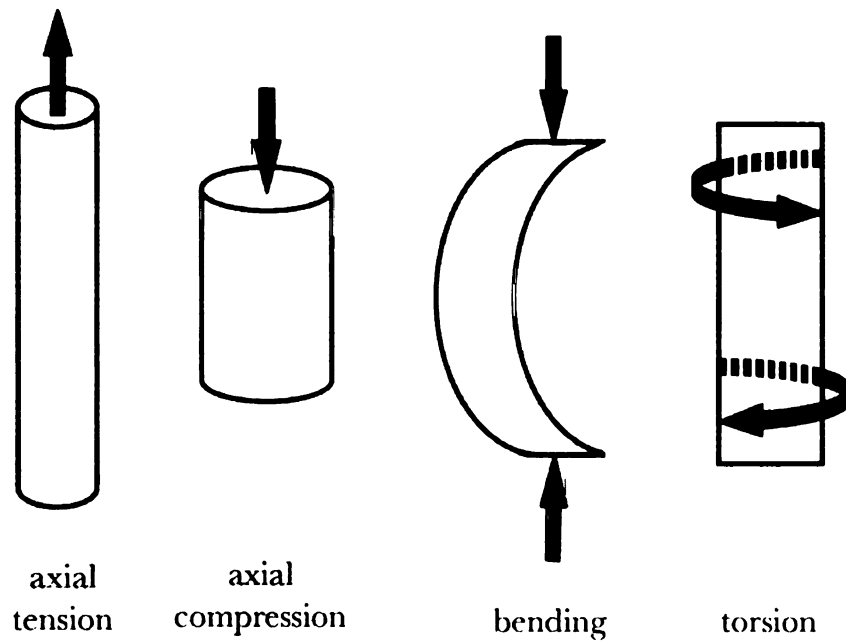


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Figure 2-2. External
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(a)



(b)

Figure 2-2. External forces and modes of loading. (a) Depending on the point of **application**, forces can be normal (tension or compression) or shear. (b) Modes of **loading**: axial tension, axial compression, bending, and torsion (twisting).

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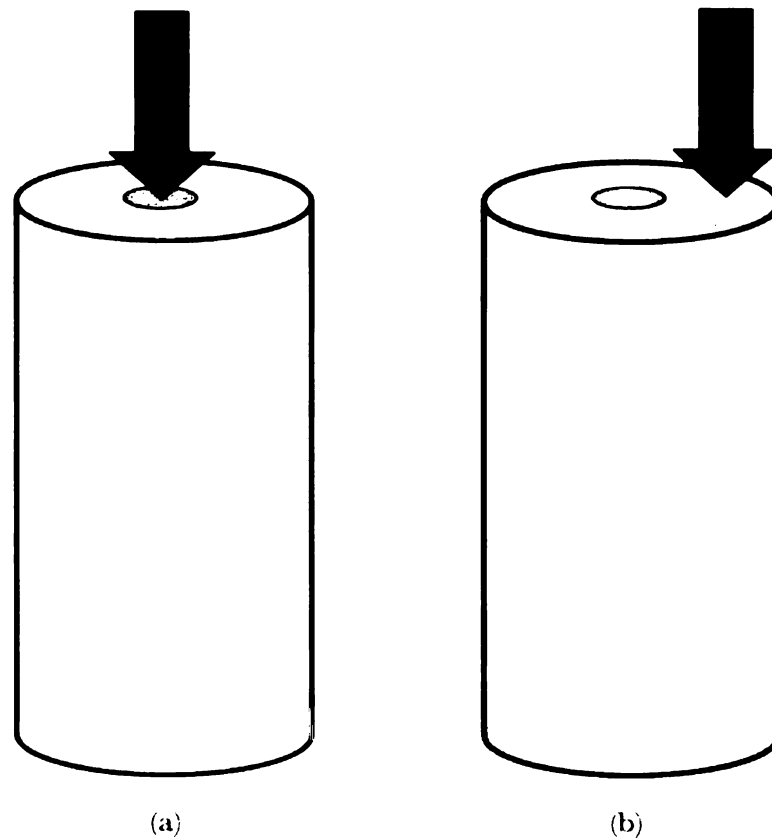


Figure 2-3. Axial loading. (a) Centric loading. (b) Eccentric loading.

bending in addition to direct compression (Figure 2-4a). Therefore, in addition to axial compressive strains, bending superimposes additional compressive strain on the concave side of the diaphysis, and places the convex side under tension. Consequently, compressive strains in long bones are typically greater in magnitude than tensile strains. Maximum compressive and tensile strains and stresses are found at the surface of the bone, and diminish toward its center eventually decreasing to zero in the plane where the transition from compression to tension occurs. This is referred to as the neutral plane. Bending results from other loading configurations as well. For example, when one end of a long bone is fixed and a load is applied to the other end, the bone is said to be loaded as cantilever beam (Figure 2-4b). In this situation, the free end of the bone is deflected resulting in the creation of bending moments along the shaft of the bone. The greatest

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tensile and compressive stresses are located closest to the fixed end of the bone. Bones subjected to bending also experience shear stresses and strains.

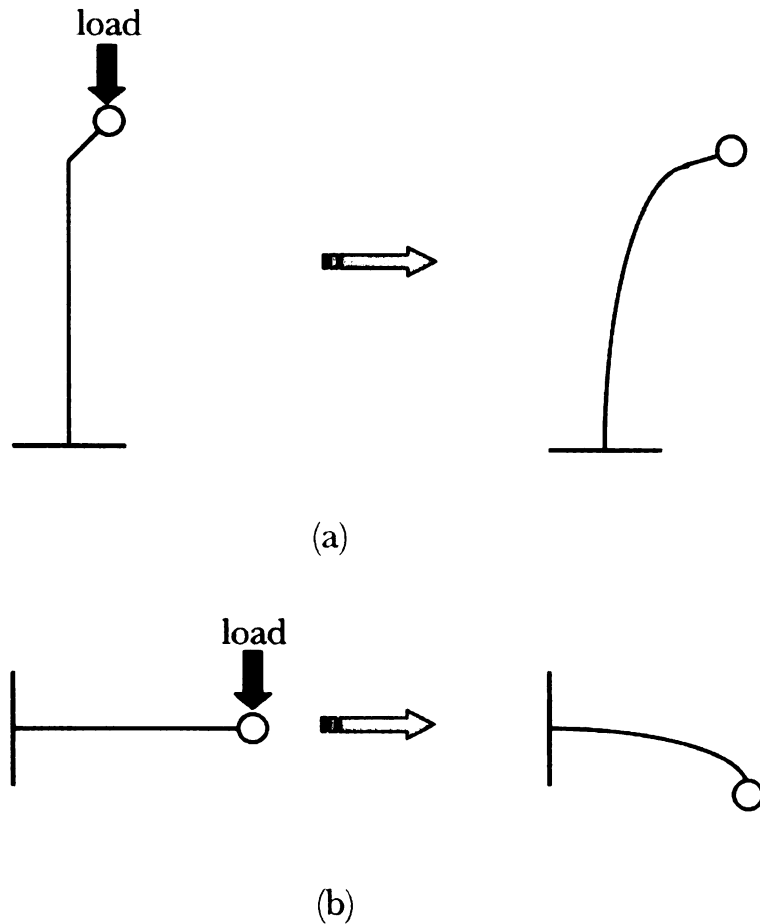


Figure 2-4. Loads that produce bending of long bones. (a) Eccentric column loading. (b) Cantilever beam loading.

To empirically test the mechanical behavior of a bone, a static load is applied until the bone breaks. The resultant deformation can be plotted against the load producing a load-deformation curve (Figure 2-5a). From this curve, the structural properties, such as strength and rigidity, can be ascertained. The load-deformation curve has two distinct regions; the first is called the elastic deformation region, and the second is

called the plastic

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Figure 2-5b .

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called the plastic deformation region. The regions are separated by the proportional limit, a point in the curve where the slope becomes non-linear and begins to level off. The graph of the elastic region is a straight line because the initial increase in deformation is directly proportional to the load, a phenomenon known as Hooke's Law. If the load is removed in this region, the bone will return to its original shape. The slope of the elastic region represents the rigidity of the structure, a measure of its resistance to deformation. Rigidity varies inversely with the length and directly with the thickness of a structure. In other words, a longer bone must be thicker to resist deforming under the same load as a shorter bone. In the plastic region of the curve, a permanent deformation remains even after the load is removed. The point in the curve where this occurs is called the yield point, and the yield strength is the load at which plastic deformation commences. Continual loading will eventually cause the bone to break. The load at failure is known as the ultimate load, and it defines the ultimate or breaking strength of the bone, often simply referred to as the "strength" of a bone.

To determine the mechanical properties of a material, e.g., bone tissue, the effects of geometry are factored out by converting load (force) to stress (F/A) and deformation (change in length, ΔL) to strain ($\Delta L/L$). The resultant curve is called a stress-strain curve (Figure 2-5b). The slope of the stress-strain curve within the elastic region is known as the elastic modulus or Young's modulus (E), and is a measure of the intrinsic stiffness of the material in compression and tension. For shear loading, this property is called the shear modulus. Young's modulus varies within a cross-section and along the length of a bone (Currey 2002). The area under the curve represents the toughness of the material, a

measure of the ability of a bone to resist failure. Factors that influence bone include density, orientation, fatigue, etc.

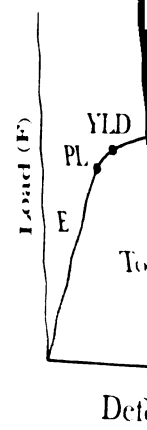


Figure 2-5. Stress-strain curve of bone. E=elastic region, PL=plastic region, UTS=ultimate tensile strength, F=fracture. The curve represents the relationship between load and deformation.

The curve exhibits complex material strength. Bone is loaded in a complex manner, also anisotropic and dependent on the direction of loading.

Work is defined as the product of force and displacement.

measure of the amount of energy absorbed (or work¹) to failure. Toughness relates to the ability of a bone to resist crack propagation. Factors that affect the material properties of bone include degree of mineralization, porosity, microarchitecture, collagen fiber orientation, fatigue microdamage, and rate of deformation (i.e., strain rate).

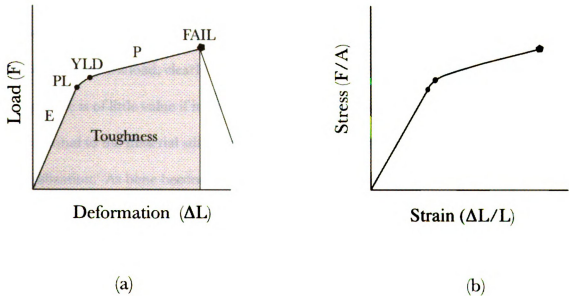


Figure 2-5. Structural and material properties. (a) Load-Deformation curve. E=elastic region of the curve, the slope of this region represents the rigidity of the structure; P=plastic region of the curve; PL=proportional limit; YLD=yield point; FAIL=failure point (=ultimate or failure strength of the structure); the shaded area under the curve represents the energy absorbed to failure (toughness). (b) Stress-Strain curve.

The combination of mineral and collagen makes bone a composite material that exhibits complex mechanical behavior. Bone is weakly viscoelastic, which means that its material strength and elastic properties are somewhat dependent on the rate at which the bone is loaded. In fact, these properties increase with higher rates of loading. Bone is also anisotropic, which means that material properties, such as Young's modulus, are dependent on the direction of loading. This is because bone, like wood, has a "grain"

¹ Work is defined as force acting over a distance. Its units are the newton-meter (Nm) or Joule (J)

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that is partly due to collagen fiber orientation and partly due to the longitudinal orientation of secondary osteons. Bone is stronger and stiffer when loaded in the longitudinal direction, than in the transverse direction.

The mechanical properties of bone often represent a compromise. As Currey (2002) pointed out, one might assume that the ultimate strength of a bone is most important; however, because the efficiency of muscle contractions requires that bones do not deform under a load, clearly, for many bones, rigidity is of foremost importance. A strong bone is of little value if it bends when the muscle contracts. Rigidity is proportional to the material stiffness (E), which is largely dependent on degree of mineralization. As bone becomes more mineralized, stiffness increases but so does brittleness; therefore, toughness decreases—“Bones cannot be both very tough and very stiff” (Currey 2002: 136). Martin et al. (1998: 140) point out, “Different bones have different functions, and the best solution to the conflicting mechanical demands need not be the same for every bone.” The specific evolutionary compromises struck vary throughout the skeleton, and likely contribute to the differential response to loading observed among bones.

Most of the foregoing discussion dealt with the mechanical properties of bones under conditions of static (monotonic) loading (i.e., loads that are continuously applied); however, in life, bones typically experience dynamic loads, in other words, repetitive loading cycles (i.e., repeated cycles of loading and unloading; also referred to as cyclical loading). Repetitive loading generates microscopic fatigue damage (e.g., microcracks), which alters the mechanical behavior of bone. Failure resulting from the accumulation of fatigue damage (fatigue failure) occurs at smaller loads than the ultimate strength of bone. Studies have shown that dynamic not static loading is osteogenic (Lanyon and Rubin

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1984; Rubin and Lanyon 1984b), and it has been hypothesized that bones may be “designed” to minimize fatigue damage (Carter 1984; Frost 2000) rather than maximize ultimate strength. This hypothesis makes sense when it is considered that bones “can only respond to the strains to which they are actually subjected” (Lanyon 1987: 1086)—“the cellular population responsible for functional adaptation can only respond to the strain it experiences while swinging through the trees, not the potential for falling from high branches” (Rubin 1984: S17). In fact, it has been observed that some aspects of normal bone architecture, such as long bone curvature, may actually increase functional strains, but also “control” the direction of bending (Bertram and Biewener 1988; Rubin 1984). One explanation for this is that because bones cannot foresee potential future catastrophic strains, high but predictable functional strains provide a mechanism by which bones can adapt to their typical strain environment (Bertram and Biewener 1988; Lanyon 1987). This would be advantageous as long as repair mechanisms can keep up with the microdamage that results from higher strains.

Concepts in skeletal mechanobiology

Mechanobiology is the study of how the biological processes in bone produce adaptation to mechanical loading. The following are some of the questions mechanobiology research is attempting to answer (Hart 2001; Rubin et al. 1992; van der Meulen and Huiskes 2002): 1) What is the mechanosensor? 2) What mechanical loading variable is being “sensed,” i.e., what is the nature of the mechanical signal? 3) What are the pathways involved in the transduction of the mechanical signal into a cellular response? 4) Is the adaptive process the same throughout the skeleton, or does it vary by bone and location? While there has been significant progress in the field of

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mechanobiology, there are still no definitive answers (Burger 2001; Cowin and Moss 2001; Hart 2001). The following discussion highlights some of the predominant issues and contemporary hypotheses.

The ability of bone to adapt its architecture to mechanical usage would seem to necessitate the existence of a self-regulating biological feedback mechanism. A generally accepted schema of skeletal adaptation is as follows (Cowin and Moss 2001; Lanyon 1993). Osteocytes sense some aspect of their strain environment via the flow of interstitial fluid through the lacunocanalicular network. The osteocytes then transmit a chemical or electrical signal to bone-lining cells, which recruit the effector cells (i.e., osteoclasts and osteoblasts). The effector cells respond by removing or adding bone tissue thereby adapting the bone's architecture to suit its mechanical environment. Once the bone is sufficiently adapted, the signal diminishes to an acceptable level, and the feedback loop is closed.

Research suggests that the “mechanosensory organ” of bone is the “connected cell network” (CCN) and its associated lacunocanalicular network (Burger 2001; Burger and Klein-Nulend 1999; Cowin and Moss 2001; Turner and Forwood 1995). Cowin and Moss (2001) describe the CCN as a “functional syncytium” consisting of osteocytes, bone-lining cells, and osteoblasts, which functions as the “site of intracellular stimulus reception, signal transduction, and intercellular signal transmission” (p. 29-3). Within the CCN, osteocytes are considered the mechanosensor cells (Lanyon 1993). Their distribution within the bony matrix and their numerous cellular connections make them ideally suited to detect local changes in the mechanical environment, and transmit the information to other cells in the network.

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remodeling, the normal response of osteocytes to mechanical usage is to transmit inhibitory signals to bone-lining cells (Martin 2000). This assumes that in the absence of an inhibitory signal, the normal behavior of bone-lining cells is to activate remodeling. This inhibition is released when generation of the signal ceases due to disuse or osteocyte death, or the transmission pathway of the signal is disrupted, which could occur through the formation of microcracks. In this view, microdamage mimics localized disuse. According to Martin (*ibid*), this hypothesis is consistent with and explains the apparently contradictory observation that remodeling activity is increased in both disuse and overload situations.

Just how osteocytes sense a mechanical signal is the subject of much research (Burger 2001; Burger and Klein-Nulend 1999; Turner et al. 1994). The predominant hypothesis is that osteocytes sense mechanical loads via interstitial fluid flow through the lacunocanalicular network. In vitro studies of cultured osteocytes have shown several effects of fluid flow on osteocytes including enhanced production of nitric oxide and prostaglandins, paracrine messenger molecules known to increase following mechanical loading (Burger and Klein-Nulend 1999; Burger 2001; Nomura and Takano-Yamamoto 2000). The mechanism of interstitial fluid flow involves deformation of the bone matrix by dynamic mechanical loading, particularly loads which produce bending. Bending creates pressure gradients, which in turn forces interstitial fluid through the lacunocanalicular network (Tate 2001) from regions of compression to regions of tension. Interestingly, there is some evidence that increased venous pressure and the heartbeat also produce interstitial fluid flow through cortical bone (*ibid*). The flow of interstitial fluid can affect osteocytes either by transduction into an electrical signal (e.g., streaming potentials) or by direct mechanical deformation of the cell (e.g., fluid shear stress).

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Streaming potentials fall under the category of stress-generated potentials, which also includes piezoelectricity. Initial interest in electromechanical phenomena in bone focused on the piezoelectric effect (Currey 2002). The direct piezoelectric effect is an electrical charge produced by deformation of crystal structures—an electrical potential is created by the separation of charged particles resulting in polarization of the crystal. However, piezoelectricity is not thought to play a role in the adaptive process, and researchers have instead turned their attention to streaming potentials (Pollack 2001)—electrical currents generated by the flow of an ionized fluid along a charged solid surface (e.g., through the lacunocanalicular network). The flow of interstitial fluid can also produce direct mechanical deformation of cells through the effects of fluid shear stress. The magnitude of the shear stress is related to the strain generated by mechanical loading; therefore, shear stress provides a direct source of information for osteocytes regarding their local strain environment (Burger and Klein-Nulend 1999). The issue of whether osteocytes are stimulated by streaming potentials, fluid shear stress, both, or neither is currently unresolved (Cowin and Moss 2001).

While there is general agreement that mechanical stimuli are essential in determining and maintaining the structural integrity of the skeleton, “controversies arise in identifying those specific parameters of the complex physical milieu which are actually responsible for modulating or initiating...adaptive processes” (Rubin et al. 1992). Possibilities include stress, strain, or microdamage (Prendergast and Huiskes 1995). Most models assume that some time-averaged stress or strain variable (i.e., loading history) is involved, and most research suggests that bone responds to changes in the strain environment rather than stress (Burr 1992; Burr et al. 1989; Frost 1990b; Lanyon 1981, 1984, 1987; Martin and Burr 1989; Rubin et al. 1992; Tate 2001). Many possible strain

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variables have been proposed as the primary stimulus for mechanical adaptation including: strain mode, strain magnitude, strain rate, strain gradient, strain frequency, and strain energy density (Burr 1992; Martin and Burr 1989; Rubin et al. 1992). Burr (1992) and Lanyon (1984, 1987) have suggested that it is likely the actual “signal” is some interactive combination of variables, such as strain rate, distribution, and magnitude. Rubin et al. (1992) suggest that bone adaptation is also frequency dependent. In spite of significant research on the subject, this issue is unresolved for lack of consensus (Currey 2002).

Since the late 19th century it has been hypothesized that bones become functionally adapted to their mechanical environment by way of an error-driven feedback process (Roesler 1987). In other words, some optimal level of adaptation exists, and deviation from this optimum initiates a corrective response. Relative to the mechanical properties of a bone, mechanical usage can generate strains that are too low, too high, or normal. Strains that are too high or too low initiate biological processes (i.e., modeling or remodeling), which either increase or decrease bone mass and modify the bone’s architecture, thereby normalizing the strains experienced by the bone. The “mechanostat” model was proposed by Frost (1987, 1996) to explain under what conditions (i.e., “when”) the adaptive mechanisms are activated. The mechanostat is a negative feedback model analogous to a thermostat—the adaptive system is turned “on” when there is a mismatch between mechanical usage and bone architecture, and is turned “off” when they are brought into parity. The mechanostat model employs two concepts: 1) threshold values or set points, which Frost has named minimal effective strains (MES), and 2) “usage windows,” which are ranges of strain values that entail a specific set of adaptive responses (Figure 2-6). Because there are probably more strain variables

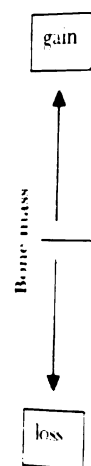


Figure 2-6. The modeling and remodeling window, lies below MOW=mild overload window design intend to Metab 18: 278-2

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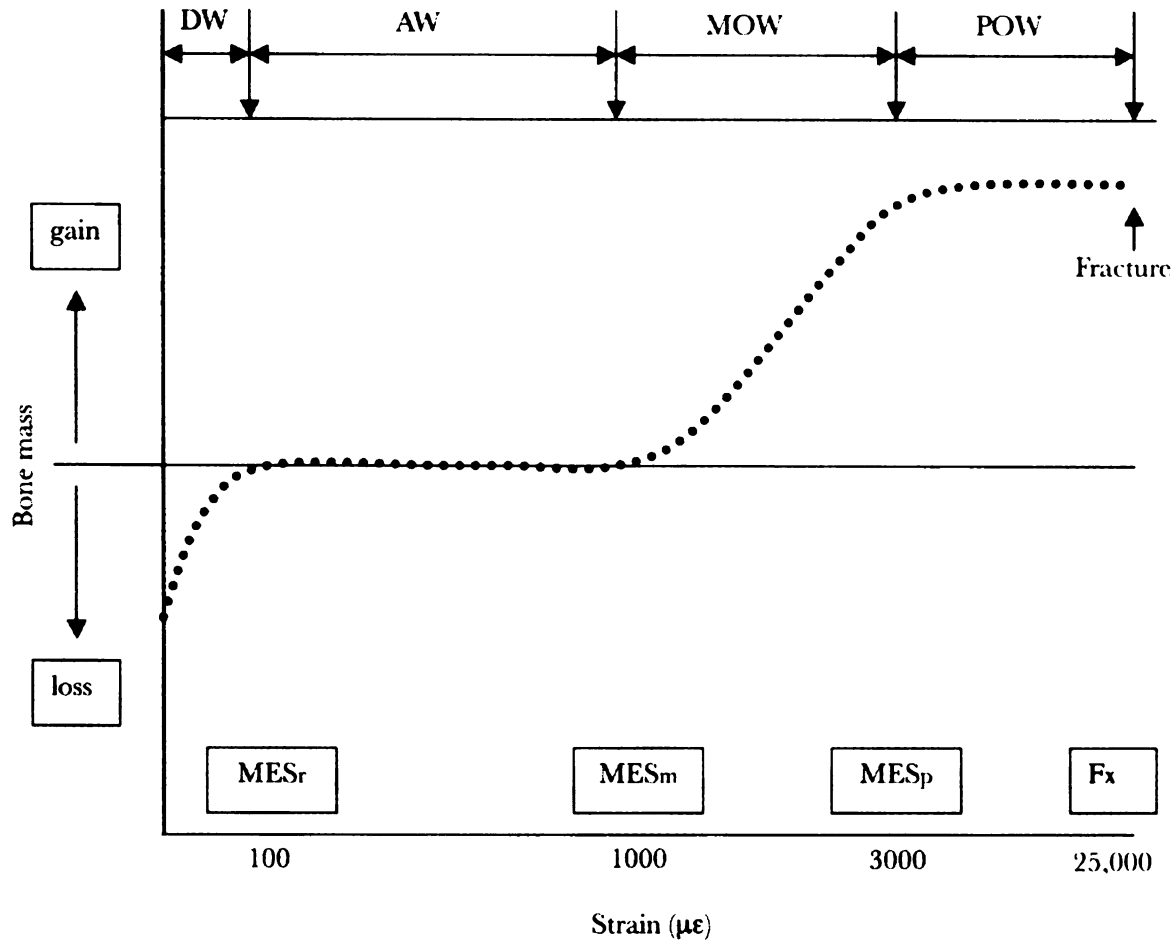


Figure 2-6. The “mechanostat” model. The dotted curve represents the net effects of modeling and remodeling on bone mass within the four usage windows: DW=disuse window, lies below the MES_r; AW=adapted window, lies between the MES_r and MES_m; MOW=mild overuse window, lies between the MES_m and MES_p; POW=pathological overload window, lies above the MES_p. Adapted from Frost, HM (2000) Does bone design intend to minimize fatigue failures? A case for the affirmative. *J Bone Miner Metab* 18: 278-282.

involved in stimulating bone adaptation than simply peak strain magnitude Lanyon (1987) proposed the acronym MESS (minimum effective strain-related stimulus) as an alternative to MES. The current version of the mechanostat model includes four threshold values and four usage windows (Frost 2000). There is an MES for remodeling (MES_r; ~50 - 100μϵ), an MES for modeling (MES_m; ~1000μϵ), an MES for microdamage (MES_p; ~3000μϵ), and a threshold value for fracture (F_x; ~25,000μϵ) (Frost 1997a, 2000). Below the MES_r lies the “disuse window” in which disuse-mode

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remodeling is activated, modeling is inhibited, and bone mass is reduced due to remodeling-dependent bone loss. Between MES_r and MES_m there is a physiological range of strain values that do not initiate an adaptive response, and baseline (conservation-mode) remodeling occurs primarily in response to metabolic demands. In this model, the “goal” of adaptation is to maintain bone strains within this “adapted window.” Frost has also defined two overload windows. The “mild overload window” lies between MES_m and MES_p , and the “pathological overload window” lies above the MES_p . In conditions of mild overload, formation-mode modeling may be activated resulting in the apposition of lamellar bone on periosteal or endosteal bone surfaces. According to Frost, remodeling is inhibited in conditions of mild overload. However, remodeling may be initiated or redirected to remove microdamage. Within the pathological overload window the accumulation of microdamage resulting from extremely high peak strain magnitudes (i.e., greater than those typically generated during normal voluntary activities in adults) is hypothesized to outpace the bone’s ability to repair itself through remodeling. This triggers a type of modeling in which woven rather than lamellar bone is deposited. There is some debate as to whether this is a pathological or a normal adaptive response to extreme overloading (Bertram and Swartz 1991; Burr et al. 1989).

The mechanostat model predicts that mechanical usage will have opposite effects on the processes of modeling and remodeling, which nevertheless produce similar adaptive consequences. For example, stimulation of modeling and inhibition of remodeling both tend to increase bone mass. Because modeling and remodeling activities vary with age and exhibit envelope specificity, the architectural consequences of mechanical usage differ between skeletally immature and mature individuals (Frost 1987).

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Prior to skeletal maturity, increased mechanical usage involves gains in bone mass 1) by formation-mode modeling on periosteal surfaces, and 2) by suppression of remodeling, which conserves bone on endosteal surfaces. Architectural consequences include increased external diameter, decreased medullary cavity diameter, thicker cortical bone, and greater cortical area. In contrast, increased mechanical usage in adults primarily conserves bone mass by suppressing remodeling-dependent bone loss on endosteal and trabecular envelopes. It is not known whether increased mechanical usage produces a normal modeling response in adults, and it is still an open question as to whether adult bone can achieve similar increases in external diameter as seen in younger individuals. This issue is addressed in more detail in chapter 6. Under conditions of extreme overloading (i.e., within the pathological overload window) adults and juveniles might experience a form of modeling involving the addition of woven bone on periosteal or endosteal surfaces. Decreased mechanical usage inhibits modeling and stimulates remodeling. In skeletally immature individuals, the decrease in bone formation produces bones with smaller external dimensions. The architectural consequences of decreased mechanical usage in adult bones are increased medullary cavity diameter and thinned cortices resulting from resorption of endosteal bone. Additionally, because the periosteal envelope tends to experience a net positive bone balance throughout life, increased remodeling does not tend to reduce the external diameter of a bone, and may in fact produce a slight increase in diameter (Frost 2000).

An important concept of the mechanostat, which will be further addressed in chapters 5 and 6, is that changes in the MES setpoints can mimic changes in the strain environment of the bone—an increase mimics disuse, a decrease mimics overload. Consequently, changing the setpoints results in alterations of bone architecture that are

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indistinguishable from those produced by changes in mechanical loading (Frost 1996). Furthermore, the mechanostat model predicts that nonmechanical agents, such as nutrition, genetics, hormones, and disease are responsible for changing the setpoints (Burr 1992; Frost 1996; Jee 2001; Martin et al. 1998). In other words, “the *effect* of the mechanical stimulus is dependent on the nonmechanical environment” (Jee 2001: 1-37, emphasis added).

The mechanostat is not the only model of skeletal adaptation to mechanical usage (Burr 1992; Martin et al. 1998; Turner 1999); however, it is probably the most cited. Inconsistencies between Frost’s mechanostat and experimental data led Turner (1999) to recently propose “the principle of cellular accommodation” as an alternative to the concept of minimal effective strain. Turner claims the mechanostat predicts that under conditions of complete disuse, bones would be completely resorbed (i.e., reduced to a density of zero). Because this does not happen, Turner suggests the mechanostat must be the wrong model. Whereas the mechanostat proposes that bone cells respond to certain threshold values, the principle of cellular accommodation assumes that “bone cells react strongly to transients in their environment, but weakly to steady state signals...[which convey] no new information to the cells” (ibid: 467). Turner suggests that the initial, rapid adaptation response dies out as “bone cells ‘accommodate’ to the new environment” through “changes in the cell’s sensitivity to external stimuli” (ibid: 467). A second weakness of the mechanostat, according to Turner, is the assumption that the MES is the same throughout the skeleton. A variable setpoint explains why weight-bearing bones are more affected by disuse than non-weight-bearing bones, and why the bones of the cranial vault do not erode away even though they are routinely subjected to much lower strains than bones of the appendicular skeleton. Turner claims that the

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principle of cellular accommodation “predicts that the set point...will vary from site to site within the skeleton depending upon the local strain environment to which the cells have become accommodated” (ibid: 468). Of course, it is also possible that the MES is site specific, and the question of whether bone cells “know where they are” is considered an important one in mechanobiology (Currey 2002). A third distinguishing feature of the principle of cellular accommodation is “that final bone mass will be dependent upon the temporal sequence of preceding mechanical loading/hormonal events” (ibid: 469). In other words, the final structure of a bone can be seen as an example of historical contingency; it is dependent on a sequence of unique antecedent states.

Frost’s “mechanostat” and Turner’s “principle of cellular accommodation” are both viable models, but it is likely that neither is, as Frost (1995) would say, “the whole truth.” Even a relatively casual perusal of the literature demonstrates that our current understanding of the biology of mechanical adaptation is still extremely incomplete, and research seems to produce more questions than answers (Cowin 2001a; Currey 2002). The significance of competing models to the topic of this dissertation is that each implies a different relationship between physical activity and bone architecture, and the choice of model will impact the interpretation of group variation in cross-sectional geometry. According to Frost (1997a, 1997b), long-distance running does not necessitate large bones because it generates peak strains within the “adapted window.” Therefore, no amount of running is likely to result in an adaptive modeling response. Running will however help to conserve existing bone. In contrast, according to Frost, the high peak strains generated weight-lifting does result in bigger, stronger bones. If the principle of cellular accommodation is correct, the deciding factor in determining whether running or weight-lifting will produce an adaptive response does not depend on the peak strains involved,

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but rather on the strain environment to which the cells have become accommodated. Furthermore, until the mechanical stimulus is known the relationship of specific physical activities to bone structural variation is speculative at best. For example, if Lanyon's (1987: 1088) "theoretical prediction" is correct that "regardless of peak strain magnitude no adaptive response will be engendered providing the strain distribution is normal" then differences in the intensity level of an activity are not likely to explain group variation in cross-sectional geometry.

Technical overview of cross-sectional geometry

The application of mechanical engineering principles to biological materials is known as biomechanics. Biomechanical properties of the human skeleton have been studied by anthropologists since the mid-20th century; however, it was not until the early 1980s that technological innovations, e.g., computed tomography (CT) and computer software, allowed the application of biomechanical principles to archaeological populations (Larsen 1997; Ruff and Larsen 1990). Pioneering studies by Ruff and colleagues (e.g., Brock and Ruff 1988; Ruff and Hayes 1983a, 1983b; Ruff and Larsen 1990; Ruff et al. 1984, 1987) resulted in, what might be considered, a paradigm shift in bioarchaeology whereby structural variation of the human postcranial skeleton, and long bones in particular, became interpreted in a functional, rather than a nutritional context. "The application of this biomechanical approach in the analysis of archaeological skeletal remains has represented an important breakthrough in bioarchaeological study, especially in the elucidation of specific levels and types of activities in now-extinct human groups" (Larsen et al. 1996: 96). This shift in focus led to research projects aimed at using cross-sectional geometry to elucidate changes in human behaviors coincident with

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Terminology

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Terminology and definitions

This section provides an overview of relevant biomechanical concepts and terminology used throughout this dissertation.

Diaphyseal structure

By definition, long bones are significantly longer than they are wide. Long bones, such as the femur, are composed of two ends, called epiphyses, attached to a connecting shaft, or diaphysis. The transitional region between each epiphysis and the diaphysis is called the metaphysis. Prior to skeletal maturity, the growth plate or physis is located at the junction of the epiphysis and the metaphysis. These three regions of a long bone, the epiphysis, metaphysis, and diaphysis, are to a certain extent structurally and functionally distinct. Typically the epiphyses of long bones are broader than the diaphysis, and function as articular regions, forming joints with other bones. The metaphysis, as a structurally transitional zone between the broad epiphysis and the narrower diaphysis, is usually tapered, and functions to transmit and mitigate joint forces from the epiphysis to the diaphysis. The diaphysis of an adult long bone is essentially composed of an outer shell of cortical bone surrounding a “hollow” center, or medullary canal, which, in life, contains yellow (fatty) bone marrow and a negligible amount of trabecular bone (Ruff 1983). Epiphyses and metaphyses have a relatively thin cortex and contain a significant amount of trabecular bone even into adulthood. Interpretation of their mechanical properties is more complex than for the diaphysis.

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As discussed in the previous section, the structural properties of a bone (e.g., strength, rigidity, toughness) are dependent on both its geometry and material properties. For the purposes of behavioral interpretation, it is assumed that alterations in mechanical loading patterns (e.g., physical activities) principally result in adaptive changes to bone geometry, and that material properties remain unchanged (Larsen 1997; Ruff 2000b; Ruff and Hayes 1983a; Ruff and Larsen 1990; Ruff et al. 1984). This is largely borne out by experimental research (Haapasalo et al. 2000; Heinonen et al. 2001; Woo et al. 1981), although changes to material properties have also been reported (e.g., Matsuda et al. 1986). While adaptive changes can theoretically occur in any skeletal element, the focus of anthropological studies of bone biomechanics has been on long bone diaphyses.

Direct measurement of whole bone strength and rigidity requires empirical testing of a fresh specimen with uncompromised material properties. However, “Because the effects of climate, immersion, and time on skeletal tissue are severe, the direct measurement of strength in archaeological specimens is not possible” (Lovejoy et al. 1976), and indirect methods that estimate mechanical properties must be used. Biomechanical analyses employing engineering beam theory allow estimation of the rigidity of a bone, and more indirectly, its strength² via analysis of diaphyseal cross-sectional geometry. The theory behind biomechanical analysis is that the tubular shape of long bone diaphyses allows them to be modeled as hollow beams. Just as civil or mechanical engineers determine the mechanical behavior of beams used in construction,

² The terms rigidity and strength are often used interchangeably in the bioarchaeological literature (Ruff and Hayes 1983a). Although they are correlated, as noted earlier, they are in fact distinct properties.

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biomechanists can determine the mechanical behavior of long bones (Larsen 1997). Cross-sectional geometric properties reflect the amount and distribution of diaphyseal cortical bone within a specific cross-section. Estimates of rigidity and strength based on cross-sectional geometry correlate with theoretical and experimentally derived (in vitro) values, as long as the section location is not too near the ends of the bone (Ruff 1983)—“beam theory is adequate for representation of stresses in the femoral diaphysis, but seriously overestimates stress in the trochanteric and femoral neck region...beam model geometric analyses of metaphyseal and epiphyseal areas of long bones are inappropriate” (ibid: 143).

Cross-sectional geometric properties fall into two categories, cross-sectional areas and second moments of area. Cross-sectional areas measure the amount of bone in the cross-section, and include total subperiosteal area (TA), medullary area (MA), and cortical area (CA). TA represents the total area contained within the outer (subperiosteal) boundary of the cross-section, and thus includes both the actual area taken up by cortical bone (CA) as well as the “empty” space of the medullary canal (MA). Cortical area is the difference between the total subperiosteal area and the medullary area ($CA = TA - MA$), and reflects the bone’s resistance to the axial forces of tension and compression. A larger cross-sectional area is more effective at resisting deformation due to pure axial loads because the forces are distributed over a larger surface resulting in lower strains and stresses. Axial rigidity is equal to the product of Young’s modulus (E) and cross-sectional area.

Second moments of area (SMA; also known as area moments of inertia) are determined by the amount and distribution of bone within the cross-section. Second moments of area predict structural behavior in bending and torsion with reference to a

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specific neutral plane or neutral axis. Larsen (1997: 200) claims they are “more accurate indicators of bone strength and mechanical function than areas alone.” Generally speaking, the further the bone tissue is distributed from the neutral plane or axis, the more rigid the bone. Slight increases in external diameter produce large increases in rigidity; however, outward distribution of bone tissue is not without cost. “Redistribution of a set amount of material to produce a more rigid structure will not always produce a stronger structure in terms of overall load that can be sustained. As the material gets further and further from the centrum and becomes too thin, strength eventually becomes limited when part of the structure fails by buckling” (Cochran 1982: 151).

The SMA designated by the letter I predicts bending rigidity with reference to a specific neutral plane of bending. Bending rigidity is equal to the product of Young’s modulus (E) and I . For each cross-section there are as many possible values of I as there are potential planes of reference, but for simplicity, biomechanical studies focus on four: I_x , I_y , I_{max} , and I_{min} . I_x and I_y represent bending rigidity in the anterior-posterior and medial-lateral planes, respectively, and reflect the distribution of bone *relative* to the medial-lateral (x -axis) and anterior-posterior (y -axis) planes of the bone. In other words, a cross-section with bone tissue more outwardly distributed in the anterior-posterior plane (i.e., exhibits a greater anterior-posterior diameter) would have a greater value for I_x , because the bone tissue is located further from the x -axis (medial-lateral plane) (Figure 2-7). I_{max} and I_{min} , known as the principal second moments of area, are measures of maximum and minimum bending rigidity relative to two empirically derived orthogonal planes. A bone’s resistance to torsional loading (i.e., loads that produce twisting or rotation of material about an axis) is predicted by the polar second moment of area, symbolized by J , and is equal to the sum of any two values of I relative to two

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perpendicular planes (e.g., $I_x + I_y$ or $I_{\max} + I_{\min}$). Therefore, J is also seen as representing “an average bending rigidity about all planes through the section...a useful measure of overall bending/torsional rigidity” (Ruff 1999: 296). The calculated value of J is most accurate for cross-sections that do not deviate significantly from circularity (Burr and Piotrowski 1982; Ruff and Hayes 1983a).

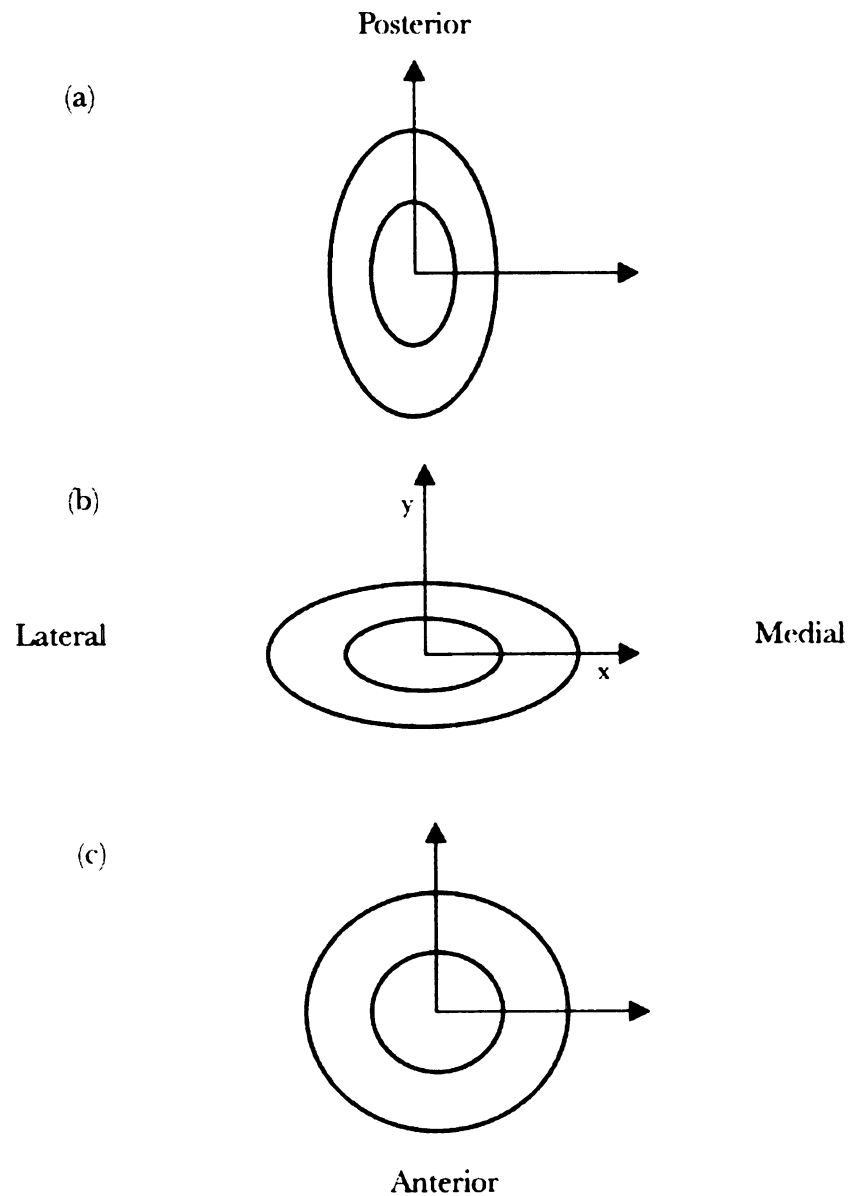


Figure 2-7. Second moments of area. (a) Anterior-posterior expanded cross-section; $I_x > I_y$. (b) Medial-lateral expanded cross-section; $I_y > I_x$. (c) Circular cross-section; $I_x = I_y$.

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Ruff and colleagues (Ruff 1987; Ruff and Hayes 1983a; Ruff et al. 1984) have identified cross-sectional “shape” as an important indicator of behavior. Cross-sectional shape in this usage refers to ratios or indices of second moments of area (SMA), such as I_x/I_y and I_{max}/I_{min} . Ratios approaching 1.0 have a more circular cross-section. Temporal and geographic differences in these SMA ratios, particularly I_x/I_y of the femoral midshaft, are seen as reflecting changes in types of activities, such as mobility.

External diaphyseal dimensions

Some of the earliest bioarchaeological studies of long bone diaphyseal structure focused exclusively on external diaphyseal dimensions, such as midshaft medial-lateral and anterior-posterior diameters, rather than cross-sectional geometric properties (e.g., Larsen 1981). In these studies, skeletal “robusticity” is typically represented as a ratio of external diaphyseal dimensions to a measure of overall long bone size, such as length. Many studies continue to utilize external dimensions in structural analyses, usually in addition to cross-sectional geometry (Bridges 1989; Bridges et al. 2000; Ruff 1987; Wescott 2001), primarily because this standard anthropometric technique is less hampered by fragmentary or poorly preserved remains (Larsen 1997). Moreover, in spite of technological improvements, calculation of cross-sectional properties is a time-consuming and expensive procedure (Wescott 2001).

Larsen and Ruff (Larsen 1997, 2002; Larsen and Ruff 1991; Ruff 2000; Ruff et al. 1984) have maintained that external dimensions, while correlated with cross-sectional properties, are much less precise in terms of reflecting biomechanical strength because they do not consider the internal architecture of the bone (such as the medullary and cortical areas). In a bioarchaeology review article Larsen (2002: 135) stated, “measuring

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the external dimensions of long bones...does not allow the analysis of distribution of bone, which is the most meaningful attribute of bone strength for inferring lifestyle.” However, Wescott (2001) has argued that external dimensions accurately predict all cross-sectional geometric properties, except cortical area, and provide equivalent results to biomechanical analyses. For the purposes of this dissertation, the critique of using cross-sectional geometry to reconstruct behavior can be considered to apply to studies that utilize external diaphyseal dimensions as well.

CHAPTER 3 BEHA

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CHAPTER 3—LITERATURE REVIEW: BIOMECHANICAL ANALYSES AND BEHAVIORAL RECONSTRUCTION IN BIOARCHAEOLOGY

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Justus von Liebig

Introduction

This chapter reviews the anthropological literature pertaining to behavioral reconstruction from cross-sectional geometric analyses. The chapter is not intended to provide a comprehensive summary of all anthropological studies of cross-sectional geometry, but rather focuses on the conclusions of the research that are most relevant to this dissertation.

Literature review

A large body of anthropological literature deals with the application of long bone cross-sectional geometry to behavioral reconstruction. For ease of presentation, this literature is divided into two broad categories. The first category includes articles emphasizing the methodology and theory behind the application of cross-sectional geometry in anthropology. The second category includes bioarchaeological studies that apply cross-sectional geometric analyses to the reconstruction of behavior in archaeologically derived populations from the United States, Europe, Asia, and Africa.

Methodological and theoretical literature

Since the mid-1970s, anthropologists have investigated a variety of issues pertaining to the biomechanical structure of long bones, including locational variation in

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the cross-sectional properties of the femur and tibia (Lovejoy et al. 1976; Ruff and Hayes 1983a), and group variation with regard to sex, age, and side (Ruff 1987; Ruff and Hayes 1983b; Trinkaus et al. 1994). These studies have also examined long bone structure with regard to allometry (Ruff 1984, 2000; Ruff et al. 1993), ontogeny (Ruff et al. 1994), and trends in hominid evolution (Ruff et al. 1993, 1994; Trinkaus et al. 1994). By interpreting observed variation in cross-sectional geometric properties of paleontological, archaeological, and modern samples within a framework of theoretical and experimental research in biomechanics, Ruff and colleagues have attempted to define a causal relationship between long bone structure and the mechanical loading patterns generated by physical activity. Collectively this research has generated a biomechanical model that provides the basis for “reconstructing” the behavior of archaeological populations.

Bone architecture and mechanical function

Utilizing a large sample of femora and tibiae from the Pecos Pueblo archaeological population, Ruff and Hayes (1983a) investigated the general pattern of variation in cross-sectional properties within the lower limb. To accomplish this they examined six femoral section locations (5 diaphyseal plus the femoral neck), and five tibial (all diaphyseal). Diaphyseal sections were located by percentage of bone length, i.e., 20%, 35%, 50%, 65%, and 80%, with 20% most distal, 50% at midshaft, and 80% most proximal (e.g., the femoral subtrochanteric location). Results of this investigation demonstrated that bone geometric properties are not uniformly distributed along the diaphysis, but rather vary by section location. For example, in the femur, I_{max} is oriented more mediolaterally in the 80%, 65%, and 20% sections, and more anteroposteriorly in the 50% and 35% section locations. Additionally, by examining the ratio of the principal

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second moments of area ($I_{\max}/I_{\min}$), it was found that the femur is most circular at midshaft, and least circular proximally.

Experimental and theoretical predictions of *in vivo* mechanical loadings and stresses of the lower limb “generally correspond” (Ruff and Hayes 1983a: 379) to the observed pattern of variation in cross-sectional geometry suggesting that the distribution of cortical bone within the diaphysis reflects localized adaptation to specific types of loadings. For example, a more circular section is best adapted to either torsional loading or to relatively equal bending forces in two perpendicular planes. A bone section that is elongated (e.g., ovoid) is better adapted to bending in just one plane. This structure-function relationship, originally proposed by Lovejoy et al. (1976) as an explanation for differences in tibial shape between prehistoric Native American populations and modern urban populations, forms the core of the hypothesis that long bone cross-sectional shape can be used to infer specific types of activity (Ruff et al. 1984).

Sexual dimorphism and “the mobility index”

Building on the observations discussed above, studies of sexual dimorphism in cross-sectional properties by Ruff and Hayes (1983b) and Ruff (1987) led to the development of “the mobility index,” the ratio of anterior-posterior to medial-lateral bending strength (I_x/I_y) of the femoral midshaft. In analyzing sex differences in Pecos Pueblo femora and tibiae, Ruff and Hayes (1983b) observed that the lower limb bones of males are generally more “adapted” to anterior-posterior bending loads, and females more medial-lateral. This is most apparent when comparing the cross-sectional shape ratio I_x/I_y , which is greater in males, and especially pronounced around the knee (distal femur and proximal tibia). Sex differences in this ratio are virtually non-existent for the

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proximal femur and distal tibia, where expected in vivo anterior-posterior bending loads are minimal. To explain these findings the authors propose that sex differences in pelvic structure lead to increased medial-lateral bending loads in the proximal femur of females. However, since this anatomical difference in pelvic structure does not account for the observation that the greatest amount of sexual dimorphism in I_x/I_y is around the knee, the authors suggested, “a second factor...related to a probable behavioral difference between males and females of the Pecos Pueblo...[such as] long distance running” (Ruff and Hayes 1983b: 394).

Ruff (1987) expanded this study of sexual dimorphism in cross-sectional shape to include a modern U.S. sample and published diaphyseal shape data from a variety of other samples, in order to elucidate temporal trends related to changes in subsistence strategy. Samples were classified as hunter-gatherer, agricultural, or industrial. Population comparisons suggested that hunter-gatherers show the greatest degree of sexual dimorphism in I_x/I_y , industrialists the least, and agriculturalists an intermediate amount. According to Ruff (1987), this is due to a decrease in mobility among males over time, combined with reduction in sexual division of labor (sex-specific behavior).

Age and cross-sectional geometry

Cross-sectional properties not only vary between the sexes, but by age as well. Loss of cortical bone from the endosteal surface with compensatory subperiosteal apposition has been documented as an age-related process (reviewed in Ruff and Hayes 1983b). Using the Pecos Pueblo archaeological population, Ruff and Hayes (1983b) examined the effects of age on long bone cross-sectional geometry. In summary, they found that total subperiosteal area (TA) increased over all age categories in both sexes.

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However, following a peak in cortical area (CA) during the fourth decade, the subsequent increase in medullary area (MA) outpaced the increase in TA, resulting in an overall decline in CA during the last decades of life. This effect was greater in females than males. The net result of this age-related phenomenon is a thinner cortex with greater medullary and subperiosteal areas. This more outwardly distributed bone also leads to increased values for second moments of area (SMA). The authors noted sex-specific regions of greatest increase in SMAs—males increase most in the midshaft region of the femur and tibia, and females in the proximal femur.

Bilateral asymmetry

Bilateral asymmetry, particularly of the upper limb, has received a great deal of attention in anthropological studies (e.g., Bridges 1989; Bridges et al. 2000; Fresia et al. 1990; Ruff 2000b; Trinkaus et al. 1994). Individuals exhibit varying amounts of size and strength difference between the bones of their right and left sides, with the right side typically larger and stronger in the upper limb (the opposite is typical of the lower limb). These differences have most often been interpreted in terms of handedness. In addition, the relative amount of difference between the two sides (i.e., the degree of bilateral asymmetry) varies among populations. Trinkaus et al. (1994) have argued that the high degree of bilateral asymmetry in cross-sectional properties exhibited by professional tennis players and some Neanderthal specimens strongly supports the idea of extreme developmental plasticity of bone structure in response to life-long differences in mechanical loading. Consequently, population variation in degree of upper limb bone bilateral asymmetry is hypothesized to reflect variation in mechanical loading patterns of the right and left arm (i.e., differential use of the upper limb).

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Ruff et al. (1994) evaluated the influence of developmental age on the effects of increased mechanical loading on the cross-sectional geometry of long bones. While, the ultimate purpose of the study was to provide a basis for interpreting the biomechanical properties of juvenile fossil hominids, the findings are pertinent to any evaluation of long bone structural adaptation. As part of this study, the authors reanalyzed the data from a classic study of professional tennis players who were found to exhibit significant humeral bilateral asymmetry related to side-dominance of the playing arm (Jones et al. 1977). It was found that the dominant playing arm of tennis players exhibited increased total subperiosteal area (TA) and decreased medullary area (MA), resulting in increased cortical area (CA) and torsional strength (J) over the non-playing arm.

To examine the effects of age on the development of extreme bilateral asymmetry, Ruff et al. (1994) performed correlation analyses between TA, CA, and J and three timing factors (age of subject at the time of the original study, age at which play began, and number of years played). Only age at which play began showed a statistically significant correlation with the cross-sectional properties. Further analysis of three of the tennis players by Ruff et al. (1994) produced the following observations: 1) From childhood through early adolescence, the primary effect of increased mechanical loading is periosteal expansion, leading to relatively greater increases in TA, and consequently torsional strength (J). 2) Following mid-adolescence, the primary response of bone to increased mechanical loading is conservation of endosteal bone leading to a reduction in MA, and less dramatic increases in J. An important overall conclusion of this study is that “mechanical stimuli may have different effects on diaphyseal modeling/remodeling

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Allometry and size standardization

Cross-sectional properties have been shown to vary by sex, age, and side. They also vary in relation to body size and body shape (Ruff 1984; Ruff et al. 1993; Ruff 2000a). As explained by Lovejoy et al. (1976: 497), “Two beams of identical cross section will therefore withstand equal loads only if they are also the same length.” Therefore, in order to interpret differences in bone strength among different population samples, cross-sectional properties must be “size-standardized”. Lovejoy et al. (1976) originally proposed dividing cross-sectional properties by the square of bone length, however, Ruff and Hayes (1983a) argued for the importance of studying the allometric³ relationships between body size and shape and long bone structure, prior to adopting a specific size-standardization factor. Subsequently, Ruff and colleagues have conducted several studies of allometry and size-standardization on human skeletal samples (Ruff 1984; Ruff et al. 1993; Ruff 2000b).

Ruff (1984) examined the dependence of cross-sectional properties on bone length utilizing femora and tibiae from the Pecos Pueblo and Georgia coast archaeological samples, as well as modern autopsy material. Based on this original study, Ruff suggested that the relationship of cross-sectional properties to long bone length is isometric⁴. To standardize for differences in body size, he proposed that cross-sectional areas be divided by bone length squared and second moments of area by bone length to the fourth power. He concluded that, “Significant differences between populations after this standardization

³Allometric refers to the change in proportion or shape of parts of an organism during growth and development.

⁴ Isometric refers to equality of proportion; in other words, no effect of size on shape.

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should be indicative of relative differences in mechanical loadings of the bones under study” (ibid: 356), and proposed four factors that could produce population differences in size-standardized cross-sectional properties: 1) different activity levels, 2) different activity types, 3) different body weight/height ratios or different limb length proportions, and 4) different body shape (e.g., short and broad versus tall and slim).

Ruff’s (1984) standardization methodology was subsequently revised (Ruff et al. 1993; Ruff 2000b), based on the hypothesis that cross-sectional properties vary relative to body mass and body shape, rather than simply bone length (i.e., stature). Ruff et al. (1993: 25) defined “skeletal ‘robusticity’...as the *strength or rigidity of a structure relative to the mechanically relevant measure of body size*,” and proposed that for the weight-bearing portion of the skeleton (e.g., the lower limb bones), the “mechanically relevant measure of body size” is body mass. Ruff et al. (1993) rejected Ruff’s (1984) earlier contention that the relationship between bone length and cross-sectional properties is isometric, and proposed a new size-standardization method—dividing cross-sectional areas by bone length cubed and second moments of area by bone length to the 5.33 power.

Ruff (2000b) expanded the findings of Ruff et al. (1993) further emphasizing the critical importance of controlling for differences in body shape as well as body size in biomechanical analyses. “[I]n order to distinguish the effects of specific behavioral use of the limbs on limb bone structure, it is necessary to first account or control for the effects of both body size and body shape on diaphyseal morphology” (Ruff 2000b: 270). He added, “it is potentially misleading to use unadjusted bone length alone as a ‘size’ measure against which to compare cross-sectional diaphyseal dimensions...raising bone length to a different power has no effect...” (ibid: 282). Ruff suggested that a “correction factor for body shape should be incorporated” (ibid: 269) when there are potentially

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significant differences in body shape among groups. In a separate publication (Ruff 2000a) proposed using articular dimensions, such as femoral head size, to standardize the data. Unfortunately, while strongly arguing for the importance of controlling for body shape differences between groups, Ruff does not specify the criteria used to determine what constitutes “*significant*” body shape variation, thereby casting doubt on the behavior-related conclusions of any study that does not explicitly take body shape into consideration.

Studies by both Ruff et al. (1993) and Ruff (2000b) indicated that the cross-sectional properties of the humerus as well as the femur scale with body mass, in spite of the observation that, “The upper limb of bipedal hominids, whose primary function is not locomotor and therefore not weight-bearing, should probably not be scaled strictly to body mass” (Ruff et al. 1993: 25). Ruff (2000b) also found that the proximal femur scales differently from the femoral midshaft, being more dependent on pelvic breadth than femur length. These results suggest that relationship between cross-sectional properties and body size and shape may be rather complex, and that the appropriate standardization method may vary by section location.

Evolutionary trends

The apparent existence of long-term evolutionary trends in long bone robusticity and biomechanical strength has contributed to the theoretical basis for drawing inferences about behavior from population differences in cross-sectional properties (see reviews by Bridges 1995 and Ruff 2000a). Cross-sectional geometric properties of long bones have been reported for a variety of fossil hominid specimens (Lovejoy and Trinkaus 1980; Ruff et al. 1993, 1994; Trinkaus et al. 1994). These studies have demonstrated a

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“worldwide trend” of decreased postcranial robusticity throughout human evolution and continuing into recent human prehistory. Ruff (2000b: 79) wrote, “The simplest explanation for this general trend is that as cultural mechanisms for interacting with the physical environment elaborated during the last two million years (i.e., technological sophistication increased), biological mechanisms—in this case, bone strength—decreased in importance.” Juvenile fossil hominids also exhibit “increased postcranial robusticity relative to Recent humans” interpreted as being “consistent with increased mechanical loading of the skeleton throughout life” (Ruff et al. 1994: 53).

Comparisons of degree of sexual dimorphism of femoral I_x/I_y ratios between Late Pleistocene samples (archaic *Homo sapiens*, i.e., Neanderthals, and early modern *Homo sapiens*) and Holocene samples, suggests that sexual division of labor in Late Pleistocene groups was similar to that of more recent hunter-gatherers. Interestingly, though demonstrating a degree of sexual dimorphism in femoral midshaft shape similar in magnitude to Holocene hunter-gatherers, the Neanderthal femoral midshaft is more circular (Bridges 1995; Ruff 2000b). Based on Ruff’s mobility index (I_x/I_y) described earlier, this would suggest that Neanderthals were less mobile than groups that are more recent. However, the authors reason that because it does not seem probable that Neanderthals lived a more sedentary lifestyle than more recent hunter-gatherers (Bridges 1995), this finding more likely reflects a Neanderthal body shape “quite different from that of later humans” (Ruff 2000b: 86). It is worth noting that when the existing preconception regarding a specific type of behavior, namely Neanderthal mobility, did not fit the biomechanical model (i.e., I_x/I_y as an indicator of mobility), it was the biomechanical model that was modified, not the assumption about Neanderthal mobility. This would seem to call into question the claim that biomechanical analyses yield

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Bioarchaeological studies of cross-sectional geometry

Numerous anthropological studies have interpreted population variation in cross-sectional geometric properties in the context of changes in human adaptive strategies that have occurred throughout the course of human cultural evolution. Specifically, this literature addresses changes in long bone structure presumed to have resulted directly from differing patterns of activities (level and type of physical activity) and sexual division of labor associated with transitions in subsistence and mobility strategies, as well as, in response to European contact. Research has also looked at population variation in cross-sectional geometry in relation to the physical environment (e.g., terrain). Anthropologists approach these issues by quantifying variation in external dimensions and cross-sectional geometric properties, as well as, changes in degree of sexual dimorphism and bilateral asymmetry within, between, and among sample populations.

These studies have been divided into two broad categories based on geography: bioarchaeological studies of North American populations and bioarchaeological studies of non-North American populations. For each study, the results and conclusions most germane to this dissertation are presented. A major thesis of this dissertation is that the data from many of these studies have been over-interpreted (see chapter 5). In other words, the authors' conclusions are frequently based on statistically non-significant group differences and non-significant "trends" in sample means. Therefore, it should be noted that most of the findings summarized here are taken directly from the authors' data

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tables, and not from the written “results” portion of each publication. Only those findings that are statistically significant ($p < 0.05$) or near-significant ($p < 0.10$) are included in this review. This is done to facilitate an evaluation of the relationship between the actual data and the conclusions reached by the authors, and to minimize the impact of interpretive bias. In keeping with the main focus of this dissertation, which is a critical analysis of the application of biomechanical analyses to behavioral interpretations, conclusions related to changes in cross-sectional geometric properties (as opposed to variation in external dimensions) are emphasized.

Bioarchaeology of North American populations

By far, the majority of research has been conducted on archaeologically derived skeletal collections representing a variety of prehistoric and early historic groups from the eastern and western United States.

Eastern United States

In the eastern United States, studies of variation in cross-sectional geometry have been conducted on populations primarily from three main regions, the southeast coast (Freesia et al. 1990; Larsen 1981; Larsen and Ruff 1991; Larsen et al. 1996, 2001; Ruff and Larsen 1990, 2001; Ruff et al. 1984), northwest Alabama (Bridges 1989, 1991), and west-central Illinois (Bridges et al. 2000). A single study has examined populations from Michigan and New York (Barondess 1998).

The most comprehensive investigation of temporal changes in long bone diaphyseal structure has been conducted on samples from a geographic region known as La Florida or Spanish Florida (Larsen et al. 2001), which includes archaeological sites

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from the Georgia coast and northern Florida. While the earliest of these studies focused on the transition from hunting and gathering to maize agriculture along the Georgia coast (Larsen 1981; Ruff et al. 1984), this long-term research project subsequently included samples representing populations from the Spanish mission period in order to study behavioral changes associated with European contact (e.g., Ruff and Larsen 1990). This research examined temporal changes in long bone size (external dimensions) and biomechanical properties of femora and humeri from males and females of precontact preagricultural, precontact agricultural, and postcontact agricultural periods.

Larsen's (1981) anthropometric study of external diaphyseal dimensions of femora, tibiae, and humeri laid the groundwork for subsequent research on long bone structural adaptation in this geographic region. Comparisons of hunter-gatherers to agriculturalists demonstrated that long bone dimensions, including measures of diaphyseal size and long bone length, decreased over time in both sexes, but that the magnitude of the changes was greater in females. Larsen (ibid: 498) concluded, "Analysis of skeletal size on the prehistoric Georgia coast presents us with a trend of skeletal size reduction that is probably associated with the adoption of an agricultural lifeway.... While degradation of nutrition may have been a factor, it seems most likely that the cause for this reduction is centered on change in degree of functional demand with the shift in economic focus."

Following this original analysis, Ruff et al. (1984) conducted the first study of changes in cross-sectional geometric properties of the same hunter-gatherer and agricultural populations, focusing on the femur. Because Larsen (1981) had documented a decrease in long bone length for this region, the authors "standardized" the data to facilitate interpretation of group comparisons.

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Group differences were determined by ANOVA and t-tests. Results of statistical analyses of size-standardized cross-sectional properties demonstrated relatively few statistically significant differences between sample means, particularly in the midshaft region. In males at midshaft, only medullary area (MA) and I_x/I_y were significantly lower in the agricultural group. In contrast, a greater number of significant changes were identified for the subtrochanteric section; MA, TA, I_{max} , I_{min} , J, and I_{max}/I_{min} were all significantly reduced in male agriculturalists. In females, *only* total subperiosteal area (TA)—for both the midshaft and subtrochanteric sections—was significantly lower among agriculturalists. Female differences in midshaft and subtrochanteric MA and subtrochanteric torsional strength (J) reached near-significant levels. The authors claim, “All of these changes in the distribution of bone tissue within cross sections *strongly suggest* a reduction in mechanical loading of the femur in the agricultural group” (ibid: 131, emphasis added).

Subsequent studies of the Georgia coast archaeological populations continued to expand on these two studies ultimately including samples from post-European contact populations, and adding the humerus to the structural analysis. Ruff and Larsen (1990) reported the results of the first biomechanical study to include femora and humeri from three temporal/cultural periods (precontact pre-agricultural, precontact agricultural, and post-contact). This study also expanded on the results of Ruff et al.’s (1984) comparison of the two precontact populations.

Ruff and Larsen (1990) demonstrated that the statistically significant decrease in I_x/I_y previously reported for male agriculturalists (Ruff et al. 1984) was due to a near-significant decrease in I_x . In addition to the decrease in femoral midshaft TA documented by Ruff et al. (1984), females also showed significant decreases in both I_x and

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I_y. Between the two precontact populations, male humeri showed significant reductions in I_{min}, I_y, and J, and near-significant reductions in T_A, I_{max}, and I_x; whereas, female humeri showed *no significant differences*.

Between the pre-contact agricultural and contact populations, an increase in medullary area (MA) was the only change seen in the femoral midshaft of males. No significant (or near-significant) change in any other size-standardized midshaft geometric property, *including cross-sectional shape*, was observed between the males of these two periods. In contrast, all size-standardized properties except cortical area (CA) were significantly larger at the femoral subtrochanteric location in contact period males.

Contact period females exhibited significant increases in all size-standardized femoral cross-sectional properties except midshaft and subtrochanteric MA and subtrochanteric I_{max}. Female subtrochanteric I_{max}/I_{min} showed a significant decrease in the contact period. *No significant*, or even near-significant, differences were found between the precontact agricultural and contact periods for *any* size-standardized cross-sectional property of the humerus for either sex. The humeral shape ratio I_x/I_y showed a near-significant increase in males following contact.

Sexual dimorphism was found to be significant for most cross-sectional properties, at all section locations, and in all temporal periods. The primary exception was cross-sectional shape ratios, for which male-female differences were generally *not significant*. Sexual dimorphism of femoral midshaft I_x/I_y was not significant for any temporal period, but reached near-significance in the contact period. Subtrochanteric I_{max}/I_{min} was significantly dimorphic *only* in the precontact agricultural period, and humeral cross-sectional shape was significantly sexually dimorphic *only* in the precontact preagricultural period.

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The authors discussed their findings at some length, and reached the following conclusions. 1) “In the Georgia coast samples studied here, females decline through time in the femoral midshaft I_x/I_y ratio, while males first decline in the precontact agricultural period, then increase in the contact period” (Ruff and Larsen 1990: 110). It should be reiterated at this point that the only statistically significant change in this ratio, for either sex, was a decrease in males between the two precontact periods. No other significant or near-significant difference was observed. In fact, the one-way ANOVA of femoral midshaft I_x/I_y among periods within sex was not statistically significant. The authors also discussed the finding that among contact period males the I_x/I_y distribution is bimodal, with 5 of 11 males showing an extremely high mean value for this ratio. These “changes” in midshaft cross-sectional shape were interpreted in terms of mobility, “Thus, these results indicate that among some of the males in the contact period, long-distance travel had increased greatly from the average levels documented prior to contact, while in other males and all females, long-distance travel either stayed about the same or declined” (ibid: 112). They suggested that this is consistent with historic records documenting that some contact period males were forced by the Spanish “to make periodic long-distance trips” as part of the “*repartimiento*” labor system. 2) The authors suggested that the decrease in subtrochanteric I_{max}/I_{min} over time in males and females “is indicative of a decrease in *general* activity level” (ibid: 113). In males, the significant decrease in I_{max}/I_{min} occurred between the two precontact periods, with only a near-significant decrease following contact. In females, the decrease occurred following contact with the two precontact periods showing almost identical values. 3) The authors noted that an hypothesis of decreasing general activity levels over time (based on subtrochanteric I_{max}/I_{min}) seems inconsistent with the finding that femora of contact period males and females show

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increases in cross-sectional areas and second moments of area. They offered the following explanation: “it is plausible that body weight/stature increased in the missionized Guale relative to previous or nonmissionized contemporary populations due to increased sedentism...confinement...and increased consumption of carbohydrates...This in turn would increase the body weight/bone length ratio, and thus the length-standardized cross-sectional properties in the lower limb...despite a generally lower activity level” (ibid: 115-116). Unfortunately, it is impossible to test this hypothesis because weight (i.e., body mass) cannot be determined from skeletal remains. 4) With regard to the upper limb the authors stated, “geometric properties of the femora and humeri in the present study sample tend to follow similar temporal trends, with one major exception. Unlike femora (or male humeri), female humeri continue to decrease in strength relative to bone length in the contact period. Thus, it appears that females in the contact period were placing relatively lower mechanical loads on their upper limbs than in any other period” (ibid: 116). This was interpreted as being “consistent with the hypothesized changes in general activity level and relative body weight among the missionized Guale” (ibid: 117). The authors also claimed that the biomechanical analysis of male humeri suggests that males became “more involved in agricultural tasks during the contact period” (ibid: 117). These interpretations are not supported by the data. Results of the one-way ANOVA among periods within sex for the humerus were not significant, and t-tests for precontact agricultural-contact period comparisons showed no significant differences for either sex. In their final comments the authors asserted, “Male and female differences in use of the upper limb continued to decline [in the contact period], possibly reflecting more male participation in agricultural responsibilities” (ibid: 120). This is in direct conflict with the data, which show sexual dimorphism of humeral

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properties at its maximum during the contact period, a point the authors noted earlier in the paper, “sexual dimorphism in humeral properties first declines from precontact preagricultural to precontact agricultural, then increases to its largest values in the contact period” (ibid: 108).

In a companion study to Ruff and Larsen (1990), Fresia et al. (1990) examined temporal changes in bilateral asymmetry (calculated as percent side difference) of humeral length and mid-distal humeral cross-sectional properties. A one-way ANOVA of percent side difference among groups within sex was significant for TA, Ix, Iy, and J; near significant for length; and not significant for CA, MA, or humeral cross-sectional shape Ix/Iy. This study did not include post-hoc t-tests (e.g., Tukey HSD test) for pairwise comparison of group means, so it is unclear which periods showed significant differences in the above properties. However, examining the data reveals that for cross-sectional areas, bilateral asymmetry decreased most dramatically between the two precontact periods then remained unchanged into the contact period for both sexes. For second moments of area (SMA), the results differ somewhat between the sexes. In males, degree of bilateral asymmetry of Ix and J is similar between the two precontact periods, but decreases in the contact period, whereas bilateral asymmetry of Iy decreases between the two precontact periods, and does not change in the contact period. In females, bilateral asymmetry of all three SMAs decreased dramatically with the transition from hunting and gathering to agriculture, but was unchanged following Spanish contact.

Significant differences between right and left sides (i.e., bilateral asymmetry) were evaluated by t-tests for paired comparisons. For statistically significant side differences, total subperiosteal area (TA) and cortical area (CA) were found to be typically greater on the right side with medullary area (MA) greater on the left side in both sexes. Very few

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statistically significant side differences in second moments of area were detected. In males, no right-left SMA comparisons reached the level of statistical significance. In other words, males of all three periods were nearly symmetrical in terms of humeral “strength.” For females, the right humerus was significantly stronger than the left only during the precontact preagricultural period. Female right and left humeri were essentially symmetrical during the other two periods.

In summary, male humeri were virtually symmetrical in all periods, but the mean percent side difference for some properties changed over time; TA asymmetry decreased between the two precontact periods and second moments of area asymmetry decreased following contact. Female humeri were significantly asymmetric only during the precontact preagricultural period, and became bilaterally symmetrical coincident with the transition to agriculture.

The authors asserted, “changes in bilateral asymmetry...reflect alterations in mechanical loadings, and thus activity patterns” (ibid: 121). They concluded, “Comparisons of the temporal periods reveal a decline in asymmetry of the upper limb...[that] reflects activity patterns involving change in the use of the upper limbs in the shift to a lifeway that involves agriculture...[and] females were affected to a relatively greater degree in the shift to agriculture than males” (ibid: 131). With regard to bilateral asymmetry of humeral shape the authors asserted, “females of the precontact periods exhibit greater anterior-posterior bending strength on the left side, males...on the right side” (ibid: 130). However, results of paired t-tests for side differences in shape showed no significant asymmetry in shape for females of any period, or for males in the precontact preagricultural and contact periods (only male precontact agriculturalists showed significant shape asymmetry). In fact, for anterior-posterior bending rigidity (I_x)

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specifically, females showed statistically significant side dominance *only* during the precontact preagricultural period, where the right side (not the left) was greater, and *no* significant asymmetry for the other two periods. In addition, as noted above, one-way ANOVA among periods within sex was not significant for humeral shape.

Continuing the trend of building on earlier research of Georgia coast populations Larsen et al. (1996) expanded their study with the addition of a late contact period sample; therefore, in this study the contact period is represented by early contact and late contact groups. Results of comparisons among the two precontact and early contact period populations are consistent with those already reviewed (Ruff and Larsen 1990). Statistically significant differences between the early and late contact periods were restricted to females, who experienced an increase in medullary area (MA) of the femur (both midshaft and subtrochanteric sections) and humerus, and an increase in humeral total subperiosteal area (TA). No other statistically significant differences between the early and late contact periods were detected. Nevertheless, based on the results of this study the authors stated, “In both Early and Late Contact males and Late Contact females, an increase in bone strength in the humerus suggests increased use of their upper limbs...likely related to the increase in demands placed on these populations by the Spanish in labor-related projects...that structural properties increase during the Late Contact period in both females and males suggests that during this time both sexes may have engaged in similar types of activities, or at least activities involving similar loading modes” (Larsen et al. 1996: 113). The authors acknowledged that a higher average age-at-death of the late contact sample could have contributed to observed findings, but maintained that, “the increases in second moments of area during the Contact period [are most likely explained by] behavioral factors” (ibid: 115). Neither sex showed a

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statistically significant increase in second moments of area. The significant increases in TA and MA observed in late contact period females are consistent with an increase in mean age of this sample, as discussed earlier in this chapter (Ruff and Hayes 1983b).

Ruff and Larsen (2001; see also Larsen et al. 2001) revamped their study of long bone structural adaptation on the southeast coast to include samples from northern Florida. In both studies, six samples were compared, three from Georgia and three from Florida, representing different subsistence strategies and temporal periods. Following Ruff and Larsen (2001) they are referred to as Early Prehistoric Guale (EPG), Late Prehistoric Guale (LPG), Early Mission Guale (EMG), Late Mission Guale (LMG), Early Mission Yamasee (EMY), and Early Mission Timucua (EMT). The authors (*ibid.*) noted that some of the samples previously categorized as preagricultural (i.e., EPG) (Ruff and Larsen 1990) were, in the current study, included with the LPG, a horticultural group. These studies also employed a different size-standardization method—following Ruff et al. (1993) cross-sectional areas are divided by (bone length)³ and SMAs by (bone length)^{5.33}.

As compared to previous studies, the number of cross-sectional variables analyzed was reduced to CA and J for the femur (subtrochanteric region and midshaft) and humerus, Ix/Iy for the femoral midshaft and humerus, and I_{max}/I_{min} for the femoral subtrochanteric region (Ruff and Larsen 2001). Results of a two-way ANOVA by sex and group (with age included as a covariate) revealed statistically significant differences among groups in femoral midshaft J and Ix/Iy, femoral subtrochanteric J and I_{max}/I_{min}, and humeral CA and J. The following statistically significant differences between temporally contiguous groups were found. Between the EPG and LPG femoral

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subtrochanteric J, as well as humeral CA and J decreased. Between the LPG and EMG/EMY groups femoral subtrochanteric I_{max}/I_{min} decreased. No statistically significant changes occurred between early mission EMG and late mission LMG groups. No differences among the Early Mission groups⁵ (EMG, EMY) were detected in the analysis.

Overall, these findings are consistent with those already presented. However, unlike the results reported in Ruff and Larsen (1990) this study failed to detect any significant changes in the femoral midshaft I_x/I_y between the two precontact (EPG and LPG) groups (the only significant group difference in this ratio is between the EPG and LMG, which are not temporally or culturally contiguous groups). Behavioral interpretations do not deviate from those already reported (Larsen et al. 1996; Ruff and Larsen 1990) with respect to the EPG, LPG, EMG, and LMG. With regard to the Early Mission Yamasee, the authors proposed the following: “The Yamasee early mission sample is...in many respects...more similar to the late pre-mission Guale group (LPG) than the mission period Guale or is intermediate between this group and the EMG group...[i]n particular...variation among males in long-range mobility [is] not increased in the Yamasee” (Ruff and Larsen 2001: 138). They asserted that this is suggestive of a people who were “less acculturated during the mission period.” Results of pair-wise group comparisons show that the EMY significantly differ from the EPG in subtrochanteric I_{max}/I_{min} , and humeral CA and J, and they differ from the LPG in subtrochanteric I_{max}/I_{min} . The EMY do not differ significantly for any property from

⁵ Ruff and Larsen’s (2001) interpretations of the EMT will not be presented in this dissertation because, by the authors’ own admission, “Results for the Timucuan ossuary sample must be treated cautiously, since the exact sex composition of this sample is unknown, and sex was seen to be an important influence on biomechanical properties in the other samples” (p. 139).

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the EMG or LMG. With respect to group means for femoral midshaft I_x/I_y (the mobility index), the EMY do not differ significantly from any of the other groups. Therefore it would seem that, statistically, the EMY are, in most respects, similar to all of the other groups studied. In fact, the authors' interpretation of similarity between the EMY and LPG is based primarily on the *coefficient of variation*⁶ for midshaft I_x/I_y in males, which is similar in magnitude between the two groups.

Bridges (1989, 1991) studied temporal changes in upper and lower limb external dimensions and cross-sectional geometry (CA, I_{max} , I_{min} , J) associated with the transition from hunting and gathering to maize agriculture in northwestern Alabama. This research "examine[d] evidence for changes in both the level and the types of subsistence activities between the Archaic and Mississippian time periods" (Bridges 1991: 89). Based on ethnographic and ethnohistoric literature, Bridges (1989, 1991) hypothesized that the subsistence transition would have entailed a change in the types of activities and an increase in the level of activity for Mississippian populations. In addition, she predicted that the changes would be more pronounced in females because they typically take on most of the responsibilities associated with food production in agricultural societies.

The results (Bridges 1989, 1991) revealed an increase in femoral cross-sectional properties in the Mississippian population for both sexes, but with the changes more pronounced and uniform in male femora. Size-standardized humeral dimensions (i.e., robusticity) and cross-sectional properties were not different between hunter-gatherer and agricultural males. In females, robusticity of both humeri increased in the Mississippian period, as did biomechanical "strength" of the left mid-distal humerus (cross-sectional

⁶ The coefficient of variation compares the variability between samples with different means. It is the ratio of the standard deviation to the group mean.

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properties of right humeri were not studied). Both sexes exhibited decreased bilateral asymmetry in humeral robusticity in the Mississippian sample (no data is available for bilateral asymmetry of humeral cross-sectional properties), attributed to more equal usage of the right and left arms.

Bridges (1989: 391) states, “Differing patterns of changes in males and females suggest a change in the division of labor coinciding with the shift to maize agriculture.” In females, the combination of increased humeral size and strength, particularly on the left side near the elbow, and decreased bilateral asymmetry is attributed to “pounding corn in the traditional manner of southeastern Indian women” (Bridges 1991: 98). For males, the decrease in humeral bilateral asymmetry was tentatively attributed to the adoption of the bow and arrow (Bridges 1989, 1991). The increase in femoral size and strength in males is referred to as “an unexpected result” (Bridges 1991: 98), which Bridges attributed, not to “long-distance running”, but rather to “a variety of activities...includ[ing] long-distance raiding and hunting, agricultural or building chores, and possibly increasing involvement in the ball game, a vigorous sport regarded as preparation for warfare...” (ibid: 99). Bridges (1991: 99) concluded, “the adoption of maize agriculture involved a major increase in workload” in northwestern Alabama. The difference in results between this region and the Georgia and Florida coastal populations is attributed to regional variation in practices associated with the adoption of agriculture.

Bridges et al. (2000) applied a similar research design to populations from west-central Illinois to examine temporal changes in long bone diaphyseal structure (both external dimensions and cross-sectional geometry) of upper and lower limbs. However, this study emphasized skeletal adaptation associated with increasing “horticultural intensification” in order to “link activity levels with specific subsistence economies, rather

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than with somewhat simplistic categories such as ‘agriculturalists’” (ibid: 218). The samples were derived from populations representing four subsistence stages: 1) Middle Woodland—“low-level horticulturalists relying on native seeds”, 2) Early Late Woodland—“intensive horticulturalists using the same crops,” 3) Later Late Woodland—intensive horticulturalists following the initial introduction of maize, and 4) Mississippian— “intensive maize agriculturalists” (ibid: 218).

Cross-sectional properties examined in this study were CA, I_{max}, I_{min}, J, and I_{max}/I_{min}. Results of the analysis of male femora and humeri demonstrated *no significant* differences in cross-sectional properties among the time-periods examined. The only statistically significant findings for female femora were greater midshaft CA, I_{min}, and J in the Later Late Woodland period as compared to the Middle Woodland period. Female humeri, on the other hand, showed several significant differences between time-periods, but only on the left side (the right side showed no differences). The cross-sectional properties of the left humeri of Later Late Woodland females were greater than Middle Woodland females. Mississippian females showed a subsequent decline from both Late Woodland periods in the geometric properties of their left humeri, a reduction to levels statistically indistinguishable from those of the Middle Woodland period. Only one Early Late Woodland variable, left midshaft I_{max}, showed a statistically significant increase over the Middle Woodland period. In other words, Later Late Woodland females (but not Early Late Woodland females) had “stronger” left humeri than Middle Woodland females, while Mississippian females had left humeri that were weaker than both Early and Later Late Woodland females, but similar in strength to Middle Woodland females.

These results suggest that there was an increase in left humeral strength in females that preceded the adoption of intensive maize agriculture as the primary mode of

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subsistence in Mississippian times, i.e., it occurred at some point during the Late Woodland period. The subsequent decrease in left arm strength of Mississippian females was unanticipated by the authors—"The increasing reliance on starchy seeds, especially maize, in the Mississippian period would be expected to coincide with a greater need for processing, a chore traditionally carried out by females. If so, female arm strength should continue to increase in the Mississippian period. That it did not, but actually decreases, requires rethinking this hypothesis" (ibid: 232). The authors suggest the decrease in left arm strength might reflect a technological improvement in corn processing, such as soaking in lye or boiling, which ultimately led to reduction in the physical labor necessary for this subsistence chore.

The results were also interpreted in terms of sexual division of labor. "Overall, male and female changes in strength occur largely independently of each other, suggesting that their roles in society differed as well...Given that females historically conducted the majority of agricultural tasks, including both growing and processing crops, and that variation in female strength in this study fits well with the observed archaeological sequence of subsistence change, it can be assumed that females were also largely responsible for growing crops in the Woodland period as well as later in Mississippian times" (ibid: 235).

Barondess (1998) evaluated humeri and femora from prehistoric and historic groups in Michigan, and from hunter-gatherer and agricultural groups in western New York State to detect structural differences "that may have resulted from concomitant changes in physical activity" (ibid: 93). This study analyzed both external diaphyseal dimensions and biomechanical strength (cross-sectional properties).

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female femora demonstrated a statistically significant increase in many cross-sectional properties of both the proximal and distal femur, but not the midshaft. Male femora exhibited significant increases only in midshaft and distal MA and TA. Most of the statistically significant differences between female humeral samples were localized to the midshaft region. Male humeri showed few significant differences, confined to an increase in both TA and torsional strength of the distal humerus, and TA only of the midshaft. Based on these findings, Barondess accepted the null hypothesis (no difference in cross-sectional properties) for male femora, and both male and female proximal humeri. However, he rejected the null hypothesis for female femora at proximal and distal section locations, and for male and female humeral distal and midshaft locations.

Biomechanical data from New York hunter-gatherer and agricultural samples were restricted to male femora and female humeri. Group comparisons revealed few statistically significant differences for any biomechanical variable. Barondess accepted the null hypothesis for male femora. For female humeri, he accepted the null hypothesis for the proximal humerus, where no significant differences were found, but rejected the null hypothesis for the distal humerus, where only MA increased significantly, and for the midshaft humerus where MA increased and CA decreased.

According to Barondess (1998: 110), “Interpreted within the context of physical activity, the increases in the cross-sectional area and strength measures provide evidence for increased biomechanical demand, for both sexes, in the Michigan historic period.” He observed that the magnitude of the changes was greater for females, and suggested, “the level of activity changed more dramatically for females than for males between the two periods” (ibid: 110-111). Barondess concluded that there is no biomechanical evidence for a change in workload with the adoption of agriculture in New York.

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Variation in cross-sectional geometry has also been investigated in archaeological populations of the western United States including the Southwest, Great Basin, and Great Plains.

Some of the earliest work on cross-sectional geometry utilizing an archaeological sample was performed on the Pecos Pueblo of New Mexico (Ruff and Hayes 1983a, 1983b). The major findings of this work are presented in the previous section of this chapter dealing with methodological and theoretical issues. Studies of the Pecos Pueblo have provided a foundation for all subsequent research in this area. In addition, the data from the Pecos Pueblo sample has served as a basis for several regional comparisons (e.g., Ruff et al. 1984; Larsen and Ruff 1995). Ruff et al. (1984) compared Georgia coast preagricultural and agricultural femoral samples with the Pecos Pueblo sample, which represents an agricultural adaptation roughly contemporaneous with the Georgia agricultural sample. They found that for most cross-sectional properties, particularly of the midshaft, the Pecos Pueblo femora exhibited strength and robusticity more similar to the Georgia preagricultural sample, and greater than the Georgia agricultural group. The most significant exception to this was cross-sectional shape, midshaft I_x/I_y and subtrochanteric I_{max}/I_{min} , where both agricultural groups had lower values for these ratios (i.e., increased circularity). Ruff et al. (1984: 134) conclude “a possible scenario of less running and climbing, and more walking and possibly other more sedentary pursuits such as lifting and carrying in the two agricultural groups, is at least consistent with the available biomechanical data. The relatively more robust Pecos femora may indicate that while the basic types of activities were similar in the two agricultural groups, they were more difficult and mechanically demanding at Pecos than on the Georgia coast.”

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Brock and Ruff (1988) studied structural changes in the lower limb of three skeletal samples representing a temporal-cultural sequence in prehistoric New Mexico: Early Villages, Abandonments, and Aggregated Villages. These cultural periods presumably practiced different mobility and subsistence strategies, ranging from mobile hunter-gatherers in the Early Villages period to sedentary maize agriculturalists in the Aggregated Villages period, with the Abandonments period categorized as transitional, typified by “disequilibrium and restructuring of communities” (ibid: 116). The authors examined cross-sectional properties of male and female femora from each of these periods in order to test the hypothesis that levels of mobility were greatest in the Abandonments period and lowest in the Aggregated Villages period.

For females, results of statistical analyses of the data revealed no statistical differences among periods for *any* cross-sectional property, including shape (I_x/I_y and I_{max}/I_{min}). In males, no statistically significant group differences were found for any cross-sectional property, except the cross-sectional shape index I_{max}/I_{min} . Midshaft I_{max}/I_{min} was lowest in the Aggregated Villages period, and subtrochanteric I_{max}/I_{min} was lower during the Abandonments period than the Aggregated Villages period. There was no significant difference in I_{max}/I_{min} between the Early Village and Abandonments periods for either section location (midshaft or subtrochanteric), and there was *no significant difference* in midshaft I_x/I_y (the mobility index) for males among the three cultural periods. Somewhat surprisingly, considering the lack of significant differences between sample means in this study, the authors concluded, “The temporal patterns in femoral geometry suggest that activity levels in the prehistoric American Southwest increased between the Early Villages and Abandonments periods, then declined during Aggregated Villages in both sexes” (Brock and Ruff 1988: 125).

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Larsen et al. (1995) studied the prehistoric Stillwater Marsh people of the western Great Basin. According to the authors (ibid: 107), “With regard to Great Basin prehistoric populations, a debate has centered on the relative degree of mobility of human groups and the degree of importance of dietary resources extracted from marsh versus upland settings.” Patterns of osteoarthritis along with cross-sectional geometric properties of humeri and femora were examined, “in order to shed light on patterns of physical activity, resource acquisition, and settlement in the prehistoric Stillwater populations” (ibid: 107). This summary focuses on the results of the biomechanical analysis.

Cross-sectional properties (CA, J, I_x/I_y) of the Stillwater Marsh sample were compared to those published for a variety of prehistoric population samples representing “different topographic and subsistence contexts” (ibid: 125). No indication of statistical significance (i.e., P-value) was provided for any of the group comparisons discussed by the authors; statistical analyses were either not performed or simply not reported.

Larsen et al. (1995) reported that in comparison to other populations, the Stillwater Marsh remains have relatively low CA, but high TA, resulting in relatively high values for second moments of area (e.g., J). Among males, the authors asserted that variation in torsional rigidity of the femoral midshaft “closely parallels subsistence strategy; that is, hunter-gatherers are highest and agriculturalists are lowest” (ibid: 128). This association was not found in females, however, whose femoral torsional rigidity values “seem to correspond to degree of ruggedness of terrain, with Great Basin and Southwestern (Pecos) populations showing the highest values, Georgia coastal populations the lowest, and Plains populations intermediate between the other two regions” (ibid: 128). The low cortical area in combination with high torsional rigidity of the Stillwater Marsh femoral sample was interpreted as suggesting “episodic undernutrition” (ibid: 131),

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but with a high degree of mechanical loading. The authors claimed this conclusion is supported because relative to the femora, the Stillwater Marsh humeri also have low cortical area, reflecting a systemic factor (e.g., nutrition), but are comparatively biomechanically weak, reflecting localized mechanical loading patterns.

According to Larsen et al. (1995: 132), relative to the other population samples, the Stillwater Marsh males have a relatively high femoral midshaft I_x/I_y value indicating, "...shapes are modified such that they reflect highly mobile behaviors (e.g., long-distance travel)." The Stillwater Marsh people also exhibited a high degree of sexual dimorphism for femoral shape, which the authors consider "a striking characteristic of hunter-gatherers in general...probably the result of a sexual division of labor" (ibid: 129). The authors claimed, "This study of structural morphology, then, appears to support a reconstruction of a mobile lifeway for men *and women*, but with males being more mobile than females" (ibid: 132, emphasis added). Parenthetically, the I_x/I_y value for Stillwater females was reported as 1.0. This was the second lowest value among the six populations compared and indicates a circular cross-section, a result that in other studies has been interpreted as indicative of low mobility or sedentism. The authors concluded, "Far from leading a leisurely existence, these populations likely followed a highly physically demanding lifeway that involved frequent travel over rugged terrain...including the nearby uplands...subsistence strategies were not focused entirely on the marsh" (ibid: 133).

Subsequently Ruff (1999) expanded his Great Basin study to include samples from Stillwater Marsh, Malheur Lake, and the Great Salt Lake regions. Results were again compared to those published for the Southwest, Georgia coast, the northern Great Plains, and northwestern Alabama. This study sought to evaluate the relationship of cross-

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sectional geometric variation of femora and humeri with geographic terrain (mountainous, plains, coastal), subsistence strategy (pre-agricultural, agricultural), and sex. The Stillwater Marsh, Malheur Lake, and Great Salt Lake samples are all described as hunter-fisher-gatherers, with the Great Salt Lake population differing from the other two by incorporating corn agriculture.

“In this study, CA and J are taken as the principal indicators of bone rigidity or strength, while other second moments of area, considered as ratios, are used to examine cross-sectional shape differences or relative strengths in different planes” (ibid: 296). Group differences were analyzed using two-way ANOVA (sex and group) and Tukey post hoc t-tests for between-group comparisons. The effects of terrain, subsistence, and sex on femoral cross-sectional properties were tested by three-way ANOVA. Cross-sectional properties were size-standardized following Ruff et al. (1993).

Results of comparisons among the Great Basin samples demonstrated few statistically significant differences in cross-sectional properties. In the femur, midshaft I_x/I_y was lower in the Malheur Lake sample than either of the other two, and subtrochanteric CA was lower in Stillwater than Malheur Lake, and near-significantly lower than Great Salt Lake. Humeral I_x/I_y was lower in Stillwater than Malheur Lake. Sex differences were confined to cross-sectional shape ratios, namely femoral midshaft I_x/I_y , where male values are greater than female, and subtrochanteric I_{max}/I_{min} , where females are greater than males.

Femoral midshaft comparisons between the combined Great Basin sample and two other combined samples (one representing various other Native American groups, and another representing other hunter-gatherer populations) show the Great Basin femora to have the greatest torsional rigidity. Differences in other midshaft properties

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were not significant. Results of the three-way ANOVA of all samples combined demonstrated a statistically significant effect of terrain on femoral midshaft CA and J, with samples from mountainous regions exhibiting greater values than samples from the plains (CA) and coastal (CA and J) regions. Subsistence strategy was found to have *no effect* on any midshaft cross-sectional property. Not surprisingly, sex was an important factor for CA, J and Ix/Iy with males having greater values than females. Interestingly, while differing between the sexes, Ix/Iy did not vary with either terrain or subsistence strategy. Sexual dimorphism in Ix/Iy was significant among hunter-gatherers, but not agriculturalists.

In combination, these results were interpreted as “indicat[ing] that the increase in femoral robusticity in the Great Basin is most likely related to the ruggedness of the terrain in this region...Hunter-gatherers from other regions, who presumably shared broadly similar patterns of behavior, have significantly less robust femora...[which] supports this interpretation” (ibid: 312). Ruff added, “Another possible explanation is that the Great Basin inhabitants...had to travel farther during foraging than most other American Indian groups, thereby imposing more prolonged mechanical loading of the lower limbs” (ibid: 312). Although, subsistence strategy had no effect on cross-sectional properties, Ruff maintained that it does have an effect on sexual dimorphism of femoral midshaft shape, in which hunter-gatherers exhibited greater sex differences than agriculturalists. The high degree of sexual dimorphism in Ix/Iy exhibited by the Great Basin samples is “consistent with very different degrees of mobility in males and females” (ibid: 315). Ruff discussed the finding that the Malheur Lake sample had significantly lower Ix/Iy than the other two Great Basin samples, “the lower [midshaft Ix/Iy] in the Malheur sample, particularly among males, could indicate a somewhat more sedentary

life-style when compared to the Stillwater and eastern Great Basin samples. This index in isolation must be interpreted cautiously, however, since population differences in other factors, such as general body build, can also influence femoral diaphyseal shape.... It is possible that this sample as a whole had an overall physically demanding yet more geographically limited life-style than the other two Great Basin samples, with males remaining more mobile than females..." (ibid: 317).

Ruff (1994) also studied variation in femoral midshaft geometry from samples representing a cultural/temporal sequence in the northern Great Plains, and a single sample from the southern Great Plains. As in previous studies, Ruff compared the data from these samples to those published for the Georgia coast pre-contact and Pecos Pueblo groups. Results demonstrated few differences in size-standardized geometric properties among the various geographic regions (Georgia, Southwest, Northern Plains, and Southern Plains), as well as among the Great Plains samples (only MA varied significantly, and only among females). The primary exception was in the midshaft cross-sectional shape ratios, where the Southern Plains sample was greater in magnitude than any other groups, and significantly greater than the other Great Plains samples. Sexual dimorphism of these ratios was also greatest in the Southern Plains sample. The different cultural/temporal groups from the Northern Plains exhibited virtually no variation in midshaft cross-sectional shape. Furthermore, within the Northern Plains, Ruff found no significant changes in femoral midshaft structure following the introduction of the horse.

The dramatic anterior-posterior elongation of the midshaft femur and high degree of sexual dimorphism in midshaft cross-sectional shape of the Southern Plains sample is described as "an apparent paradox" (ibid: 242) because it placed this *agricultural* group at the high end of the range of I_x/I_y values Ruff has reported for hunter-gatherers. Ruff

suggested that this “could indicate a very unusual behavior pattern, with generally high levels of mobility in both males and females, but particularly high levels among males,” and concluded, “the present data indicate significant variation in mechanical loading and behavioral use of the lower limb among the Plains Village sites, with a possible North-South dichotomy” (ibid: 243).

Wescott (2001) applied a biomechanical approach in a large-scale, comprehensive study of long bone structural variation within and among groups from the American Great Plains, Great Basin, Southwest, and Texas gulf coast, as well as, early and late modern industrial populations. Wescott assigned ordinal scores for activity level, mobility level, and ruggedness of the physical terrain to his sample populations to analyze their effects on long bone morphology. Results of statistical analyses revealed that significant group differences did not correspond to degree of mobility, nor did hunter-gatherer male femora exhibit “greater anteroposterior elongation of the femoral midshaft than horticulturalists, agriculturalists, or modern industrialists” (ibid: 184). Wescott stated, “very little of the total variation in the humerus or femur is explained by activity level...[except] between lower-level activity groups...and higher-level activity groups” (ibid: 184-185). Greater activity level was correlated with increased medial-lateral femoral diameter leading to increased torsional strength. Wescott’s results also showed that, “males tend to cluster by subsistence technology but females do not” (ibid: 185). Females clustered by geographic region; however, Wescott did not interpret this as an effect of physical terrain, as has been suggested (Larsen et al. 1995), because “Females cluster nearly identically whether femoral or humeral dimensions are used” (ibid: 185). In fact, this study provided no evidence for a strong relationship between terrain and femoral robusticity. Similar to what has been observed in other studies, sexual

dimorphism of the femur was found to correlate somewhat with subsistence strategy, with “broad-spectrum hunter-gatherers” most dimorphic at the femoral midshaft. Exactly the opposite relationship was found for the midshaft humerus. Wescott concluded, “Within a tightly controlled geographical region, patterns of behavior can probably be reliably interpreted from long bone structural morphology, but variation in mobility within subsistence groups, cultural practices, diet, health and other factors probably preclude the broad generalizations about the type of activity based on long bone morphology” (ibid: 195).

Bioarchaeology of non-North American populations

Fewer studies of cross-sectional geometry have been published for population samples from outside of North America. However, studies have been conducted on skeletal populations from Great Britain, Africa, and Asia.

Mays (1999) applied a biomechanical approach to the assessment of differences in physical activity patterns among three skeletal groups buried in a medieval period cemetery in York, England. The study samples consisted of humeri from adult female and male laypeople and a male monastic group. Results showed significant female-male differences in bilateral asymmetry between the laypeople, but no statistical difference between the male samples, or between the female layperson and male monastic samples. In addition, the lay-male humeri had greater torsional strength than monastic male humeri. Mays concluded that males (but not females) typically participated in activities requiring differential use of the upper limbs, and that laymen were more involved in manual labor than monastic males.

Ledger et al. (2000) evaluated the cross-sectional properties of tibiae and humeri

from an 18th century Cobern Street burial site in Cape Town, South Africa for the purpose of “more accurately quantify[ing] the physical demands (type and level of activity) of this group” (p. 208). This sample, of “slaves or ‘free black’ people of low socioeconomic standing” (ibid: 207), was compared to two other samples, 1) a modern cadaver collection representing the likely descendants of the burial population, and 2) a South African hunter-gatherer population dating to 2000-4000 years BP.

Statistical comparisons of sample means showed no significant differences between the Cobern Street and modern samples for tibiae of either sex. Almost all of the significant differences were between the hunter-gatherer sample and one or both of the other two groups. Male hunter-gatherer tibiae had significantly greater cortical area than both the Cobern Street and modern samples, and significantly greater torsional strength than the Cobern Street sample. Female hunter-gatherer tibiae had significantly lower I_y than both the Cobern Street and modern samples. For the humerus, again no significant differences were found between the Cobern Street and modern samples for any biomechanical property (CA, I_x , I_y). Male hunter-gatherer humeri had lower I_y than both the Cobern Street and modern samples, and lower torsional strength than the Cobern Street sample. For female humeri, both I_x and I_y were lower in the hunter-gatherer sample than in the other two. Humeral bilateral asymmetry was greatest in the hunter-gatherer sample for both sexes, but similar between the Cobern Street and modern samples.

In spite of the lack of statistically significant differences between the Cobern Street and modern samples, the authors concluded, “The Cobern Street people appear to have been manual laborers living a more physically demanding lifestyle than their descendants have in the modern group” (ibid: 215). The differences between the hunter-gatherer and

the other two samples was attributed to “their high mobility... [that required] a greater strength of their lower limbs than of their upper limbs” (ibid: 214).

Stock and Pfeiffer (2001) utilized a slightly different approach in their study of variation in cross-sectional geometry. They looked for evidence of systemic versus localized mechanical loading influences by studying skeletal adaptation in the upper limb (humerus, clavicle) versus the lower limb (femora, tibiae, 1st metatarsals) from two different foraging populations with “well-documented evidence” (ibid: 338) for different patterns and modes of mobility. The skeletal samples were derived from two groups: 1) a Later Stone Age (11,000 to 2000 years BP) group from coastal South Africa, and 2) a group of protohistoric (ca. 19th century) Andaman Islanders. According to the authors, Later Stone Age group subsistence “is characterized by the hunting of small game, terrestrial foraging, and the intensive exploitation of coastal marine resources... [requiring]...negotiation of rugged terrain” (ibid: 339-340). The Andaman Islanders subsistence was also both terrestrial and marine based, but with frequent use of canoe for exploiting both marine and terrestrial resources. Swimming was also a common activity in this group, beginning at an early age. The authors characterized these two groups as having high terrestrial mobility and high marine mobility, respectively. Based on this classification of habitual activity, the authors predicted greater lower limb strength for the Later Stone Age group, and greater upper limb strength for the Andaman Islanders. This hypothesis was generally confirmed by the statistical analysis of sample means for most cross-sectional properties analyzed.

A critique of bioarchaeological studies of behavior

In addition to the original research summarized above, proponents of the

biomechanical approach in bioarchaeology have published a number of review articles (Larsen 1995, 1997, 2000, 2002; Bridges 1995; Ruff 2000b) promoting cross-sectional geometry as a viable approach to inferring behavior from skeletal remains. In stark contrast, Jurmain (1999) has published a critique of the research calling into question the conclusions of biomechanical analyses. In his book, Jurmain dubbed the tendency for anthropologists to focus on behavioral explanations for observed patterns of variation in cross-sectional geometry “activity-only myopia” (ibid: 262), and pointed out that interpretations based exclusively on mechanical hypotheses ignore alternative explanations, and the inherent biological complexity of skeletal adaptation. Furthermore, he argued for continued research on the effects of known levels and types of physical activity on bone geometry.

Jurmain also strongly criticized these studies for constructing “just-so” stories (ibid: 254) based on ethnographic and archaeological data, and stated that, “such data, by no means, provide an adequate test for any functional hypothesis” (ibid: 249). He added, “What is immediately obvious here is that activity is assumed to explain all the variation present, regardless of the complexities of the patterns expressed. Moreover, what is being assumed is exactly what such analyses should be trying to demonstrate” (ibid: 253).

Are biomechanical data used to reconstruct behavior, or are presuppositions about behavior used to interpret the biomechanical data? Many of the studies reviewed in this chapter claimed that the purpose of the study was to determine whether physical activity patterns changed with the transition from hunting and gathering to agriculture, or following European contact. To what extent has this purpose been fulfilled? In actuality, just as Jurmain has pointed out, the discussion section of most publications involves using archaeological, ethnohistoric, and ethnographic information to *explain* the

biomechanical data, not the other way round. In other words, the behavioral reconstruction of a population is considered the “known” variable. It is “known” that agriculturalists are more sedentary than hunter-gatherers; therefore, decreases in femoral strength or changes in femoral shape in agricultural groups are the result of decreased mobility. It is “known” that female agriculturalists spend hours each day pounding corn; therefore, a decrease in humeral bilateral asymmetry in Mississippian females can be explained by this activity. When humeral strength was found to have decreased in Mississippian females when it was expected to have increased (Bridges et al. 2000), again, the explanation was sought in archaeological and ethnohistoric data. When the biomechanical data revealed opposite findings in Alabama and Georgia, regional *variation* in the transition from hunting and gathering to agriculture was the *assumed* explanation. Where the archaeological record is not specific enough to generate plausible explanations for the biomechanical data, the results are considered non-interpretable or simply attributable to general increases or decreases in activity level (e.g., Larsen et al. 1995; Ruff and Larsen 1990).

The problem with basing conclusions on the fact that the biomechanical data are “consistent” with the archaeological record is that the archaeological record is incomplete, and interpretations of it may be flawed. It is simply not known, and cannot be estimated in any reliable sense, how labor-intensive one prehistoric lifestyle was relative to another. This was the promise of biomechanical analyses, yet in order for biomechanical data to be an independent source of information about such things, the archaeological record cannot be used to explain the biomechanical findings. Could bioarchaeologists be correct in their “behavioral reconstructions”? The answer is yes, of course, they could; however, their conclusions rarely deviate from what is already

“known” or inferred from other, more traditional sources of information.

Jurmain refers to this practice of confirming hypotheses regarding physical activity from equally unsubstantiated sources of evidence as “circular reasoning.” He is particularly critical of the “mobility index” (I_x/I_y):

What is perhaps most disturbing is that this very tentative interpretation of the etiology of altered femoral shaft shape, i.e., A/P expansion due *specifically* to long-distance travel, has been repeated numerous times elsewhere.... Given enough repetitions, the hypothesis now appears to be accepted (uncritically) as established. But, to my knowledge, there is not one single clinical study which has demonstrated a relationship between activity levels and consistent changes in the shape of the femoral diaphysis. Given this lack of even a general functional correlation, the claims that such changes are the result of a *specific* activity are even more speculative. Of course, the hypothesis may eventually be confirmed, and would prove the suggestion to be a brilliant (and most useful) insight. Clearly, however, until substantiation is forthcoming, judicious restraint is called for (ibid: 249-250).

Summary

As the literature review in this chapter illustrates, behavioral reconstructions of past populations based on biomechanical analyses of long bone structure are numerous. Although, the biomechanical approach in bioarchaeology has evolved since its inception, it is still essentially grounded in the initial biomechanical model produced in the early 1980s. These early anthropological studies showed that locational variation of cross-sectional geometric properties within the lower limb bones corresponds to theoretically predicted levels of mechanical stress generated by activities such as walking and running. Subsequently, it was hypothesized that group variation in cross-sectional geometric properties could be explained primarily by differences in mechanical loading patterns

generated by physical activity, as long as sex, age-at-death, side of the body, body size, and body shape factors are taken into consideration.

When attempting to look for general patterns of variation in cross-sectional properties, it is worth noting that the results of many of the studies, even those conducted by the same researchers, are not necessarily comparable. Over the past twenty years there have been some methodological changes. For example, the method used to size-standardize the raw cross-sectional data has undergone revision. There are also methodological differences between studies in terms of the section locations analyzed, the specific geometric properties measured, and the statistical procedures employed (e.g., compare Ruff and Larsen 1990 with Bridges 1989). Moreover, the specific results of the studies differ (i.e., whether biomechanical variables, sexual dimorphism or bilateral asymmetry increased or decreased over time).

In spite of the obvious differences in methodology and results, as well as a notable lack of statistically significant findings in many studies, most authors' contend that their initial research hypotheses, usually based on a combination of archaeological, ethnographic, and ethnohistoric evidence, were supported by the biomechanical data. While occasionally circumspect and tentative in their conclusions about the *specific* activities that produced the observed variation in cross-sectional properties, most of the authors in this literature review have not seriously questioned the ability of the biomechanical model to test behavioral hypotheses.

CHAPTER 4—METHOD OF ANALYSIS

'There is a deductive logic, and an inductive logic--and there is seductive 'logic'

Arnold Kiamiat (1936)

Application of critical reasoning

As reviewed in chapter 3, several biological anthropologists, most notably Ruff and colleagues, have generated a biomechanical model in which long bone cross-sectional geometric variation among archaeological populations is attributed to differences in behavior (i.e., patterns of physical activity). Fundamentally, the purpose of this dissertation is to answer the question: Is this model supported by scientific evidence? Bioarchaeologists who employ a biomechanical approach have presented their rationale in the publications reviewed in chapter 3. This dissertation applies concepts and analytical techniques from the discipline of informal logic⁷ to reconstruct and critically evaluate their line of reasoning using the model of an inductive argument.

Inductive arguments

In logic, an argument is modeled as a series of statements called propositions; one is the conclusion, the rest are premises intended to support the conclusion. Arguments are categorized as either deductive or inductive (Cederblom and Paulsen 2001; Copi and Cohen 1990). In a deductive argument, the truth of the premises guarantees the truth of the conclusion. The following is a classic example of a deductive argument (Copi and

⁷ Informal logic uses logical principles to analyze natural-language arguments from everyday contexts (Cederblom and Paulsen 2000); whereas, formal logic employs symbolic language to analyze the formal structure of arguments.

Cohen 1990):

(1) All humans are mortal.

(2) Socrates is human.

Therefore, Socrates is mortal.

In this argument, the conclusion is logically inevitable if the premises are true. Validity is a concept that refers to the “truth-preserving” form of deductive arguments (Warburton 2000). If an argument is valid, no additional information can change the conclusion of the argument (Copi and Cohen 1990). A flaw in the structure or form of the argument results in a formal fallacy, i.e., an invalid argument. The following is an example of a formal fallacy:

(1) All humans are mortal.

(2) Socrates is mortal.

Therefore, Socrates is human.

Although similar to the previous valid form of the argument, the form of this argument does not guarantee the truth of the conclusion. Both premises are true, but Socrates could be a dog. There are several types of formal fallacies. Distinguishing between valid deductive arguments and formal fallacies is the subject of formal logic. A valid deductive argument with true premises, and therefore a true conclusion, is a sound argument (Warburton 2000).

In inductive arguments, true premises do not guarantee a true conclusion (Cederblom and Paulsen 2001; Copi and Cohen 1990); all the premises of an inductive argument can be true and yet the conclusion false. This is because the relationship between the premises and the conclusion is probabilistic rather than deterministic. The probability that the conclusion of an inductive argument follows from its premises is “a

matter of degree and dependent upon what else may be the case” (Copi and Cohen 1990: 49).

Inductive arguments are never valid. In logic, the concept of validity, as a criterion for determining whether an argument is “successful,” only applies to arguments intended to be deductive. In contrast, inductive arguments are evaluated based on the degree of support they provide for the conclusion (Copi and Cohen 1990). A successful or “strong” inductive argument is one in which the conclusion is highly probable. The potential weaknesses of inductive arguments are 1) false or poorly supported premises, and 2) a conclusion that does not follow from the premises even if the premises are true.

Although truth-preserving, the deductive process adds no new information; it is said to be “non-ampliative” because the conclusion is essentially contained in the premises (Bird 1998; Pennock 2000). Logical and mathematical proofs are deductive. In contrast, the empirical sciences (e.g., chemistry, physics, biology, geology) are fundamentally based on an inductive process (Bird 1998). Only induction allows predictions (i.e., conclusions) regarding unknown situations or future events to be made based on observations of past events. Induction has been criticized as flawed in the sense that its conclusions are always tentative. Although it would be a strong inductive argument to suggest that because the sun has always risen in the past it will rise tomorrow, there is no guarantee that it will.

Induction is often defined as the process of deriving general principles from specific observations. However, this is not always the case. Induction, in the broadest sense of the word, simply means non-deductive (Bird 1998). There are several forms of inductive argument (Cederblom and Paulsen 2001). Three of these are addressed below: 1) sampling arguments, 2) arguments with statistical premises, and 3) arguments from

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Sampling arguments lead to an inductive or empirical generalization; they argue from particular instances to a general conclusion, and thus fit the standard definition of induction. The following is an example of a sampling argument:

- (1) Observation A showed an increase in bone mass following physical activity.
- (2) Observation B showed an increase in bone mass following physical activity.
- (3) Observation C showed an increase in bone mass following physical activity.

Probable conclusion: Bone mass increases following physical activity.

Causal arguments are a special form of sampling arguments. If observations A, B, and C are the results of controlled experiments designed to establish a cause-effect relationship between physical activity and bone mass, the premises might be statements to the effect that bone mass directly correlates with physical activity, and the conclusion of the argument could be a theoretical statement: **Physical activity causes increases in bone mass.**

In contrast to sampling arguments, some inductive arguments have a statistical generalization as a premise. Arguments of this type move from a general premise to a particular conclusion. The following is an example of this type of argument:

- (1) Most people who participate in vigorous physical activities have greater bone mass than people who do not.
- (2) Bob participates in vigorous physical activities.
- (3) Tom does not participate in vigorous physical activities.

Probable conclusion: Bob has greater bone mass than Tom.

In this argument, premise 1 is a generalization, presumably the conclusion of a sampling argument. If all the premises are true, then the statistical probability represented by the

word “most” in premise 1, to a large degree, determines the strength of the above argument; that is, if most equals 99%, then the conclusion is much more likely to be true than if most equals 60%.

Arguments from analogy are based on a comparison between two things that are allegedly similar. These arguments rely on the principle that if two things share some characteristics they are likely to share others. The following represents an argument from analogy:

- (1) Populations A and B are both Native American.
- (2) Populations A and B both represent stratified societies.
- (3) Populations A and B are both agricultural.
- (4) The females of population A are more involved in agricultural activities than the males.

Probable conclusion: The females of population B are more involved in agricultural activities than the males.

Analytical procedure

The critical analysis presented in this dissertation involved three basic steps (based on Cederblom and Paulsen 2000): 1) Reconstruction of the argument, 2) Evaluation of the argument, and 3) Determination of whether to accept or reject the conclusion of the argument.

The argument presented in chapter 5 was reconstructed by identifying the premises and the conclusion embedded in the prose of the research articles and dissertations reviewed in chapter 3. The premises of an argument are sometimes indicated by key words and phrases, including: since, because, as, follows from, as

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shown/indicated by, the reason is, may be inferred/derived/deduced from (Copi and Cohen 1990). Likewise, conclusion statements often have indicator words or phrases: in conclusion, therefore, so, hence, thus, accordingly, as a result, suggests, implies, for this reason.

The conclusions were relatively easy to identify because they were found explicitly stated at the end of the discussion or in a separate conclusion section. The premises were more difficult to identify. This is partly because much of the text of a scientific article is exposition intended to provide the reader with background information necessary to understand the subject matter, and does not actually contribute to the argument. In order to reconstruct the argument as fairly as possible, it was assumed that if a statement was necessary to complete the line of reasoning or strengthen the argument being made, it was included as a premise. Not every premise was articulated in each research article; however, the majority of the premises were derived from the earlier works of Ruff and colleagues (Ruff 1987; Ruff and Hayes 1983a; Ruff and Larsen 1990; Ruff et al. 1993, 1994; Trinkaus et al. 1994). Once identified, the premises and conclusion were summarized and paraphrased, making sure to preserve the author's original intent. This was done so that the reconstructed argument would be easier to follow. The argument was then evaluated to determine whether the conclusion should be accepted or rejected. This step involved reviewing the non-anthropological theoretical, experimental, and clinical literature on skeletal biology and mechanobiology to determine how well the premises were supported, and whether the conclusion followed from the premises based on all available relevant evidence.

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Techniques for criticizing inductive arguments

Sampling arguments and arguments with statistical premises can both be criticized by: 1) Casting doubt on the premises, and 2) Demonstrating that the argument does not use all available relevant evidence (Cederblom and Paulsen 2000; Copi and Cohen 1990). Obviously if the premises of an argument are false, the conclusion of the argument has not been supported. It is important to note that this does not prove that the conclusion is false, only that it does not follow from the premises. Sampling arguments can be criticized by pointing out problems with the data or the research design, which could cast doubt on the premises. For example, the sample size could be small or the group non-representative. Alternatively, the study outcome may have been affected by confounding variables⁸. Causal arguments can also suffer from post hoc errors, i.e., confusion of correlation with causation.

Unlike the case of a valid deductive argument, the addition of relevant new information to an inductive argument can lead to a different conclusion. For example, additional information can show that the supposed regularity of an inductive generalization does not actually exist, i.e., introducing counterevidence can potentially refute the generalization. This is demonstrated by adding premises 4 and 5 to the previous example of a sampling argument:

- (1) Observation A showed an increase in bone mass following physical activity.
- (2) Observation B showed an increase in bone mass following physical activity.
- (3) Observation C showed an increase in bone mass following physical activity.
- (4) Observation D showed no change in bone mass following physical activity.

⁸ A confounding variable is defined as “any uncontrolled variable that might affect the outcome of a study” (Graziano and Raulin 1989: 384).

(5) Observation E showed a reduction in bone mass following physical activity.

Probable conclusion: 60% of the time bone mass increases following physical activity.

It is clear that the previous inductive generalization is not as strongly supported when the information contained in the new premises is brought to bear on the argument.

Likewise, the introduction of more specific information into an argument with statistical premises can lead to a different conclusion. This is demonstrated using the previous example of an argument with statistical premises:

- (1) Most people who participate in vigorous physical activities have greater bone mass than people who do not.
- (2) Bob participates in vigorous physical activities.
- (3) Tom does not participate in vigorous physical activities.
- (4) Bob carries a gene that reduces the sensitivity of his osteocytes to mechanical strain.

Probable conclusion: Bob and Tom will have similar bone mass.

Arguments from analogy can be criticized by showing that the analogy itself is flawed. For example, relevant *dissimilarities* between the two things being compared make it less likely that they share the additional characteristic inferred in the conclusion. Furthermore, the conclusion is made less likely by showing that the alleged similarities do not exist, or that there is no real connection between the shared characteristics and the additional characteristic in question. In the previous example of an argument from analogy, the strength of the argument is partly dependent on whether the two populations in question actually share the characteristics proposed in premises 1 through 3. In other words, the conclusion that the females of population B are more involved in agricultural

activities than the males is much less likely if there is little evidence to show that population B is agricultural. Likewise, the conclusion is weakened if it can be shown that there is no consistent relationship between sexual division of labor and the shared characteristics. An example of a Native American, stratified, or agricultural population in which the males were more involved in agricultural activities would cast doubt on the conclusion.

Begging the question

Jurmain (1999) has accused bioarchaeologists of circular reasoning. In logic, circular reasoning, also known as “begging the question,” is considered an informal fallacy⁹ that occurs when the premises presuppose the conclusion (Walton 1989), as when a premise is either a restatement of the conclusion or a proposition that will be equally doubtful for reasons similar to those which make the conclusion doubtful. Begging the question is considered particularly “uninformative” (Warburton 2000) because the premises do not provide a reason to accept the conclusion. Most examples of begging the question represent arguments with unsupported premises (Copi and Cohen 1990).

⁹ An informal fallacy is any type of faulty reasoning other than a formal fallacy (an invalid argument resulting from a flawed formal structure).

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CHAPTER 5—RECONSTRUCTION AND EVALUATION OF THE ARGUMENT

If it was so, it might be; and if it were so, it would be; but as it isn't, it ain't. That's logic.

Lewis Carroll

Introduction

Since the early 1980s, numerous bioarchaeological studies have applied a biomechanical approach to the problem of “reconstructing” physical activity patterns (i.e., behavior) from archaeological skeletal remains. Ultimately, the written presentations of these research projects are more than a simple reporting of results; they are an attempt by the authors to persuade the reader that the conclusions they have drawn from their data are correct. In other words, they construct an argument. The purpose of this chapter is to reconstruct and critically analyze the argument.

Reconstruction of the argument

The argument for inferring physical activity patterns from biomechanical variables, e.g., cross-sectional geometry of long bone diaphyses, is embedded in the prose of the bioarchaeological literature reviewed in chapter 3. It is not within the scope of this dissertation to systematically reconstruct and evaluate the nuances of each author's specific argument. For example, it is not my intent to reconstruct Bridges' (1989) argument for her conclusion that, in northwestern Alabama, the transition from hunting and gathering to agriculture entailed an increase in the workload in females, or the argument presented by Ruff and Larsen (1990) for their conclusion that the exact opposite occurred following the adoption of agriculture on the Georgia coast. Rather, I

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present a reconstruction and critique of the overall argument for the ability to draw behavioral conclusions from long bone diaphyseal structure. This argument is summarized by the propositions listed in figure 5-1.

The propositions that comprise the argument represent paraphrased statements from the introductions, discussions, and conclusions of the journal articles, book chapters, and dissertations reviewed in chapter 3. Not all of the propositions are explicitly articulated in each manuscript; however, they are all necessary to present the complete line of reasoning. They are listed here more-or-less in order of increasing specificity, from the general theoretical statement in the first premise to the specific interpretation represented by the conclusion. The overall argument is best described as an inductive argument with statistical premises.

Critical analysis of the argument

The overall argument (Figure 5-1) is analyzed as two separate arguments connected by a linking proposition. The first argument, represented by premises 1 through 5, provides the explanatory framework for inferring behavior from bone structure. This will be referred to as the ‘theoretical argument’ (Figure 5-2). Its purpose is to link long bone cross-sectional geometry with physical activity. That is, it promotes mechanical loading patterns resulting from different physical activities as a principal cause of long bone structural variation. Premise 5 is the conclusion of this theoretical argument; it is inferred from the first four premises. This conclusion then functions as the main premise in the second argument, represented by premises 5 and 6. This argument is used by bioarchaeologists when drawing specific conclusions about behavior from comparisons of cross-sectional properties between two or more samples. It is referred to

as the ‘empirical argument’ (Figure 5-3) because the conclusion is based on empirical evidence generated by a specific bioarchaeological study.

Figure 5-1. Reconstruction of the overall argument.

Premise 1	Bones are capable of adapting to alterations in the mechanical loads to which they are subjected by adding bone tissue where it is needed, and removing it from where it is not needed, i.e., changing the amount and distribution of bone tissue to suit functional demands (Wolff’s Law).
Premise 2	Physical activity places mechanical loads on the bones of the skeleton.
Premise 3	Bones adapt to physical activity through changes in the amount and distribution of bone tissue.
Premise 3a	Bone material properties are not altered by physical activity.
Premise 4	The cross-sectional geometric properties of a long bone diaphysis measure the amount and distribution of bone tissue.
Premise 5	Variation in cross-sectional geometric properties reflects differences in patterns of physical activity.
Premise 5a	Larger values for cross-sectional properties (i.e., cortical area and second moments or area) indicate higher levels of physical activity, while smaller values indicate lower levels of physical activity.
Premise 5b	Group differences in the amount of bone (i.e., measured by cortical area) are less informative for interpreting behavior than group differences in the distribution of bone tissue (i.e., measured by second moments of area).
Premise 5c	Group differences in second moments of area reflect group differences in the <i>level</i> of physical activity.
Premise 5d	Group differences in cross-sectional shape, represented by ratios of second moments of area, suggest group differences in <i>types</i> of physical activities.
Premise 5e	Non-mechanical factors do <i>not</i> produce localized skeletal effects, i.e., localized changes in the distribution of bone.
Premise 6	A difference in cross-sectional properties exists between groups.
Conclusion	It is probable that the type/level of physical activity differs between groups.

In the reconstruction of the argument, premise 5 subsumes a series of additional

premises, identified as 5a through 5c. These premises merit special consideration. First, they are essential to drawing specific conclusions about physical activity from observed patterns of cross-sectional geometric variation. Premises 5a through 5d attribute specific meaning to patterns of cross-sectional geometric variation. Premise 5c, on the other hand, is posited as a means of ruling out the potential confounding effects on skeletal structure of non-mechanical variables, such as group differences in nutrition and genetics (Ruff et al. 1984). It asserts that observed variation in cross-sectional geometry, specifically localized variation in bone tissue distribution and “cross-sectional shape,” is mechanical in nature, and not the result of other factors. Second, these five premises (5a – 5c) were originally conclusions inferred from ‘empirical arguments’ based on early studies of cross-sectional geometric variation among a variety of prehistoric, early historic and modern groups (Ruff 1987; Ruff and Hayes 1983a; Ruff et al. 1984). One problem with these propositions is that they represent inductive generalizations of arguments that used fallacious reasoning; they begged the question. A brief discussion and example of their derivation is presented in the last section of this chapter; however, a thorough critique of these premises is beyond the scope of this dissertation because it involves the reconstruction and evaluation of five specific arguments. Instead, the purpose of this dissertation is to critically analyze the overall argument for inferring behavior from variation in long bone diaphyseal structure. Obviously, the primary critique of the theoretical argument has profound implications regarding the acceptance of premises 5a through 5c and their subsequent application to behavioral reconstruction in bioarchaeological research.

Analysis of the ‘theoretical argument’

The theoretical argument represents a plausible line of reasoning, and the conclusion would be as plausible as the least plausible premise (Walton 1989), *if* no other relevant information was brought to bear. However, the latter point is the crux of this critique. The strength of an inductive argument with statistical premises is primarily based on the truth (amount of support for) the premises, and whether the argument makes use of *all available relevant information*, including information relating to other possible alternative explanations, such as the effects of confounding variables. Acceptance of the conclusion of the theoretical argument hinges on two primary issues: 1) The evidentiary value and relevance of the first premise, which is the primary theoretical proposition, and 2) Whether there are viable alternative explanations for variation in cross-sectional geometry, i.e., are there confounding variables?

Figure 5-2. Reconstruction of the ‘theoretical argument’.

Premise 1	Bones are capable of adapting to alterations in the mechanical loads to which they are subjected by adding bone tissue where it is needed, and removing it from where it is not needed, i.e., optimizing the amount and distribution of bone tissue to suit functional demands (Wolff’s Law).
Premise 2	Physical activity places mechanical loads on the bones of the skeleton.
Premise 3	Bones adapt to physical activity through changes in the amount and distribution of bone tissue.
Premise 3a	Bone material properties are not altered by physical activity.
Premise 4	The cross-sectional geometric properties of a long bone diaphysis measure the amount and distribution of bone tissue.
Conclusion (Premise 5)	Variation in cross-sectional geometric properties reflects differences in patterns of physical activity.

Figure 5-3. Reconstruction of the ‘empirical argument’.

Premise 5	Variation in cross-sectional geometric properties reflects differences in patterns of physical activity.
Premise 5a	Larger values for cross-sectional properties (i.e., cortical area and second moments or area) indicate higher levels of physical activity, while smaller values indicate lower levels of physical activity.
Premise 5b	Group differences in the amount of bone (i.e., measured by cortical area) are less informative for interpreting behavior than group differences in the distribution of bone tissue (i.e., measured by second moments of area).
Premise 5c	Group differences in second moments of area reflect group differences in the <i>level</i> of physical activity.
Premise 5d	Group differences in cross-sectional shape, represented by ratios of second moments of area, suggest group differences in <i>types</i> of physical activities.
Premise 5e	Non-mechanical factors do <i>not</i> produce localized skeletal effects, i.e., localized changes in the distribution of bone.
Premise 6	A difference in cross-sectional properties exists between groups.
Conclusion	It is probable that the type/level of physical activity differs between groups.

The theoretical proposition

The proposition that bone adapts to its mechanical environment is considered a fundamental principle of skeletal biology, typically referred to as Wolff’s Law. In a sense, Wolff’s Law is an explanation for the structure of bone, asserting the biological axiom that form follows function; consequently, changes in function produce changes in form. Alterations in mechanical loading generate new patterns of forces that necessitate modifications in the quantity and distribution of bone.

There are two primary problems with the application of Wolff’s Law in bioarchaeology. The first is that Wolff’s Law is fundamentally flawed in its derivation, and the second is that it is not, in fact, a “law.” In other words, the implied certainty or regularity of a scientific law does not exist. Wolff’s Law is based on a flawed argument

from analogy. Its originator Julius Wolff compared two things that appeared similar, namely an engineered crane and the proximal end of a human femur, and concluded that because they shared some similarities, the femur must, like the crane, follow mathematical laws of construction. Chapter 6 demonstrates that the analogy is not supported. However, it is argued that current usage of the phrase “Wolff’s Law” is simply a synonym for the concept of functional adaptation (Cowin 2001b).

The concept of functional adaptation, as opposed to Wolff’s Law *per se*, is an inductive generalization based on a sampling argument. When evidence from a variety of studies is examined, the implied regularity of the generalization does not appear to exist. There are a number of counterexamples in which bone either does not seem to adapt to increased physical activity, or does so in a manner that is contrary to expectations (see chapter 6).

The theoretical argument, which relies on “Wolff’s Law” or functional adaptation as its primary theoretical foundation, fails to make use of all available relevant evidence. Bioarchaeologists have not kept pace with developments in the field of skeletal mechanobiology over the past two decades (as evidenced by a lack of citations). While there is abundant empirical evidence that many biological tissues, including bone, are capable of adapting to their functional milieu, there are still many critical details about the process that remain unknown. This precludes the ability to associate cross-sectional geometry with physical activity at this time.

According to most of the researchers whose studies were reviewed in chapter 3, Wolff’s Law provides the theoretical basis for reconstructing behavior from biomechanical analyses, by directly linking physical activity to long bone cross-sectional geometry (Barondess 1998; Bridges 1989; Larsen 1997, 2000, 2002; Larsen and Ruff

1991; Larsen et al. 1995; Ruff and Hayes 1983a; Ruff and Larsen 1990; Stock and Pfeiffer 2001; Wescott 2001). Bridges (1989: 387), citing Wolff (1892), stated, “Reconstructing changes in prehistoric activities from long bone diaphyseal dimensions and cross-sectional structure is possible because the cross-sectional structure of a bone is related to the forces acting upon it during life.” This interpretation is reiterated by Larsen (1997: 195), “Julius Wolff, a leading nineteenth century German anatomist and orthopedic surgeon, recognized the great sensitivity of bones to mechanical stimuli, especially with regard to their ability to adjust size and shape in response to external forces.” One of the strongest statements in support of the importance of Wolff’s Law was made by Barondess (1998: 8) in his Ph.D. dissertation, “Wolff’s Law provides the theoretical underpinning for understanding how it is that a skeleton’s final form provides a window through which the external stimuli (i.e., mechanical forces) to which an individual’s skeleton is subjected throughout life can be examined and interpreted.” However, it was the groundbreaking publication by Ruff and Hayes (1983a: 371) that provided the most thoroughly articulated explanation of the pivotal role played by Wolff’s Law, “It is commonly stated that living bone alters its structure in accordance with specific mechanical loadings, a concept first popularized by Julius Wolff...and frequently referred to as ‘Wolff’s Law.’ This implies not only that mechanical stresses and strains developed under loading will influence bone morphology, but also that preserved bone morphology may be used to reconstruct past in-vivo bone loadings.” This interpretation of Wolff’s Law laid the foundation for future studies of the biomechanical adaptation in archaeological populations.

During the same period of time in which biomechanical analyses were gaining acceptance in bioarchaeology, non-anthropological skeletal biologists and biomechanists

published critiques of Wolff's Law (e.g., Bertram and Swartz 1991; Dibbets 1992; Lee and Taylor 1999; Roesler 1981, 1987; Currey 1997; Cowin 2001b), and have continually reanalyzed its validity in the study of skeletal mechanobiology (e.g., Cowin 1981a; Cowin 2001a; Frost 1987, 1990a, 1990b, 1995, 1996, 1997a, 1997b, 2000, 2001; Huiskes 1995, 2000; Huiskes et al. 1987; Odgaard and Weinans 1995; Prendergast and Huiskes 1995; Turner 1992, 1999). Yet, the applicability of Wolff's Law to the anthropological problem of behavioral reconstruction from archaeological skeletal remains has never been questioned, or thoroughly analyzed by the anthropological community; Wolff's Law has simply been repeatedly paraphrased. As Roesler (1987: 1027) put it, Wolff's Law is "often quoted, hardly read."

The majority of the bioarchaeological studies reviewed in chapter 3 cite a small number of experimental studies of Wolff's Law, which were conducted in the late 1970s to mid-1980s. While these experiments (e.g., Goodship et al. 1979; Woo et al. 1981) were relatively current for the earliest behavior studies (e.g., Bridges 1989; Brock and Ruff 1988; Ruff and Hayes 1983a, 1983b), most recent bioarchaeological publications (i.e., those published within the past decade; Bridges et al. 2000; Larsen et al. 1995, 1996; Ledger 2000; Mays 1999; Ruff and Larsen 2001) do not cite any contemporaneous experimental literature dealing with Wolff's Law or skeletal mechanobiology. Either they do not include non-anthropological references at all, or they cite the same few studies as before. Thus, with respect to understanding and applying principles of skeletal mechanobiology, there seems to be an ever-widening gulf between skeletal biologists and biomechanists on one side and bioarchaeologists on the other. The reason for this seems best summarized by Larsen (2000: 52, emphasis added) in a non-technical book written for a general audience, "The premise of bone changes in response to mechanical forces is

an outgrowth of work done in the late 1800s by the eminent German anatomist and orthopedic surgeon, Julius Wolff. He observed that during life—from infancy through adulthood—bone tissue is added in areas of the skeleton where it is needed, and is taken away where it is not needed. *Such an overwhelming amount of experimental and other research has accumulated in support of Wolff's conclusions that the phenomenon is identified simply as Wolff's Law.*" The view is that Wolff's Law is axiomatic.

Confounding variables

The existence of potential confounding variables impacts the conclusion of the theoretical argument in two ways. 1) Mechanical factors other than physical activity could produce observed variation in cross-sectional geometric properties. 2) Diachronic changes (or group differences) in the amount and distribution of bone leading to variation in cross-sectional geometric properties could occur in the absence of changes in physical activity or other mechanical loading factors.

Premise 2 is the proposition that physical activity places mechanical loads on the bones of the skeleton. This fact was hypothesized long before it was empirically demonstrated using strain gauges applied to living bone (Martin et al. 1998). Since then this premise has been confirmed by numerous experimental data, and is not disputed. However, there is a caveat; factors other than physical activity can exert mechanical forces on the skeleton. So, while it is probably true that all physical activity generates mechanical loads, the inverse of this statement, all mechanical loads are generated by physical activity, is false. In addition to physical activity, body size, shape, and mass, normal muscle tone (i.e., tonus), abnormal muscle tone (e.g., spasticity or paralysis), trauma, breathing, body posture, clothing and other accoutrements, and prosthetics can

all influence the mechanical environment of the skeleton, and potentially result in bony adaptation. Of these, it is reasonable to assume that only body size (height), shape (relative body proportions), and mass (weight) are likely to have a confounding effect on patterns of variation in long bone structure, particularly at the population level.

Ruff has acknowledged the potential mechanical effects of body size, shape, and mass, especially with regard to the bones of the lower limb (Ruff 1984, 2000a, 2000b; Ruff and Hayes 1983a; Ruff et al. 1993). Standardization methods to control for group differences in body size using long bone length have been in common use since the mid-1980s; however, as reviewed in chapter 3, these standardization methods have changed over time and vary among researchers casting some doubt on the accuracy and comparability of results. Ruff (2000b) has also suggested that it is hypothetically possible to “control” for body shape differences by limiting comparisons to groups with “similar” body shape. Determination of body shape is feasible if the skeletal remains are complete enough to allow the assessment of relevant body proportions. However, at present, there is no generally accepted method to reliably estimate body mass from skeletal remains¹⁰, because this anthropometric variable is inherently dependent upon both hard and soft tissues. Ruff (2000a, 2000b) has admitted that conclusions are suspect for any study in which group differences in body shape and mass are not considered. While in most circumstances it may be “safe” to assume that ratios of body mass to body size (e.g., body mass index or BMI) did not differ significantly among prehistoric populations, the issue becomes contentious when a hypothetical group difference in body mass is invoked as a potential explanation for unexpected or otherwise non-interpretable findings (e.g., Ruff

¹⁰ Ruff (2000b; see also Ruff et al. 1993) has proposed a method of estimating body mass, using estimates of body breadth and body length.

and Larsen 1990). Furthermore, in addition to potential mechanical effects, as a confounding factor in biomechanical analyses, body mass may have metabolic effects on cross-sectional geometry as well (Reid 2002).

Ruff et al. (1984) maintain that differences in the relative size of bones (i.e., robusticity or size-standardized cross-sectional properties) and distribution of bone tissue (i.e., shape changes) as opposed to increases or decreases in body size “[seem] to suggest localized (mechanical) rather than systemic (nutritional or other) effects” (p. 135). Furthermore, Ruff (1987: 409) has stated, “dietary...explanations...may be relevant to general size differences...[however] it is difficult to see how a systemic factor like diet could have...specific effects on localized bone remodeling.” This general assertion has appeared in several other publications (Bridges 1989, 1991; Larsen 1997; Larsen et al. 1995; Ruff and Larsen 1990). With regard to differences in long bone structure between hunter-gatherers and agriculturalists in northwestern Alabama, Bridges (1991: 99, emphasis added) wrote, “Although cortical area may be affected by a variety of other factors (including genetics, diet, and age), activity differences seem to be the most plausible explanation for the changes seen here. Nutritional differences, for example, would lead to systemic differences in cortical area... Given the patterning of changes seen here, it is unlikely that they result from a major change in diet, which *should affect all bones equally*.”

The idea that mechanical loading produces localized structural adaptation is simply derived from Wolff's Law, and follows from the idea that bone structure is optimized: minimal material for maximum strength. Bone adaptation to mechanical loads is need-based. When confronted with increased mechanical stresses or strains bone cells do not add bone tissue anywhere, they add new tissue where it is necessary to resist

the new forces, and they remove it from where it is no longer necessary, thus redistributing it. The implication that nutrition, genetics and other non-mechanical factors do *not* produce localized effects is an untested hypothesis, not a well-supported premise (designated as premise 5e, Figures 5-1 and 5-3). Empirical evidence for this hypothesis is of critical importance to bioarchaeologists because many of the group comparisons involve populations where dietary (i.e., nutritional) and genetic differences are highly likely (e.g., comparisons of hunter-gatherers and agriculturalists, or Pecos Pueblo and Georgia coast populations). Because Ruff et al. (1984) provide no citations for research supporting their hypothesis (premise 5e), the literature was reviewed for evidence that might *refute* their assertion. The results of this review are included in chapter 6. While not conclusive, studies suggest that genetics and nutrition *can* produce differential changes in cortical geometry either directly, or indirectly, through primary effects on the amount and distribution of lean and fat body mass, bone quality (i.e., material properties), or the processes involved in skeletal adaptation (e.g., mechanotransduction).

Individual (and group) variation in the *response* of bone to mechanical usage, and by extension, response to physical activity contributes potentially numerous confounding variables. Ruff and colleagues (Ruff and Hayes 1983b; Ruff et al. 1994) have discussed the influential role of sex and age in skeletal adaptation, and consequently on the interpretation of variation in skeletal structure. It is recognized that inherent sex-related differences (e.g., hormonal status) render direct comparison of cross-sectional properties between males and females impossible. Therefore, studies are limited to evaluating relative male-female differences in terms of degree of sexual dimorphism. In addition, due to the normal age-related bone loss, the structural properties of individuals of

different ages cannot be directly compared, and bioarchaeologists strive to control for age-at-death in their samples¹¹. Even so, group differences in mean age are sometimes overlooked or too readily dismissed as contributing factors in geometric variation (e.g., Larsen et al. 1996; Ruff and Larsen 1990).

Furthermore, Ruff and colleagues (Ruff et al. 1994) have pointed out that there are ontogenetic differences in the response of bone to mechanical usage; the same physical activity will produce a different response depending upon the point it is performed within the life cycle. It is well recognized that mechanical loads are most osteogenic prior to skeletal maturity, and especially during puberty (Duncan et al. 2001; Frost 1986, 1997a, 1997b; Forwood and Burr 1993; Haapasalo et al. 2000; Heinonen et al. 2000; Jee 2001; Kannus et al. 1995; Khan et al. 2000; Martin et al. 1998; Ogden 2000; Seeman 2002; Slemenda et al. 1991). Thereafter, physical activity tends to maintain bone mass rather than increase it (Forwood and Burr 1993; Frost 1997a). Research suggests that the cross-sectional properties of adult bones are strongly influenced by activities performed earlier in life, and differences in cross-sectional geometric properties among samples might be due to group differences in the *timing* of the activities relative to skeletal maturity, rather than group differences in the activities. This “timing” factor, as potential confounding variable, cannot be addressed by controlling for the mean age-at-death of the sample. It must be known in order to interpret the results. The assertion by bioarchaeologists that bone structure provides a record of activities performed over a lifetime may be true, but the inability to control for the “timing”

¹¹ Because of methodological difficulties in aging prehistoric skeletal remains (Jacks 2000; Larsen 2002), and the inherent population specificity of techniques such as functional dental wear (Russell et al. 1990), there is reason to question whether it is actually possible to control for age-at-death *among* different population samples.

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variable precludes the interpretation of this record with a reasonable degree of confidence.

In addition, research on skeletal mechanobiology has shown mechanotransduction to be a complicated phenomenon, influenced by a large number of regulatory factors (Cowin and Moss 2001), many of which are likely under genetic control (Akhter et al. 1998; Burr 1992; Drake et al. 2001; Ishijima et al. 2001; Kodama et al. 2000; Mikic et al. 1996; Pedersen et al. 1999; Robling and Turner 2002; Slemenda et al. 1996; van der Meulen and Huiskes 2002; Young and Xu 2001). It has been hypothesized that metabolic factors can change the threshold (e.g., MES set-point) necessary to initiate bone adaptation, thereby increasing or decreasing an individual's sensitivity to mechanical loading (Burr 1992; Hernandez 2000). If true, this implies that although mechanical loading may be the principal stimulus in bone structural adaptation, the *biological processes* involved in adaptation may be amplified or attenuated by other non-mechanical factors; metabolic differences between individuals could lead to differences in bone structure in the absence of absolute differences in mechanical loads. Metabolic factors may be under either genetic or environmental control.

In the context of bioarchaeology, regulation of skeletal adaptive processes by non-mechanical factors provides yet another alternative explanation for observed group variation in cross-sectional geometric properties. For example, the extreme level of humeral bilateral asymmetry seen in professional tennis players and certain Neanderthal specimens, is usually touted as virtually irrefutable evidence for the primary role of the mechanical environment in determining skeletal structure (Trinkaus et al. 1994). Because right-left side differences within an individual are said to provide the ultimate control for confounding variables such as age, sex, nutrition, and genetics, bilateral

asymmetry is usually attributed to differential use of the upper limbs (Bridges 1995; Fresia et al. 1990). However, differences in mechanosensitivity (e.g., through changes in the MES setpoints) could also hypothetically explain group differences in degree of humeral bilateral asymmetry. For example, a hypothetical allele responsible for increasing the sensitivity of bone to mechanical loading could exist at a high frequency in a population. For individuals with this allele, a relatively small difference in loading between the right and left upper limb, such as that which typically occurs in an individual who is right- or left-handed, could lead to significant bilateral asymmetry as compared to someone who was less sensitive to mechanical loads. At the population level, genetic differences in mechanosensitivity could lead to statistically significant differences between group means even if there were no differences in the type or level of activity performed. Thus, while the final structure of bone may not be directly controlled by genetics, as has been argued (Bridges 1995; Trinkaus et al. 1994), it is likely that the sensitivity of bone to mechanical usage and the processes that regulate bone adaptation on a localized level are genetically controlled, and potentially influenced by non-genetic metabolic factors (e.g., hormones, nutritional status, health, age, etc.) as well. Therefore, unknown metabolic and genetic differences among study samples further limit interpretation of variation in bone structure.

Analysis of the ‘empirical argument’

Acceptance of the conclusion of the empirical argument (Figure 5-3) rests on: 1) The degree of support for premise 5 (including 5a – 5e), and 2) The existence of group differences in cross-sectional geometric properties. Premise 5 states that variation in cross-sectional properties reflects differences in patterns of physical activity. Because this

is the conclusion of the theoretical argument, which has already been analyzed, it is not necessary to further discuss the degree of support for this proposition. However, the issue of the existence of group differences (premise 6) warrants discussion. While this would seem to be a simple procedural matter of measuring the cross-sectional geometric variables in question and statistically analyzing the data; it is actually somewhat problematic in terms of the empirical argument put forth to support the specific conclusions of bioarchaeological studies of long bone structural adaptation.

The premise that a difference in cross-sectional properties exists between the samples under investigation (premise 6) is, in fact, what the individual research projects were designed to demonstrate; it is empirical. The specific formulation of premise 6 (i.e., whether a difference exists and what the specific differences are) is derived solely from the skeletal data, and it varies from study to study. Therefore, the specific conclusion, based on premise 6, will also vary among studies.

Most of the bioarchaeological studies reviewed in chapter 3 had specific research hypotheses that were tested via the analysis of cross-sectional geometric data. The crux of hypothesis testing is determining whether the observed group difference in the variable of interest can be attributed to chance or to some potential causal factor. “Ruling out the null hypothesis is a necessary first step” (Graziano and Raulin 1989: 164) in establishing a causal link, in this case between physical activity and cross-sectional geometry. To avoid subjective bias when interpreting the meaning of group differences it is common practice for researchers to employ statistical methods. Selection of an appropriate statistical method is considered of paramount importance in any research design intended to establish a cause or correlation (Graziano and Raulin 1989). For the purposes of this dissertation, it is assumed that the researchers have selected an appropriate statistical

method (c.g., that the data do not violate the assumptions of the statistical test), and that the reported results are accurate.

The most common statistical methods employed in bioarchaeological studies are the Student's t-test and one-way analysis of variance (ANOVA). Some studies employing ANOVA follow with post hoc Tukey HSD tests for pair-wise group differences. These tests allow the researcher to determine the statistical significance of the differences between or among group means, which is reported as a significance level or P-value. It is generally accepted, and indeed stated in the studies reviewed that a P-value of less than 0.05 is considered statistically significant (when reported, P-values less than 0.10 are considered "near-significant").

While most studies report significance levels, a surprising number of researchers have drawn specific behavioral conclusions even in the near-total absence of statistically significant (or even near-significant) group differences in the cross-sectional properties ascertained by the study (e.g., Bridges et al. 2000; Brock and Ruff 1988; Fresia et al. 1990; Larsen and Ruff 1990; Larsen et al. 1996; Ledger 1999; Ruff and Larsen 2001; Ruff et al. 1984). Much of the alleged support for mechanically based explanations of long bone structural variation has come from these statistically non-significant group differences. I would argue that without statistically significant differences between sample means, the results of a comparative study do not provide support for any activity-related conclusion. In fact, in these instances the most appropriate tack would seem to be accepting the *null* hypothesis. Only Barondess (1998) approached his results in this manner, and ultimately had to accept the null hypothesis for a large proportion of his comparisons.

There is an apparent tendency to over-interpret data, and draw conclusions where there are none to be drawn. Statistically non-significant results are discussed as temporal

“trends” (e.g., Bridges et al. 2000: 222; Brock and Ruff 1988: 120) despite the fact that the inability to assign individuals to anything other than broad temporal categories precludes the type of correlation analysis that would allow direct evaluation of the hypothesis that bone structural properties changed over time. Furthermore, the discussion presented in many papers frequently fails to distinguish between significant and non-significant findings, which are ultimately given equal weight in arriving at the conclusions (e.g., Bridges et al. 2000; Brock and Ruff 1988; Fresia et al. 1990; Ruff and Larsen 1990). In other words, by simply reading the discussion and conclusion sections of an article, one would have no idea that most of the results were not statistically significant.

As an example of the insidious nature of this problem, when summarizing Brock and Ruff's (1988) publication on femoral structural changes in the prehistoric Southwest for a review article, Larsen (1997: 217) wrote, “The ratio of I_x/I_y in the femur midshaft shows a decline in both sexes, which also suggests a reduction in bending stresses—particularly in the anteroposterior plane...These observations are consistent with archaeological reconstructions of increasing sedentism with the shift to agriculture in the American Southwest.” The problem with this interpretation is that when the results of the original study are examined, it is clear that Brock and Ruff found no statistically significant (or even near-significant) differences among their temporal/cultural groups for I_x/I_y . In fact, the values for males over the three periods in question were virtually identical (1.28, 1.27, 1.24) (Brock and Ruff 1988: 119). It is difficult to understand how these group differences can be attributed to anything other than chance (i.e., the null hypothesis should be accepted).

This discussion is concluded with an example to illustrate the importance of relying on statistically significant differences to interpret the results of a scientific study.

This discussion contrasts the conclusions drawn by Ruff et al. (1984), based on their own statistical analysis, with two other possible interpretations of their data, consistent with the premises of the overall argument as summarized in this chapter. Ruff et al. calculated the following cross-sectional properties for groups representing hunter-gatherers and agriculturalists: cortical area (CA), medullary area (MA), total subperiosteal area (TA), I_{max} , I_{min} , J , I_x/I_y , and I_{max}/I_{min} for femoral midshaft and subtrochanteric section locations. After size-standardization the following statistically significant group differences were observed: Male agriculturalists showed decreased midshaft MA and I_x/I_y , and decreased subtrochanteric MA, TA, I_{max} , J , and I_{max}/I_{min} . Females showed only decreased TA at both femoral locations. The authors concluded, “In sum, our results indicate that adoption of corn agriculture on the Georgia coast was very likely associated *in both sexes* with a decrease in mechanical stress...” (ibid: 132, emphasis added). Apparently, these authors place a great deal of weight on changes in the subtrochanteric region of the male femur for interpretation of mechanical stress in both sexes. There are at least two possible alternative interpretations using the authors’ own reasoning (Ruff et al. 1984). 1) Statistically significant decreases in several male subtrochanteric cross-sectional properties suggest some highly localized mechanical variable exerting forces on the hip and proximal femur, but with minimal effect on the midshaft region. This unknown mechanical variable, possibly activity-related, did not affect females in the same way. 2) While few statistically significant changes in cross-sectional properties were observed, all were reduced in the agriculturalists. Moreover, although not statistically significant, most of the other properties measured also showed reductions, a few reaching near-significance. Additionally, bone length was decreased in agriculturalists. Therefore, the pattern that emerges is of a nearly across-the-board

decrease in overall size and strength of the femur. These results are consistent with a change in some systemic factor such as nutrition, which is plausible because dietary differences are likely to have existed between these two groups.

The problems with premises 5a through 5e

In the brief history of bioarchaeological studies of cross-sectional geometry, propositions 5a through 5e have first appeared as inductive generalizations, then as premises, of an empirical argument. In other words, each of these premises is derived from an empirical study that applied the conclusion of the theoretical argument (i.e., premise 5) to group comparisons of cross-sectional geometric variation, and each has subsequently been utilized as a premise for interpreting cross-sectional geometry. A critical analysis of proposition 5d is provided below.

Cross-sectional shape as an indicator of mobility

Ruff, Larsen and colleagues (Larsen 1997, 2002; Ruff and Hayes 1983a; Ruff and Larsen 1990; Ruff et al. 1984) have argued that the amount of cortical bone within the cross-section (i.e., CA), is not as informative for interpreting behavior as differences in the distribution of bone, measured by the second moments of area (i.e., I and J). The reasoning is twofold. First, “bone curvature and other factors” (Ruff et al. 1984: 126) eccentrically load the long bones resulting in bending and torsional stresses (hence increased bending and torsional rigidity, or I and J), rather than pure compressive or tensile stresses. While it is true that the majority of strain experienced by long bones is due to bending, it is not necessarily true that differences in CA are any more or less informative about physical activity levels. For example, the aforementioned study of

humeral bilateral asymmetry (Jones et al. 1977; Ruff et al. 1994) demonstrated significant differences in CA between the playing and non-playing arms of tennis players. Second, it is suggested that CA “is more likely to be due to some systemic influence, such as undernutrition” (Larsen 1997). Moreover, it is suggested that group differences in the *level* of physical activity are revealed by variation in second moments of area (SMAs), while differences in the *types* of activities (i.e., specific mechanical loadings) are reflected by the shape of the cross-section, represented by ratios of SMAs (I_x/I_y and I_{max}/I_{min}). The latter statement, relating cross-sectional shape to type of physical activity grew out of some of the earliest biomechanical investigations of archaeological samples (Ruff 1987; Ruff and Hayes 1983a; Ruff and Larsen 1990; Ruff et al. 1984), and has become, perhaps, the most pivotal in drawing specific behavioral conclusions from the data. For example, Ruff et al. (1984: 134) have used this premise to infer that, “Relative reduction in A-P bending loads in the midshaft femur could be brought about by relatively less running and climbing and more walking.” The I_x/I_y ratio has earned the moniker “the mobility index,” and it is considered an indicator of “long-distance travel” (Larsen 1997; Ruff and Larsen 1990). The following assertions have been made about the I_x/I_y ratio (Ruff 1987): 1) It is higher in more mobile groups, such as hunter-gatherers, 2) It is higher in males than females, presumably because males are typically more mobile than females, and 3) Sexual dimorphism of this index is greatest in hunter-gatherers where sex differences in mobility are supposedly greatest. References to this index appear in the discussion and conclusion of many studies and review articles when addressing cross-sectional geometry of the femur (Bridges 1991, 1995; Larsen 1997; Larsen et al. 1995; Ruff 1994; Ruff and Larsen 1990, 2001). However, there is evidence that the relationships between physical activity and cross-sectional geometry are not as specific as

proposed. Some studies of skeletal adaptation to mechanical usage suggest that bones are not necessarily more reinforced in the specific maximum plane of loading (e.g., Demes et al. 1998; Demes et al. 2001). Furthermore, as previously mentioned, it is likely that group differences in genetics and nutrition *can* produce localized changes in cross-sectional properties, including shape. Therefore, the “sub” premises of premise 5 are also confounded.

The hypothesis that group differences in cross-sectional shape reflect group differences in *types* of physical activities is based on the theoretical argument (Figure 5-2) that physical activities, such as running, impose specific forces on the human skeleton, to which the bones adapt according to Wolff’s Law. Figure 5-4 presents the propositions for an argument, derived from Ruff (1987), that group differences in sexual dimorphism of I_x/I_y reflect sex differences in the level of mobility engaged in by the group.

Figure 5-4. Argument for I_x/I_y as an indicator of sex differences in mobility.

Hypothesis (Ruff 1987)	Differences in sexual dimorphism of I_x/I_y among hunter-gatherers, agriculturalists, and modern industrial populations are due to differences in sexual division of labor (sex-specific activities) involving mobility.
Premise 1 (Premise 5)	Variation in I_x/I_y reflects differences in mobility.
Premise 2	Sex differences in mobility are greatest among hunter-gatherers.
Premise 3	Sex differences in mobility are less among agriculturalists.
Premise 4	Sex differences in mobility are least among industrial populations.
Premise 5	Sexual dimorphism of I_x/I_y is highest in hunter-gatherers, lowest in industrial groups, and intermediate in agriculturalists.
Premise 6	Male I_x/I_y decreased over time, while female I_x/I_y did not.
Conclusion (Hypothesis accepted)	It is highly likely that I_x/I_y is a reflection of the relative mobility of males and females in these populations.

As with any inductive argument, the confidence one has in its conclusion is largely

based on the degree of support for (e.g., the evidentiary value of) the premises, and whether the conclusion follows from the premises. Premise 1 is an assertion made by Ruff and Hayes (1983a) based on analysis of Pecos Pueblo femora. Reasons to question premise 1 are based on the analysis of the theoretical argument, and will be further elaborated in chapter 6. Premises 2 through 4 are assertions made by Ruff, about the relative mobility levels in three broad “subsistence” categories, hunter-gatherers, agriculturalists, and modern industrial populations. The assumptions represented by premises 1 through 4 *determine* the conclusion of the argument, but they are not themselves strongly supported. For example, if instead, one were to assume that there were no sex differences in degree of mobility among the three groups, then the conclusion of the argument makes no sense. Furthermore, as Jurmain (1999) has emphatically pointed out, what these premises assume are the very questions biomechanical studies are supposed to be answering. The premises are no better supported than the conclusion itself. Therefore, the argument begs the question. Anthropologists do not *know* what the relative mobility levels were in these three categories of populations, and there are no independently verifiable means of determining relative mobility levels in prehistoric populations, apart from presupposing the conclusion that group variation in I_x/I_y is an indicator of mobility.

As with any research, there are concerns regarding the generalization of results to other circumstances—other populations, other time-periods (i.e., the external validity of the study). Therefore, even if the assumptions about the degree of mobility in these specific groups (i.e., study samples) are in fact correct, and who is to say they are not, it is certainly not known to what extent they are representative of the broad categories in which they have been placed. From this standpoint alone, it is questionable to apply the

conclusion of this study to the interpretation of variation in I_x/I_y in any other population.

Lastly, premises 5 and 6 make claims as to observed differences in I_x/I_y among hunter-gatherers, agriculturalists, and industrialists. The previous discussion of statistical significance applies again in this argument. In fact, in this study, there was no significance level reported. It is therefore unclear whether the observed pattern of variation is attributable to chance, or to some independent variable, possibly mobility. In sum, the problems with the premises cast doubt on the specific conclusion that I_x/I_y is reflective sex differences in degree of mobility, and call into question any subsequent generalization about the relationship between cross-sectional shape and type of activity.

Summary

This critical analysis has identified four problems that cast doubt on the conclusions of the reconstructed arguments presented in this chapter: 1) Wolff's Law has little evidentiary value as the primary theoretical premise in the argument used to infer behavior from long bone cross-sectional geometry. 2) The argument does not make use of all available relevant evidence; there is an ever-increasing body of literature dealing with skeletal mechanobiology. As detailed in chapter 6, this literature points to the complexities of functional adaptation to mechanical usage, which would seem to preclude drawing conclusions about physical activity patterns from cross-sectional geometry. Perhaps, more importantly, this literature calls attention to how much we do not yet know about skeletal adaptation suggesting that, at this time, any conclusions are premature. 3) The argument has failed to make a case for the ability to rule out or adequately control for a number of confounding variables, such as age, body mass, genetic constitution, timing of activity relative to skeletal maturity, nutrition, and other

metabolic factors. Consequently, while the arguments presented in this chapter represent plausible lines of reasoning, there are several potential alternative explanations for the data. Furthermore, there is no reason to rule out *a priori* the hypothesis that every group comparison represents a unique “case study” for which there is a different “cause” or set of causes responsible for observed differences in bone geometry. 4) Results of statistical analyses often failed to reject the null hypothesis for many of the cross-sectional properties ascertained (i.e., few statistically significant differences were found). In such instances, conclusions regarding group differences in physical activity are spurious. The first three of these problems are further developed in the following chapter by reviewing theoretical, experimental, and clinical literature dealing with Wolff’s Law, functional adaptation, and the non-mechanical confounding variables, genetics and nutrition.

CHAPTER 6—WOLFF’S LAW, FUNCTIONAL ADAPTATION, AND CONFOUNDING VARIABLES

It is quite possible for scientists to overlook the fact that observation is of data only: all the rest is interpretation.

James K. Feibleman (1972)

Introduction

This chapter reviews theoretical, experimental, and clinical literature to evaluate the problematic issues surrounding Wolff’s Law, functional adaptation, and confounding variables. The information bears directly on the strength of the reconstructed argument presented in chapter 5, and therefore on whether conclusions regarding specific relationships between cross-sectional geometry and types or levels of physical activity should be accepted or rejected.

The “Law” that is not a law

Wolff’s Law is proffered as the primary theoretical justification for inferring activity patterns from bone geometry. In the previous chapter Larsen (2000: 52) was quoted as claiming, “Such an overwhelming amount of experimental and other research has accumulated in support of Wolff’s conclusions that the phenomenon is identified simply as Wolff’s Law.” However, examination of the literature on skeletal biology reveals that rather than being well supported, Wolff’s Law is contentious. Its derivation is based on a “false premise” (Cowin 2001b) and a fundamental misunderstanding of bone biology (Dibbets 1992). Furthermore, the contemporary conception of Wolff’s Law, namely that bone is capable of sensing and adapting to mechanical stimuli via a cell-based, self-regulating feedback mechanism is not what Wolff proposed. As illustrated

below, there are skeletal biologists who believe that Wolff's Law is a hindrance to the field of mechanobiology.

Wolff's Law is by no means universally accepted among skeletal biologists. One of its harshest critics is John D. Currey, a renowned expert in the field of skeletal biology (Currey 1979, 1981, 1984, 1984a, 1984b, 1987, 1995, 1997, 2001, 2002; Currey and Butler 1975). In a recent publication Currey (2002: 350) wrote, "Studies on bone modeling have been bedevilled [sic] by *Wolff's law*...The unfortunate thing is that, for many workers, it seems only necessary to show that bone is adapting, invoke Wolff's law, and depart, conscious of a day's work well done." In an earlier article titled "Was Wolff Correct?" Currey (1997) expressed his gratitude for Stephen Cowin's¹² "demolition" of the fundamental premise of Wolff's Law, which relates to the alleged orientation of bony trabeculae along principal stress trajectories. Currey (1997: 265) offered the following reason for the persistent use of Wolff's Law in skeletal biology: "...Wolff, with splendid nineteenth century hubris, called his book 'Das Gesetz der Transformation der Knochen', and 'Gesetz' means 'law' whichever way you look at it. Wolff set the nomenclatural ground rules and we have obeyed them ever since."

Currey is not alone in his criticism of Wolff's Law. Huiskes (2000: 145) recently wrote, "'Wolff's Law' is a question rather than a law...it is argued that it was the wrong question, putting [biomechanicians and biologists] on the wrong foot." Further, "While the authority of Wolff's Law made biomechanicians concentrate on bone design, the 'production technology' was largely neglected. Yet, it is here that the real question is found...Nature has found its design by trial and error, over time, by creating a metabolic process responsive to environmental mechanical factors, which inherently dictate the

¹² Cowin, SC (1997) The false premise of Wolff's law of trabecular architecture. *Forma* 12: 247-262.

design requirements. By wondering about what mathematical rules bone architecture might be the answer to, we do not learn anything useful at all. The key to information is in the metabolic process of bone production and maintenance” (ibid: 154). Cowin (2001b) summarizes the status of Wolff’s Law:

There is no general agreement on the form of the rule that is to replace the ‘mathematical’ falsity or ambiguity associated with Wolff’s name (p. 30-1)...Wolff’s law in its present form is a mantra and not a statement that would pass muster in either the biological sciences or the physical sciences. The use of the phrase ‘Wolff’s law’ is an inappropriate suggestion that the concept is a concrete result generally accepted by the scientific community. It implies a dignity that the concept has not achieved. In reality, the exact meaning of Wolff’s law, other than that it is a synonym for the functional adaptation of osseous tissue, is uncertain. There is no generally accepted physiological model for Wolff’s law (p. 30-13).

Given the foregoing comments on Wolff’s Law it is difficult to justify its *continued* application to bioarchaeological research. However, these views are not entirely new. Wolff’s Law has been subjected to a continual barrage of critical analyses by preeminent skeletal biologists since long before its invocation in the first bioarchaeological study of cross-sectional geometric variation. For example, in 1922 Triepel cited 20 objections to Wolff’s Law (Cowin 2001b; Evans 1953). In 1968, Enlow made the following observation, “Wolff’s law of bone transformation has all but defied our best attempts at meaningful explanation” (p. 803). With regard to experiments designed to verify Wolff’s Law, Enlow commented:

Many workers presume that bone growth and biomechanics are virtually synonymous and that mechanical stresses are the principal (perhaps the sole) factor governing the course of skeletal morphogenesis (ibid: 804).... It would be overextending the information...to presume that, because artificially applied stress (or the removal of normal stress) can change the normal course of growth, in vivo stress thereby represents the basic influence that regulates all bone growth and remodeling. Although not

precluding such a possibility, the experiment does not in itself verify it, since a multitude of other variables and possible regulatory factors are not accounted for in its design (ibid: 806).

Just prior to publication of Ruff and Hayes' major collaborative efforts on the Pecos Pueblo archaeological population (Ruff and Hayes 1983a, 1983b), Roesler (1981: 33) wrote, "These deductions of Wolff...contain so many objective errors and misinterpretations of elastomechanical principles that it is difficult to understand why his work was not challenged by his contemporaries." Several years later Carter (1984: S19) wrote, "Although the basic concepts proposed by Roux and Wolff are now universally accepted, the 'mathematical laws' relating bone remodeling to bone stresses or strains have yet to be formulated. Furthermore, the mechanical/biological control system or systems that mediate these processes are unknown." Huiskes et al. (1987) observed, "'Wolff's Law'...as it is commonly understood, is not a scientific law in the traditional sense, but rather a series of qualitative observations and expectations...it is not a theory suitable for quantitative predictions..." (p. 1135). And in 1991 Bertram and Swartz reviewed numerous experimental and clinical studies (including those cited by Bridges, Larsen, Ruff and others) of Wolff's Law and concluded, "future progress in the study of bone structure and function will require the removal of certain conceptual blinders associated with a well-accepted but weakly supported paradigm [i.e., Wolff's Law]...the general assessment of the functional and adaptive behaviour of bone that is often cited in the introductory paragraphs of new research papers is actually based in part on poorly supported presumed 'facts' and the interpretations of the results of previous work that have been passed from paper to paper without receiving adequate critical appraisal" (p. 268). Bertram and Swartz's critical review has subsequently been cited by many skeletal

biologists (Cowin 2001b; Currey 2002; Huiskes 1994; Martin et al. 1998) as providing “a very useful antidote to a blind acceptance that [bone models adaptively to its mechanical environment]” (Currey 2002: 341).

The origin of Wolff's Law

Julius Wolff was born in 1836 and died in 1902. He was a German orthopaedic surgeon and anatomist who became interested in the relationship of form and function in bone while obtaining his medical degree in Berlin during the 1850s (Forward by Peltier, L. F. in Wolff 1988). Wolff is often depicted as an obsessed and arrogant scientist (Cowin 2001b; Currey 1997; Dobbins 1992; Roesler 1981, 1987) as well as a prolific and skillful writer (Dobbins 1992). The 1892 publication of *Das Gesetz der Transformation der Knochen*, which literally translates as “The Law of Transformation of Bone,” represents Wolff's best-known work and the culmination of ideas—some his own, many borrowed—which he had been developing in a series of publications beginning in 1869 (Roesler 1981). In his famous monograph, Wolff presented what he considered to be irrefutable mathematical proof of “the law according to which alterations of the internal architecture clearly observed and following mathematical rules, as well as secondary alterations of the external form of the bones following the same mathematical rules, occur as a consequence of primary changes in the shape and stressing or in the stressing of the bones” (Wolff 1892: 1). Wolff (ibid: 83) wrote of “the action of a determined force of nature” (i.e., “the transformation force”) that could alter the shape and architecture of bone and had tremendous potential in orthopaedics for the correction of deformities. In the 1986 translation of *Das Gesetz der Transformation der Knochen*, Maquet and Furlong modified Wolff's original work to include a “more accurate account of bone growth”

(Dibbets 1992: 2) by substituting the word “remodelling” for “transformation” throughout the book and in the title, which became *The Law of Bone Remodelling*.

Wolff’s Law has been succinctly summarized as: “Every change in the function of a bone is followed by certain definite changes in internal architecture and external conformation in accordance with mathematical laws” (Forward by Peltier, L. F. in Wolff 1988). However, as stated by Enlow (1968: 803), “Definitions or interpretations of Wolff’s law...vary widely according to the nature of the application by different authors.” One reason for a diversity of interpretations is that the current conception of Wolff’s Law is an amalgamation of three general principles (Roesler 1981, 1987), namely that the internal architecture and external shape of a bone are: 1) based on mathematical laws (the stress trajectorial theory of trabecular bone architecture), 2) determined by and adapt to changes in the “function” of the bone (the concept of functional adaptation), and 3) represent the minimum amount of material required for maximum strength (the principle of optimization).

Wolff (1892: 6) credits anatomist G. H. Meyer with having “significantly contributed to our knowledge of the internal architecture of bone,” and German bridge and railway engineer Carl Culmann for having “discovered the mathematical significance of this architecture.” In 1866 Culmann¹³ attended a talk by Meyer and was supposedly struck by the similarity between Meyer’s drawings of idealized trabecular architecture and the lines of stress drawn for engineered constructions. Following Meyer’s talk Culmann drew a “crane-like curved bar” (Roesler 1981: 28) with “the same contours as those of the proximal extremity of the human femur...then asked his students to draw

¹³ Culmann founded the 19th century science of graphic statics, which allowed complex systems of forces in engineered structures to be simplified and rendered graphically as principal stress trajectories.

the...compression and tension trajectories in the crane” (Wolff 1892: 6). Meyer originally published these drawings in 1867 with the hypothesis that “the structure of cancellous bone generally was determined by the direction of the principal stresses” (Roesler 1981: 28). Wolff (1892), however, believed that Meyer had failed to see the true mathematical significance of Culmann’s drawings and sought to correct this oversight.

With the publication of *Das Gesetz der Transformation der Knochen* Wolff intended to prove that bones were designed using the same mathematical rules of construction that engineers used for man-made structures. However, Wolff was neither a mathematician nor an engineer, and his “proof” merely consisted of series of statements derived from detailed descriptions of the internal architecture of the proximal end of a normal femur as seen in a series of longitudinal sections. According to Wolff (1892: 7) simple observation of the femoral sections “demonstrated that the cancellous trabeculae regularly intersect each other [and the surface of the bone] at right angles” just as the principal stress trajectories did in the drawings of Culmann’s crane rendered by graphic statics. This observation, which is the cornerstone of Wolff’s Law, is known as the “stress trajectorial theory of trabecular bone architecture.” Wolff also interpreted the presence of the medullary cavity as evidence of the mathematical laws of trabecular architecture as “there are no trajectories in the crane in the area which corresponds to the medullary cavity in the bone” (1892: 20). Furthermore, Wolff believed these observations supported the idea that bones are constructed with the minimal amount of material necessary to perform their function.

The medullary cavity as well as the spongy structure of the bone ends means saving material while the bone presents sufficient size for the insertion of powerful muscles. However, only after we have learnt from the mathematicians where material is necessary and where it is superfluous, and only after Culmann...can we see that material is absent

not in a somewhat arbitrary way but in areas where it would be superfluous.... Nature has built the bone as the engineer builds his bridges so that, as Culmann says, 'the most appropriate shape is obtained with a minimum expenditure of material' (Wolff 1892: 21).

Though Wolff based his "law" on the apparent similarity of trabecular orientations to stress trajectories in an engineered structure, he believed the external shape of a bone followed mathematical rules of construction as well. Just as the final curve of the crane (i.e., its external contour) represents a line connecting the end points of all the other curves, "...the surface of the bone...has to be considered as the last or limiting trabeculum of the whole trabecular system.... hence its shape, is derived from the internal bony architecture" (Wolff 1988: 5).

Wolff's Errors

Criticisms of Wolff's Law center around three issues: 1) Verification of the stress trajectorial theory of trabecular bone architecture (Cowin 2001b; Roesler 1981, 1987), 2) Wolff's notion of function (Dibbets 1992; Lee and Taylor 1999), and 3) Wolff's misunderstanding of bone biology (Dibbets 1992).

The stress trajectorial theory of trabecular bone architecture

Wolff's Law is predicated on the supposed "perfect mathematical correspondence" between the alignment of trabeculae in the proximal femur and the stress trajectories depicted in Culmann's crane (Martin et al. 1998; Roesler 1981), which to Wolff implied that bones follow the same mathematical rules of construction as engineered structures. Wolff believed bony trabeculae to be the physical embodiment of stress trajectories (Cowin 2001b). His evidence was that trabeculae, like stress trajectories,

cross each other “at right angles in the most obvious way everywhere” (Wolff 1892: 19). However, quantitative verification of this relationship has been elusive (Currey 2002; Martin et al. 1998). While there is some experimental support for the trajectorial theory (e.g., Hayes and Snyder 1981; Huiskes 2000), Huiskes (2000: 154) claims, “The correspondence between trabecular architecture and stress trajectories...is *circumstantial*, not causal.” Cowin (2001b) refers to trajectorial theory as the “false premise” of Wolff’s Law—“the law compares things that appear similar but are not” (p. 30-1).

Skeletal biologists have noted five problems with the trajectorial theory (Cowin 2001b; Dibbets 1992; Evans 1953; Martin et al. 1998; Roesler 1981). 1) Trabeculae do not **always** cross at right angles as was asserted by Wolff, whereas principal stress trajectories must, by definition. Cowin (2001b) points out, it is actually irrelevant whether *trabeculae* cross each other at right angles or not, because regardless of the angle at which they cross, the stress trajectories associated with each trabecula *do* cross at right angles. Whereas the trajectorial theory assumes a one-to-one correspondence between a trabecula and a stress trajectory, each trabecula is actually associated with an infinite number of stress trajectories (ibid). 2) The principal stress trajectories in Culmann’s crane were based on the assumption of an elastically isotropic, homogenous, and more importantly, according to Cowin (2001b), a continuous (containing no gaps) material, none of which is true of cancellous bone. Stress trajectories do not exist in a discontinuous material (Cowin 2001b; Martin et al. 1998). 3) The trajectories represented in Culmann’s crane were based on “only one static loading...while it is obvious that the living femur is subjected to many types of loading” (Roesler 1981: 38). Furthermore, the loads placed on the femur are unknown, and therefore can only be ambiguously or unrealistically specified (Cowin 2001b). 4) Culmann’s crane depicted a

finite number of stress trajectories, whereas in reality, “there are an infinite number of stress trajectories between any two points in the model” (Cowin 2001b: 30-10). The trajectories that were depicted in Culmann’s crane, being “solutions of a differential equation” were based on an arbitrary choice of initial values; “There is no obvious reason to draw only those trajectories that Culmann did” (Roesler 1981: 38). If all stress trajectories were graphically depicted, the resultant figure would not contain individual curves; it would instead be completely filled in. In other words, if bone really were the embodiment of stress trajectories there would be no cancellous tissue, only solid compact bone. 5) By reconstructing Culmann’s crane, Roesler (1981) demonstrated that the stress trajectories in the crane were likely based on a straight rectangular cantilever, which was subsequently curved to approximate the shape of the proximal femur without altering the stress distribution. These problems led Roesler (1981: 38) to conclude, “Whatever the proof for a trajectorial structure of the cancellous bone in the proximal part of the human femur may be, it is not Culmann’s crane.”

Wolff, Roux, and the concept of function

Roesler (1987: 1026) wrote, “The most surprising observation which can be made after reading the old literature on bones...is that there never has been the least doubt about the interrelation between structure and function of bone.” In fact Galileo is credited with having first recognized the relationship between bone shape and mechanical function (Martin et al. 1998). Wolff believed that his observations of trabecular patterns in both normal and pathological specimens proved that the internal architecture and the external shape of bones were a result of their function. However, according to Dibbets (1992: 8), Wolff’s concept of function was of “static...constraints to

be met” rather than “our present day notion of a dynamic process involving action.” Lee and Taylor (1999) echoed this view. According to Wolff (1892: 83; emphasis added), “The shape of bone is determined only by the *static stressing* for which bone is pre-programmed or, in other words, by its function.... Only *static usefulness* and necessity or *static superfluity* determine the existence and location of every bony element and, consequently, of the overall shape of the bone.” The equation of function with static forces or static stressing occurs repeatedly throughout the text, and at one point Wolff asserted, “...nothing much would be changed...by speaking of static shape instead of functional shape” (ibid: 82). Wolff’s belief that the normal architecture of bone is related to “function” yet at the same time, inherited (“it preexists in the foetus”; 1892: 14) further distinguishes his view of function from the current one, and also suggests a certain ambivalence toward the meaning of the word, e.g., “the femur presents its functional architecture long before the child’s first attempts at standing and walking” (1892: 71).

Wolff failed to understand that it was the dynamic process of loading and unloading that stimulated bone adaptation. This led Lee and Taylor (1999) to propose that Wolff’s Law be renamed “Roux’s Law” in recognition of the fact that it was Wilhelm Roux, not Julius Wolff, who first introduced the modern concept of function. It was also Roux, not Wolff, who first described functional adaptation as a cell-based, self-regulating biological process involving both bone resorption and formation in response to a mechanical stimulus (Roesler 1987: 1030). Nevertheless, as stated by Roesler (1987: 1027), “Wolff’s doctrine...became nearly inextricably involved with Roux’s principle of functional adaptation.”

Wolff's misunderstanding of bone biology

According to Dibbets (1992), Wolff was mistaken on two key points with regard to bone biology. First, Wolff (1892) maintained that cortical bone was merely “compressed” cancellous bone. He believed that normal trabecular architecture was latent in the cartilaginous anlage, and that the normal trabecular pattern “unfolded itself” from its compressed state in compact bone through the process of expansion (Dibbets 1992: 8). Hence, the second of his misconceptions was that bones grow by expansion, i.e., interstitially. He steadfastly rejected the position held by most of his contemporaries—“I am almost the only one so far to struggle against...[the] theory of growth by apposition and resorption only” (Wolff 1892: 91), which, in an earlier publication, he referred to as “a theory of permanent structural upheaval” (quoted in Roesler 1981: 35). Clearly, this state of “permanent structural upheaval” closely depicts what Frost has termed remodeling. Regarding this point, Dibbets (1992:7) wrote, “Wolff was so successful in attacking his opponents that he alone may be held responsible for carrying the incorrect notion of interstitial bone growth through the latter quarter of the nineteenth century into the twentieth century. Thus, it is obvious that the translation of the title¹⁴...should not include the term ‘remodeling’.” Although to be fair, translators Maquet and Furlong were probably using “remodeling” in the general sense of adaptation, not as the activation-resorption-formation sequence proposed by Frost (1986).

Functional adaptation

The preceding discussion leads to the conclusion that Wolff's Law is not a

¹⁴ Referring to Maquet and Furlong's 1986 translation of *Das Gesetz der Transformation der Knochen* as *The Law of Bone Remodelling*.

scientific law based on mathematical rules, but rather a synonym for the general concept of functional adaptation. At this point it would be reasonable to ask, if current usage of the phrase “Wolff’s Law” implies functional adaptation, then is the problem simply with the name “Wolff” or the word “Law”? The answer is, as eloquently stated by Cowin (2001b: 30-14) that, “the problem is not the lack of a reasonable terminology, but the lack of an acceptable theory for the functional adaptation of bone.”

Problems linking physical activity to cross-sectional geometry

The concept that bone functionally adapts to mechanical loading is vague, particularly with respect to establishing a causal link between physical activity and specific patterns of cross-sectional geometric variation. Rather than specifics, the literature on functional adaptation is replete with conflicting and equivocal information (Bouvier 1985; Burr 1992; Currey 2002; Martin et al. 1998). Furthermore, many details regarding the processes involved are not known (van der Meulen and Huiskes 2002). Currey (2002: 353) cautions that there is a difference between theoretical predictions and reality, and states that, “In real life, the situation is not very clear cut.” In an attempt to “(escape) the vagueness and confusion associated with the term ‘Wolff’s law’” Martin et al. (1998: 230) proposed the “mechanical adaptability hypothesis,” which “states that bone structure is regulated so as to minimize fracture risk and bone mass while simultaneously optimizing stiffness.” However, there is no consensus on what property of bone, if any, is optimized by an adaptive response (Biewener and Bertram 1986; Currey 2002; Hart 2001; Huiskes 2000; Lanyon 1984; Loitz and Zernicke 1992; Martin et al. 1998; Rubin 1984).

Reflecting a critical departure from the implied certainty of “Wolff’s Law” the authors emphasized that they were calling their idea “a hypothesis because we are not sure it is

true or how it works” (ibid: 230). In a recent survey article, van der Meulen and Huiskes (2002) summarized the status of functional adaptation research:

Adaptation experiments examining skeletal mechanobiology have been performed for more than a century and have examined the influence of both increasing and decreasing the habitual loads applied to the skeleton. Yet, despite the multitude of studies that have been completed, there are still many unanswered questions regarding the skeletal response to normal, perturbed and pathological mechanical loading (p. 403).... Answering these questions will require carefully controlled experiments with well-characterized mechanical environments (p. 405).

As discussed in chapter 2 it is still not known which mechanical loading variables, or combination thereof, are osteogenic (e.g., strain magnitude, strain rate, strain distribution, strain frequency) (Fritton et al. 2000). Judex and Zernicke (2000: 158) point out that, “Few studies...have associated the exercise-related milieu with induced morphological changes or a lack of them.” Bone does not adapt to physical activity per se, it adapts to some quality of the mechanical load generated by physical activity. Therefore, without an understanding of the stimulus responsible for an adaptive response, any attempt at associating specific cross-sectional geometries with types or levels of physical activity is purely speculative and not grounded in solid scientific evidence. For example, it could be that the type of activity, not the intensity of the activity determines whether an adaptive response will occur. Frost (1997a, 1997b) suggests the reason marathon runners have smaller, weaker bones than weight lifters is because weight-lifting increases muscle strength, which results in a much greater peak strain magnitude. In contrast, he suggests, running, no matter the distance, does not produce strain magnitudes that reach the MES for modeling, particularly in adults. Muscle mass is strongly correlated with bone mineral density (BMD) (Arden and Spector 1997). Weight

lifters have bigger, stronger muscles than runners, and muscle contractions produce the greatest, non-traumatic forces experienced by bones (Burr 1997; Frost 1997a, 1997b). Parenthetically, an additional complicating factor in the attribution of bone geometry to physical activity lies in the estimation that up to 50% of the variability in muscle mass is genetically determined (Arden and Spector 1997). Frost distinguishes between activities that require endurance and those that require increased strength, pointing out that the latter, and not the former are more likely to result in skeletal structural adaptations. An activity may be repetitive and it may be physically exhausting, but this does not mean that it will increase bone mass or alter geometry.

Research supports strain magnitude as a critical factor for inducing functional adaptation, but only once a certain threshold is reached (Fritton et al. 2000; Frost 1997a, 1997b; Hsieh et al. 2001; Robling and Turner 2002; Rubin and Lanyon 1985). Some suggest this threshold may vary within and among bones, and possibly between species (Carter 1984; Currey 2002; Fritton et al. 2000; Turner 1999; Hsieh et al. 2001). The threshold may also vary among individuals (Robling and Turner 2002). Others suggest (e.g., Frost 1997a) much greater uniformity of the strain threshold. Although the typical peak strains experienced by bones during normal activities tend to be similar across a variety of animal species (Burr et al. 1996; Currey 2002; Fritton and Rubin 2001; Rubin and Lanyon 1984a), during a specific activity such as running, the values for the strain variables experienced by the skeleton are likely to be different for different bones, and are non-uniformly distributed throughout the cortex, varying within a cross-section, as well as along the length of the shaft (Bertram and Swartz 1991; Carter 1984; Fritton et al. 2000; Judex et al. 1997; Lanyon and Baggott 1976; Loitz and Zernicke 1992). Strains resulting from the same activity also vary among individuals (e.g., Demes et al. 1998; Milgrom et

al. 2000). Consequently, strain measurements obtained from one location on one bone cannot necessarily be used to predict specific adaptive responses in other bones or other subjects (Burr et al. 1996; Milgrom et al. 2000).

It is generally accepted that there is a range of activities unlikely to initiate an adaptive response because the peak strain magnitudes they generate fall within the “adapted window” (Bertram and Swartz 1991; Burr 1992, 1997; Carter 1984; Carter et al. 1980; Currey 2002; Frost 1996, 1997a, 1997b; Martin et al. 1998). However, in addition to strain magnitude, many studies also indicate that strain rate is a key variable (Burr 1992; Hsieh et al. 2001; Lanyon 1981; Milgrom et al. 2000). Other research suggests that only mechanical loadings that produce an atypical strain distribution are osteogenic (e.g., Lanyon et al. 1982; Milgrom et al. 2000; Rubin and Lanyon 1985). A study by Judex and Zernicke (2000: 153) supports the hypothesis that the activity in question must generate a “mechanical milieu” that differs “substantially from the habitual milieu to induce significant adaptations.” In addition, Rubin et al. (1992: 89) have noted that, “Although the predominant responsibility of the skeleton may be to withstand the extremes of physical activity, it does not necessarily follow that the strains generated during this activity are what drive the skeleton’s morphology.” Fritton et al. (2000) found that the peak strains resulting from normal locomotor activities occur rather infrequently; however, during the same period of time bone experienced numerous low magnitude strains. These workers found that bone sensitivity to strain seems to be frequency-dependent, and suggest that low-magnitude high-frequency signals might play a significant role in bone adaptation (Fritton et al. 2000; Rubin et al. 1992).

Another complication in linking physical activity to specific long bone cross-sectional geometries is that the external loadings applied to bones and the consequent

stress and strain magnitudes, rates, distributions, and frequencies associated with specific activities are, for the most part, uncharacterized (Lanyon and Baggott 1976; Lanyon et al. 1979). Ruff and Hayes (1983a: 372) have noted “the importance of considering the total loading configuration when attempting to interpret structural variation.” Ruff and Hayes attempted to relate locational cross-sectional geometric variation in the femur and tibia to predictions of in vivo loading based on theoretical and in vitro loading models. However, the loads placed on long bones during normal activities are extremely complex and time variable (Burr et al. 1996; Fritton and Rubin 2001; Lanyon and Rubin 1984; Rubin et al. 1990; van der Meulen et al. 1993). Consequently, theoretical estimates of in vivo loading may have limited usefulness in predicting bone strain (Carter et al. 1980; Currey 2002; Demes et al. 1998, 2001). Bouvier (1985: 241) warns that, “relating stress patterns to bone morphology without first examining in vivo strain distributions may lead to erroneous conclusions.” Because measurement of strain parameters during activity requires attaching strain gauges directly to living bone, this type of invasive experiment is not often performed on humans. To date, in vivo strain of a long bone diaphysis has only been recorded for a single mid-diaphyseal location on the medial tibia in seven human subjects (e.g., Burr et al. 1996; Milgrom et al. 2000). Of the major long bones, the tibia is the most amenable to strain measurement (Milgrom et al. 2000) because its anteromedial surface is relatively superficial while the shafts of the femur and the humerus are surrounded by muscles.

Principal compressive and tensile strains were recorded from the midshaft tibia of a single, middle-aged male subject during a variety of “vigorous activities” including walking with and without a weighted pack, jogging and sprinting on level and inclined surfaces, and “zigzag” running uphill and downhill (Burr et al. 1996). For the most part,

strain magnitude and strain rate varied significantly between walking and running; however, the overall patterns of variability were complex. The highest strains experienced by the tibia were shear strains (calculated as the difference between the peak compressive and tensile strains) generated during uphill and downhill zigzag running; these approached $2000\mu\epsilon$. Shear strains were also high during level sprinting and uphill running. During most activities peak compressive and tensile strains were relatively low, ranging between 350 and $1000\mu\epsilon$; only peak compressive strain exceeded $1000\mu\epsilon$ and, even then, only during zigzag running. Carrying a pack during walking made little difference in peak strain magnitude or rate. Strain rates were significantly higher during running than walking; this was particularly true for shear strain rates during sprinting on a level surface and zigzag running downhill. The experiment by Burr et al. (1996) suggests that the more vigorous the locomotor activity, the greater the strain magnitude and rate. This general conclusion was supported by the findings of Milgrom et al. (2000). The results also generally support Frost's (1997a, 1997b) hypothesis that, in adult human bone, running does not typically generate peak compressive and tensile strains that exceed the modeling threshold of $1000\mu\epsilon$ required for bone formation. However, as pointed out by Frost (1997b), the role of shear strain in initiating an osteogenic response requires further investigation.

Ruff and Hayes (1983a: 371) have claimed that, "the optimum cross-sectional 'shape' of a bone subjected only to bending in one plane would be to place as much bone as far as possible from the neutral axis of bending." They have also asserted that, "differences in bone 'shape' can be viewed largely as adaptations which reduce stress and/or strain in bones under in-vivo loading conditions" (ibid: 373). These statements reflect a confounding of two separate concepts, the second of which may or may not

follow from the first: 1) Bones with a more outward distribution of bone tissue in a single plane are more resistant to bending in that plane (i.e., they have a greater bending rigidity in that plane). 2) Increased bending loads within a single plane produce an adaptive response that results in a greater outward distribution of bone tissue, in order to minimize bending in that plane. This requires bones to be more reinforced where they are maximally loaded. Whether optimal or not, studies suggest that this is not how bones are constructed (Demes et al. 1998, 2001; Ohman and Lovejoy 2001). Demes et al. (1998) studied ulnar deformation during locomotion in rhesus macaques. From observations of macaque locomotion, the authors hypothesized that macaque ulnae experience anterior-posterior bending. In contrast, results of strain gauge recordings indicated that the ulnae primarily experienced bending in the medial-lateral plane. In addition, the authors found that macaque ulnae are *not* reinforced in the plane of maximum bending; they are instead more expanded in an anterior-posterior direction. This led them to suggest that, “Bone cross-sectional geometry may not be a simple mirror reflection of functional loads” (ibid: 96). Similar results were reported for macaque tibiae (Demes et al. 2001). The authors “caution against broad behavioral conclusions derived from long bone cross-sectional shapes” (ibid: 264).

Other research indicates that specific sites of bone formation do not correspond to predictions based on the hypothesis that bone adapts to minimize the strains it experiences during loading. Following a three-week experimental period in which mature roosters ran on a treadmill Judex et al. (1997) observed activation of periosteal surfaces in five of the eight exercised animals. However, the sites of periosteal activation did not correlate with either peak strain magnitude or strain rate, interpreted as suggesting that bone is deposited “where mechanical integrity is least challenged” (Judex

et al. 1997: 1742). To explain these and other similar findings (Rubin 1984) it has been hypothesized that the “goal” of bone adaptation, rather than minimizing strain, is to maintain a certain “type of strain” (Rubin et al. 1990). It is reported that over 80% of strain in long bones is due to bending (Rubin et al. 1990), and as obvious from the above quote from Ruff and Hayes (1983a), it is assumed that bone architecture is optimized to reduce bending by increasing rigidity. However, as discussed by Bertram and Biewener (1988), rather than minimizing bending, normal longitudinal curvature often accentuates it in a particular direction. Likewise, an elliptical cross-sectional shape in which bending rigidity is decreased in one direction can control the direction of bending through unequal second moments of area. Bertram and Biewener (1988) have suggested that bone construction “sacrifices strength for load predictability.” This would be advantageous for bones that experience “a highly variable loading environment” (ibid: 91), as limb bones do during locomotion. This hypothesis suggests an intriguing possibility: differences in cross-sectional geometry, particularly ratios of second moments of area (e.g., I_x/I_y), may be related to differences in the amount of relative curvature among bones from different populations.

Functional adaptation: an “umbrella term” for a plurality of effects

Finding therapies for the prevention or treatment of osteoporosis has been a driving force behind much of the research conducted on bone adaptation. Functional adaptation of bone to both increased and decreased mechanical loads has been studied experimentally and clinically. Experiments designed to study the effects of increased mechanical loading have utilized surgical (e.g., osteotomy) and non-surgical loading (e.g., exercise regimens) techniques in a variety of animal models (Biewener et al. 1983;

Bravenboer et al. 2001; Buhl et al. 2001; Carter 1981; Carter et al. 1980; Chamay and T'schantz 1972; Churches et al. 1979; Cullen et al. 2000; Forwood and Parker 1987; Jee et al. 1991; Kimura et al. 1979; Lanyon 1980; Lanyon and Baggott 1976; Lanyon and Bourn 1979; Lanyon et al. 1979, 1982; Raab et al. 1990; Robling et al. 2000; Steinberg and Truetta 1981; Tanck et al. 2000, 2001). Studies of decreased loading in animals have employed immobilization (casting, hind-limb suspension, space flight, simulated weightlessness) and surgical techniques (neurectomy) (Abram et al. 1988; Amtmann 1974; Jaworski et al. 1980; Martin 1990; Shaw et al. 1987; Uhthoff and Jaworski 1978; Wunder et al. 1979). Research projects involving human subjects employ either a cross-sectional, or less frequently, a longitudinal design in which bone mass, density, and occasionally geometry are compared between exercise and control groups or between athletes and non-athletes (Davee et al. 1990; Gleeson et al. 1990; Hasegawa et al. 2001; Jonsson et al. 1992; Kirk et al. 1989; Sandler et al. 1987). Clinical studies following permanent paralysis or injury resulting in temporary immobilization have provided information about decreased loading in humans (Kiratli et al. 2000), as have studies of astronauts following prolonged weightlessness in space (Bikle and Halloran 1999).

Studies of functional adaptation are far too numerous to review here. Moreover, the results are extremely varied, and difficult to interpret (Bertram and Swartz 1991; Currey 2002; Martin et al. 1998). Bertram and Swartz (1991) provide an excellent critical analysis of numerous studies conducted prior to 1990 in which they suggest that the various phenomena reported in the literature and attributed to Wolff's Law actually represent a "plurality" of effects. These authors suggest that workers have ignored alternative explanations for their findings, particularly those related to "complications arising from indirect effects of the investigative procedures on other aspects of the

organism's physiology" (p. 246). For example, bone loss during spaceflight has been interpreted as a direct response of bone to mechanical unloading, and is frequently cited as evidence for Wolff's Law (e.g., Bridges 1989). However, Bertram and Swartz suggest alternative possibilities including a generalized, systemic response to unloading, or other physiological effects, such as bone loss due to increased corticosteroid secretion from physiological stress. In addition, the extreme non-physiological loading imposed by osteotomy and external bending devices may not produce results that are equivalent to the effects of normal, voluntary activities on bone (e.g., Bertram and Swartz 1991; Martin et al. 1998). It seems likely that the studies most relevant to inferring behavior from cross-sectional geometry would be those involving activities and loads within the normal physiological repertoire of the animal. Much of the strongest evidence for functional adaptation comes from comparative studies of athletes with sedentary controls, or studies of upper limb bilateral asymmetry in people who play racquet sports (e.g., Jones et al. 1977; Bass et al. 2002). Although professional athletic activities are within the normal physiological capabilities of humans, they often fall at the upper limit. Seeman (2002: 375) refers to the "Olympian effort" required to generate such extreme structural variation in the human skeleton, and suggests that these studies tell us "what is possible, not what is feasible in day-to-day life." Extrapolation from these studies to prehistoric societies actually presumes that the behaviors and lifestyles of past peoples reflect this "Olympian effort," which again, as pointed out by Jurmain (1999), is what needs to be demonstrated, and should not be assumed.

Other researchers reiterate Bertram and Swartz's (1991) skepticism: "While bone 'adaptation' to loading is a long-standing concept in bone physiology, researchers may sometimes be too willing to accept this paradigm as an exclusive explanation of *in vivo*

tissue responses during experiments, while overlooking confounding variables, alternative (non-mechanical) explanations, and the possibility that different types of bone (*e.g.*, woven bone, Haversian bone, plexiform bone) may have different sensitivities to loading under healing *vs.* quiescent conditions” (Brunski 1999: 99). Loitz and Zernicke (1992: 14), on the other hand, suggest that the lack of consistent experimental results “may reflect complex interactions between bone remodelling and exercise intensity, animal species, and skeletal age.”

Age effects on functional adaptation

In bioarchaeological studies of past human behavior it is frequently inferred that a larger group mean for certain geometric properties, such as the polar second moment of area (J ; representing torsional rigidity or “average” bending rigidity), implies a greater level of physical activity, *i.e.*, a more strenuous lifestyle (*e.g.*, Larsen et al. 1995). However, this dissertation asserts that the effect of the “timing” of physical activity within an individual’s lifespan confounds the interpretation of cross-sectional geometric properties. “Timing” is a confounding variable because it may differ among archaeological population samples, yet it cannot be determined, cannot be controlled for, cannot be ruled out, and could potentially provide an alternative explanation for the results. In other words, conclusions regarding greater or lesser levels of activity based on cross-sectional geometry may be false because group differences in the mean values of cross-sectional geometric properties could in fact reflect population (*e.g.*, cultural) differences in the commencement of physically demanding activities. Alternatively, adult cross-sectional geometry could reflect real differences in the activity levels of younger members of the population, but have little to do with differences in lifestyle resulting from

major transitions in mobility patterns or subsistence strategies. The geometry of an adult long bone is largely dependent on activities performed earlier in life. Research has shown that physical activity has age-dependent, site-specific and variable effects on cross-sectional geometry due to differential bone formation and resorption activity on periosteal and endocortical surfaces.

Mechanical adaptation in immature versus mature individuals

It is considered an established phenomenon that the bones of children and adolescents are more responsive to mechanical loading than those of adults (Bass et al. 1998, 2002; Bertram and Swartz 1991; Bradney et al. 1998; Duncan et al. 2002; Frost 1986, 1997a, 1997b; Forwood and Burr 1993; Haapasalo et al. 1998, 2000; Heinonen et al. 2000; Jee 2001; Kannus et al. 1995; Khan et al. 2000; Kontulainen et al. 2003; Lieberman et al. 2001; Martin et al. 1998; Milgrom et al. 2000; Mosley and Lanyon 2002; Nordstrom et al. 1998; Ogden 2000; Petit et al. 2002; Ruff et al. 1994; Seeman 2002; Slemenda et al. 1991; Zanker et al. 2003). “Growth” is said to be “the single most opportune time to modify the mass and geometry of the skeleton” (Seeman 2002: 374), and according to Frost (1997b: 183), “‘Vigorous’ voluntary activities help to increase bone mass and strength in children, but in aging adults they seem to minimize bone losses instead of increasing bone mass.” This is also the interpretation of Forwood and Burr (1993). The difference in response to mechanical loading may not relate to a differential sensitivity to increased loading between the bones of young versus old individuals (Järvinen et al. 2003; Klein-Nulend et al. 2002). Järvinen et al. (2003) compared the response of the femoral neck in young and old rats to treadmill running exercise and subsequent deconditioning (cessation of activity). While both age groups showed

increases in bone mass and bone mineral density resulting in increased bone strength, the bones of young rats exhibited dramatic changes in geometric properties, whereas old rats exhibited an increase in bone mineral density with no corresponding increase in geometric properties. Both young and old rats lost a similar amount of bone as a result of deconditioning. The authors concluded that while both age groups are capable of adapting to mechanical loading (i.e., the sensitivity to mechanical loading was not reduced in the older rats), the adaptive mechanisms were different. This conclusion is supported by experimental findings that the sensitivity of cultured human osteoblastic-lineage cells to mechanical deformation was not related to donor age (Klein-Nuland et al. 2002).

In contrast to the strong support for activity-induced adaptation prior to skeletal maturity, Bertram and Swartz (1991: 246) claimed that there was no unequivocal evidence for bone adaptation in the “healthy mature appendicular skeleton.” Forwood and Burr (1993) reiterated this skepticism and pointed out the failure of studies “to consider important confounding variables” (p. 97). Seeman (2002: 374) has also recently expressed similar reservations:

There is little replicated and methodologically sound evidence to suggest that exercise during young adulthood, peri-menopause, late adulthood, or old age modifies bone size, prevents bone loss, or restores bone mass, architecture, or strength. Consistency in results is lacking; some studies suggest bone loss is prevented by exercise and others suggest bone loss is not prevented or is increased. The increase in aBMD of a few percentage points reported in some studies is probably due to a reduction in the size of the reversible remodeling space. There is little, if any, evidence of changes in bone tissue mass beyond that produced by reducing the remodeling space. There is no evidence that exercise *in adults* increases cortical thickness by increasing periosteal apposition, reducing endocortical resorption, or increasing endocortical bone formation.

The reasons for the apparent age-related difference in response to mechanical loading are not yet known, although there is speculation about the osteogenic role of growth and sex hormones in older children and adolescents (Bass et al. 1998; Khan et al. 2000; Seeman 2002). These hormones rise during early puberty, and the level of growth hormone falls immediately after the onset of menarche in females (Khan et al. 2000), thus providing physiological evidence for an increased osteogenic response around puberty. There are also fundamental differences in the mechanical properties of rapidly growing versus mature bone (Currey and Butler 1975; Currey 2001; Martin et al. 1998). For example, rapidly growing bones are less mineralized and more compliant due to the mineralization lag following bone formation. Furthermore, modeling is thought to either cease or become greatly reduced at skeletal maturity, and as Frost (1997b: 183) stated, “Modeling, not BMU-based remodeling, determines size and architecture.”

Frost’s (1997a) hypothesis, in keeping with the “mechanostat,” is that during childhood and adolescence relatively rapid increases in body mass, muscle strength, and physical activity outpace the “sluggish” ability for bones to adapt. Consequently, strains experienced by rapidly growing bone in young individuals are greater, and are more likely to exceed the modeling threshold, thus stimulating formation drifts on periosteal or endosteal bone envelopes. This would be true regardless of whether there are other age-related differences in adaptation. Once changes in body mass and muscle strength have stabilized, which occurs at some point in the late teens and early twenties, the bones “catch-up,” and strains are reduced below the modeling threshold (i.e., they fall within the “adapted window”).

Studies of the response of immature (i.e., growing) bone to exercise using animal models, such as pigs (Woo et al. 1981), rats (Forwood and Parker 1987; Li et al. 1991;

Robling et al. 2000), and roosters (Biewener and Bertram 1994; Judex and Zernicke 2000; Matsuda et al. 1986) have produced variable results. Some studies show positive effects on bone mass and strength, including increases in cross-sectional second moments of area (Biewener and Bertram 1994; Woo et al. 1981). However, several studies have demonstrated negative consequences of intense activity on growing bone including reduced long bone length (Forwood and Parker 1987; Li et al. 1991; Matsuda et al. 1986; Robling et al. 2000), reduced periosteal diameter (Matsuda et al. 1986), reduced material properties (Forwood and Parker 1987; Matsuda et al. 1986), and reduced geometric properties (Li et al. 1991). Forwood and Burr (1993) have suggested that there may be a threshold of intensity or duration, above which exercise is detrimental to growing bone. Still other studies have reported no significant difference between the bones of exercised animals and controls (Judex and Zernicke 2000; Raab et al. 1990). Studies that show either a negative response or a lack of response to increased physical activity suggest that caution should be exercised when interpreting lower values for cross-sectional geometric properties as evidence for reduced activity.

Woo et al. (1981) is the most frequently cited bone adaptation experiment among the literature reviewed in chapter 3 (Bridges 1989; Fresia et al. 1990; Larsen 1997; Ledger 2000; Mays 1999; Ruff and Hayes 1983a; Ruff and Larsen 1990; Ruff et al. 1993, 1994). In this classic study of “Wolff’s Law”, five pigs were subjected to a regimen of treadmill running for twelve months. Four additional pigs served as unexercised controls. All pigs were one-year-old and considered sexually immature at the beginning of the experiment. At the end of the experiment, there was no difference between exercised and control pigs in the external (i.e., periosteal) diameter of the femoral midshaft; however, the endosteal diameter was significantly reduced in exercised pigs. As a result, exercised pigs exhibited

significantly greater cortical thickness, cortical area, and second moments of area (I_{max} and I_{min}). It is worth noting that a similar increase in bending rigidity would have been more efficiently obtained by the addition of a small amount of bone to the periosteal surface, yet the bones adapted to increased mechanical loading by reducing the size of the medullary cavity. This is an important point with respect to interpretation of cross-sectional geometric variation. “All else being equal” (Larsen 1997) bones with a more outward distribution of bone have greater bending rigidity, consequently it has been assumed that increased bending loads result in bone deposition on the periosteal surface where bone strains are greatest. Clearly, bone adaptation does not always result in the most structurally efficient design, which suggests possible physiological constraints on the adaptive process that control the ultimate distribution of bone tissue, and therefore the bone’s geometry. It is also worth noting that in this experiment, measurement of external dimensions alone would have led to the spurious conclusion that exercise had no effect on bone mass and distribution. Woo et al. (1981) did not indicate if the increased cortical thickness was due to the addition of new bone on the endocortical surface (e.g., by formation-mode modeling); therefore, as interpreted by Martin et al. (1998) the effect of moderate exercise in these pigs was likely a reduction in the amount of bone resorbed from the endocortical surface, as would be expected in conservation-mode remodeling.

“Growth in the external size of a long bone, its cortical thickness, and the distribution of cortical bone about the neutral axis are determined by the absolute and relative behavior of the periosteal and endocortical bone surfaces along the length of the bone” (Bass et al. 2000: 2277). Therefore, interpretation of cross-sectional geometry in skeletal samples for which activity is *unknown* necessitates knowing the effects of physical activity and age on the activity of these bone surfaces. However, it is not known what

factors are responsible for whether bone adapts by periosteal expansion versus endosteal contraction (Bradney et al. 1998).

Woo et al.'s (1981) finding of reduced endosteal dimensions has been reported for other animal exercise studies involving mature (e.g., Loitz and Zernicke 1992) and immature animals (Matsuda et al. 1986), as well as humans, including children and adolescents involved in exercise intervention programs (Bass et al. 1998; Bradney et al. 1998; Petit et al. 2002; Seeman 2002), and professional athletes involved in racquet sports (Bass et al. 2002; Haapasalo et al. 1996; Jones et al. 1977; Kannus et al. 1995).

Studies of the effects of activity on femoral midshaft geometry in children and adolescents are inconclusive. While reductions in endosteal dimensions are frequently observed, effects on periosteal dimensions are more variable. Jumping exercise in early-pubertal girls produced no significant changes in femoral midshaft geometry (Petit et al. 2002). In this study, increases in periosteal diameter were non-significantly greater in the control group. In contrast, jumping exercise did produce increases in femoral neck geometry in the exercise group. Bradney et al. (1998) reported similar findings for the femoral midshaft periosteal diameter in prepubertal males. However, in this group, femoral midshaft cortical wall thickness increased in the exercise group due to a decrease in endosteal diameter. Likewise Bass et al. (1998) found no difference between female gymnasts and controls for femoral midshaft periosteal diameter; however, cortical area was greater in gymnasts, again due to a reduction in endosteal diameter. Duncan et al. (2002) compared femoral midshaft geometry among groups of female swimmers, cyclists, runners, triathletes, and sedentary controls aged 15 to 18 years. All athletes were state or national level competitors. Results showed that runners had significantly greater cortical area and second moment of area than controls, swimmers, and cyclists, but not

triathletes. The cortical area of triathletes was significantly greater than that of swimmers only. Total periosteal area, however, did not differ among groups, again suggesting a lack of periosteal expansion. Medullary area was greater in swimmers and cyclists than in runners and triathletes, which could reflect either an increase in endocortical bone resorption or a decrease in endocortical formation.

It has been stated that “Young bone has a greater potential for periosteal expansion than aging bone” (Forwood and Burr 1993), and that “the period of longitudinal growth is the only time in life when bone may be added substantially on both the inner (endosteal) and outer (periosteal)” surfaces (Haapasalo et al. 2000: 353). Based on a study of young female tennis players, Bass et al. (2000) suggested that prior to puberty the periosteal surface is most active, while during puberty both periosteal and endocortical apposition occur. If the above hypotheses are correct then increased loading prior to puberty should result in greater increases in cross-sectional second moments of area and the polar second moment of area than the same loading applied later in life. However, a tendency for increased periosteal apposition prior to puberty was not apparent from the studies reviewed above (Bass et al. 1998; Bradney et al. 1998; Duncan et al. 2002; Petit et al. 2002), which primarily show a decrease in endosteal dimensions rather than an increase in periosteal dimensions following increased activity. In contrast, studies of long-term unilateral loading in competitive tennis do show increased periosteal dimensions of the humerus (Bass et al. 2000; Haapasalo et al. 2000; Jones et al. 1977; Kontulainen et al. 2003). Whether this discrepancy reflects bone-bone (e.g., femur versus humerus) differences with respect to periosteal and endosteal adaptation, loading differences from different types of activities, or methodological differences is not known.

Another complicating factor in the evaluation of the effects of activity on bone geometry is that the relative contribution of increased periosteal and endocortical bone to observed increases in cortical area or cortical thickness has been shown to vary depending on cortical location (anterior, medial, lateral, posterior) within a given section, and along the length of the limb bones (Bass et al. 2000; Bradney et al. 1998; Duncan et al. 2002; Haapasalo et al. 1996; Seeman 2002). Within the same bone the effects of a particular activity are site-specific (Petit et al. 2002). Consequently, the selection of bone sites for analysis bears on the particular analytical outcome, and could be partly responsible for the seemingly variable response of bone to activity reported in the studies above.

The optimal period for physical activity

Many studies have attempted to determine the optimal or “critical” period in which physical activity produces maximal gains in bone strength. In this regard, the time around puberty is often described as a “window of opportunity” to increase bone strength through adaptations in bone mass and architecture (Khan et al. 2000; Mosley and Lanyon 2002; Seeman 2002). Whether the optimal period is confined to either the pre-pubertal or early pubertal years has not been determined.

Probably the most convincing research supporting adolescence as a time during which activity has the greatest effect on cortical geometry comes from studies of humeral bilateral asymmetry in long-term players of racquet sports (Bass et al. 2002; Haapasalo et al. 1996, 1998; Kannus et al. 1995; Kontulainen et al. 2003; Seeman 2002). An advantage of these studies is that the observed effects of activity on the dominant arm are not confounded by differences in genetics, nutrition, and other lifestyle factors (Khan et al. 2000), although differences in any of these factors could account for the large range of

inter-individual variation that is often observed (Kannus et al. 1995). Activities such as tennis impose large mechanical loads on the dominant playing arm, while the non-playing arm experiences loads more typical of the arms of non-players. The arms of players tend to exhibit significantly greater side-to-side differences in bone mineral content, bone mineral density, and cortical cross-sectional geometry than those of non-playing controls, although the nature and degree of the differences vary by location (e.g., proximal versus midshaft or distal humerus) (Haapasalo et al. 1996, 1998; Kannus et al. 1995). Haapasalo et al. (1996) also noted male-female differences in the specific location of greatest side differences; male side-to-side differences were greatest proximally, female's distally. Based on a reevaluation of a classic study of humeral bilateral asymmetry in professional tennis players (Jones et al. 1977), Ruff et al. (1994) demonstrated that cross-sectional properties in the dominant playing arm are inversely correlated with starting age. These results have been confirmed in studies of other players of tennis and squash (Haapasalo et al. 1996, 1998; Kannus et al. 1995; Kontulainen et al. 2003). In a study of female tennis players aged 7 to 17 years, Haapasalo et al. (1998) found that players relative side-to-side differences were not significantly different from controls until the adolescent growth spurt at puberty. Based on a separate study of young versus old starters Haapasalo et al. (1996) concluded that, "even intense physical loading of a mature bone is only marginally better in increasing the bone mass, bone density, and [cortical wall thickness] of the target bone than the normal daily use of the dominant extremity" (p. 864). In contrast to the above findings, Nara-Ashizawa et al. (2002) observed a reduction in cross-sectional properties (e.g., total area, medullary area, second moment of area) and strength in the midshaft radius of the dominant playing arm in older females who began playing recreational tennis on a routine basis after thirty years of age.

These findings contrast with side differences reported for the radial shaft in male tennis players who began playing during childhood (Haapasalo et al. 2000). Nara-Ashizawa et al. (2002: 621) suggest, “It is therefore conceivable that habitual exercise, after peak bone mass has been attained, suppresses acceleration of bone loss from the endocortical area, resulting in suppression of compensatory bone formation at the periosteal surface.” Once again, the site-specific and sometimes counter-intuitive effects of physical activity on long bone cross-sectional geometry suggest caution when interpreting group differences in levels and types of activities based on variation in cross-sectional geometric properties.

In summary, the proposed counterargument to conventional interpretations of cross-sectional geometry (i.e., those reviewed in chapter 3) is supported by evidence for the following propositions: 1) The bones of younger individuals are more likely than those of older individuals to respond to their mechanical environment in such a way as to produce localized differences cross-sectional geometry, and 2) There is a period of time during development when mechanical loading has a maximal impact, such that activities performed during this period produce more dramatic effects on cross-sectional geometry than at other points during an individual’s lifespan.

Non-mechanical confounding variables

Attributing cross-sectional geometric variation to differences in mechanical loading vis-à-vis physical activity assumes that nonmechanical factors do not influence cross-sectional geometry or that such factors can be ruled out or controlled for in the research design. There is an assumption that variation in the distribution of bone “seems to suggest localized (mechanical) rather than systemic (nutritional or other) effects” (Ruff et al. 1984: 135). Seemingly at odds with this notion is the fact that researchers who study

the effects of activity on skeletal adaptation in living humans must carefully design their research protocols to control for a number of potentially confounding variables including height, body proportions, weight, lean and fat mass, age, sex, maturation stage, genetic background, socioeconomic status, and diet (Seeman 2002). Furthermore, even when the amount and type of physical activity are known, as they are in controlled exercise intervention studies, there is a limited ability to draw strong conclusions due to the existence of confounding variables, such as selection bias (e.g., individuals who are physically stronger self-select to participate in athletic activities) and unaccounted for group differences in nutrition, socioeconomic status, and genetics (Khan et al. 2000; Seeman 2002). There is every reason to assume that a similar set of variables may confound bioarchaeological studies attempting to compare the cross-sectional geometric properties between two or more groups.

Frost believes that mechanical usage is the driving force in shaping skeletal architecture, but that nonmechanical “agents” can “optimize or impair skeletal responses to mechanical usage” (1996: 144) “by making the MES mechanisms either somewhat deaf, or somewhat overreactive, to the skeleton’s normal mechanical usage” (Frost 1987: 6). Among the nonmechanical “agents” mentioned by Frost are nutrition, genetics, hormones, and disease. As explained by Frost (1987: 6) “the bone mass effects of such agents should duplicate those of changing mechanical usage and MES setpoints with respect to kind and anatomical distribution.” For example, administration of fluoride may act by lowering the setpoints so that the bone perceives a spurious overload, and increases its mass appropriately (Frost 1987). “If a genetic factor set the MES setpoints somewhat lower than the norm for most people and races, the mechanostat should sense that a normal amount of bone is somewhat inadequate, so it would make affected

individuals accumulate somewhat more bone than the norm during growth, and then retain more bone than the norm throughout life” (Frost 1987: 7). The opposite effect would occur if a genetic factor resulted in a higher setpoint. This interpretation of the potentially significant role of nonmechanical agents in bone adaptation is echoed by Jee (2001: 1-37):

Nonmechanical agents influence the mechanical regulation and have a direct influence on bone cells and their precursors involved with biologic mechanisms that are independent of the mechanical stimuli. In addition, there are interactions between mechanical and nonmechanical factors. Such additive or synergistic influences have shown that mechanical stimuli for bone hypertrophy or atrophy can be altered by nonmechanical agents. If one maintains the view that mechanical factors dominate bone regulation, one can consider nonmechanical factors as agents that effectively alter the level of mechanical stimulus.

The specific effect a mechanical stimulus has on bone may vary depending upon a variety of factors: age, sex, previous loading history, anatomical location and function, bone material properties, nutritional status, health status, hormone levels, body composition (lean versus fat mass), total body mass, height, body proportions, and genetics. There is no reason to assume that this list is exhaustive, and there is good reason to assume that there are numerous interactions between these factors. The following sections will discuss potential genetic and dietary effects on cross-sectional geometry.

Genetic effects on cross-sectional geometry

Historically, phenotypic traits were often characterized as being under either genetic or environmental control (i.e., nature versus nurture). This is now known to be a false dichotomy. In general terms, phenotypic plasticity refers to the ability of an organism to express a different phenotype depending on its environment. At one time it

was thought that such traits were not under genetic control. More recently it has been accepted that phenotypic plasticity often has a genetic basis (Agrawal 2001). The modern definition of phenotypic plasticity includes the ability of a single genotype to generate different phenotypes in disparate environments, reflecting the interaction of genotype and environment on developmental processes. Depending on the environment, a single genotype can exhibit different chemistry, physiology, development, morphology, or behavior. Clearly, the ability of bone to adapt to its mechanical environment provides for many skeletal properties to be defined as phenotypically plastic (Lieberman 1997). Unlike many phenotypically plastic traits, which at some point during development become fixed (e.g., long bone length), some properties of the skeleton may remain phenotypically plastic throughout the life of the organism (e.g., bone mass, cross-sectional geometry, bone mineral density).

Ontogenetically, the genetic constitution of an individual is, to some unknown extent, responsible for the general build of bones, providing “the basic genetic template.” Evolutionarily, genetic differences account for a great deal of the interspecies variation in skeletal form (Goodship and Cunningham 2001). Currey (2002: 339) has stated, “the form of bones, lying latent in the genes, is the result of natural selection acting in the past on mechanically functioning skeletons.” Currey also acknowledges that, “the interaction between the genetic endowment of the cells concerned with remodeling and the strain imposed on the bone must be complex” partly because “in the mature skeleton, the kinds of stresses imposed on bones will differ from place to place” throughout the skeleton (ibid: 379).

Obviously, genetics play a fundamental role in the structure and mechanical properties of the skeleton. The initial development of the skeleton, the formation of the

cartilaginous anlage and its subsequent ossification, and the number and general form of the skeletal elements are unquestioningly under genetic control. In addition, vertebrates have evolved the physiological machinery necessary for the skeleton to sense and adapt to its environment, and there can be no doubt that the biological processes involved in this adaptive response are under the control of multiple, probably hundreds, of polymorphic genes. Furthermore, it is almost certain that these biological processes differ between species, and that these differences are genetic in origin. For example, the bones of most modern fish do not undergo remodeling, yet are “adapted” to the loads they must bear (Currey 2002: 26).

Ruff and colleagues (Ruff 1987, 2000b; Trinkaus et al. 1994), and Bridges (1995) have argued that differences in mechanical loading account for the gradual reduction in robusticity and sexual dimorphism that occurred during the evolution of the *Homo* lineage. However, as pointed out by Martin et al. (1998), an alternative explanation involving genetic differences between Neanderthals (and other archaic *Homo* species) and modern *Homo sapiens* cannot be ruled out. They suggest two possibilities, one being a genetic change in bone metabolism resulting in a lowering of the setpoint for modeling. In this situation, “ordinary loads would stimulate more bone formation through modeling in growing Neanderthals, and suppress remodeling in adults, fitting the observations equally well” as differences in physical activity (ibid: 270). A second possibility involves genetic differences in Neanderthal periosteal tissue resulting in “enhanced bone formation and larger skeletons” (ibid: 270). Other possibilities, such as endocrine differences, exist as well. Ruff, Larsen, and Bridges, while acknowledging that genetic factors play a role in skeletal structure, have also asserted that temporal and geographic variation in skeletal robusticity and cross-sectional geometric properties among more recent prehistoric and

early historic Native American groups is better explained by differences in mechanical loading than genetics. Alternatively, this dissertation suggests that genetic differences may account for some of the observed variation among recent groups as well. More definitively, in the absence of strong evidence to the contrary, genetic differences cannot be ruled out, and preclude the attribution of cross-sectional geometry to physical activity.

Certainly, it is probable that genetic differences existed between geographically distinct populations such as those from Pecos Pueblo, New Mexico and the Georgia coast. And while it may be less likely that genetic differences account for diachronic changes in cross-sectional geometric properties that coincided with the transition to agriculture on the Georgia coast¹⁵ (Ruff and Larsen 1990; Ruff et al. 1984), it is possible that some of the differences observed following Spanish contact could be genetic in origin. For example, during the contact period, Spanish mission populations may have reflected a genetically heterogeneous group composed of aggregations of various regional native populations (Larsen 1990). This could potentially explain the bimodal distribution Ruff and Larsen (1990) observed for male femoral cross-sectional shape during the contact period, which they interpreted as evidence that certain males were recruited by the Spanish for long distance travel.

Simply postulating a *potential* genetic difference between groups does not by itself create a strong argument for an alternative, genetic explanation for the observed variation in cross-sectional properties. As discussed in chapter 5, Ruff and colleagues (Ruff et al. 1984) have suggested that variation, particularly localized variation (as

¹⁵ Gene frequency differences between the preagricultural and agricultural precontact populations could exist (Ruff et al. 1984). The time frame involved encompasses 40 or more generations. It is unclear whether the preagricultural group, which included burials from a period of over 1000 – 3000 years (2200BC – AD1150, with most post-dating AD500) (Ruff and Larsen 1990; Ruff et al. 1984), demonstrated any significant within-group variation over time.

opposed to systemic skeletal variation), in long bone cortical cross-sectional geometry is more likely the result of differences in mechanical loading than other factors such as genetics or nutrition. The argument for an alternative, genetic explanation is strengthened by evidence for genetic loci involved in producing normal skeletal variation in long bone structure, including cross-sectional geometry. The argument would be further strengthened by evidence that the genetic effects could be site-specific. Therefore, an important question, within the context of this dissertation, and in response to claims that only mechanical loading results in localized differences in structure, is this: can genetic differences produce localized versus systemic effects? While there are no definitive answers, preliminary evidence suggests it is reasonable to hypothesize that genetics could produce localized variations in skeletal structure through at least three different pathways (adapted from Volkman et al. 2003): 1) By direct local control over growth, modeling, and remodeling activities during development, resulting in regional geometric size and shape differences among the different long bones of the skeleton, which persist into adulthood. 2) By indirect effects on local geometry through a primary effect on muscle strength, body shape, body mass, including distribution of lean and fat mass, or bone material properties. 3) By altering the sensitivity of bone to its mechanical environment, which could amplify or attenuate local mechanical stimuli. This could produce a regional pattern of cross-sectional geometric variation, which would appear to be due to differential mechanical loading vis-à-vis physical activity.

Skeletal biologists have long acknowledged the potential role of heredity in contributing to bone architecture (e.g., Wolff 1892). In 1968 Enlow wrote, “genetic predisposition must be included in any complete account of the composite, diverse factors that can contribute to bone morphology, growth, and differentiation.... Until the

dilemma of the local control mechanism itself is resolved, possible contribution by all such factors [including genetics] must necessarily be considered and taken into account, since the actual extent of their individual roles is not now known” (p. 810). Enlow’s remarks are as applicable today as they were thirty-five years ago, as evidenced by van der Meulen and Huiskes’ (2002: 411) recent comment, “The challenge lies in disentangling environmental modulation and genetic predisposition in the skeleton.... Successfully distinguishing adaptation from genetic programming of cell metabolism will be a great mechanobiological feat.” With numerous recent breakthroughs in molecular genetics and genetic engineering techniques (Young and Dieudonné 2001; Young and Xu 2001), this feat may yet be accomplished.

Studies (Amblard et al. 2003; Beamer et al. 2001; Volkman et al. 2003) estimate that the heritability of bone mineral density (BMD) is between fifty and ninety percent. Heritability is the proportion of variance in a phenotypic trait that is accounted for by genetic variance. In other words, somewhere between 50-90% of normal variation in BMD is genetically determined. The strong genetic component of BMD was found to be largely independent of lean muscle mass and muscle strength, which are other factors strongly associated with BMD (Arden and Spector 1997). Other researchers (e.g., Yershov et al. 2001) have reported that as much as 50-70% of bone strength is inherited. Moreover, studies have shown genetic effects on bone mass, geometry, and mechanical properties.

A survey of recent volumes of the Journal of Bone and Mineral Research reveals that the genetic basis of skeletal properties is the subject of much on-going research. There is a growing awareness of the genetic complexity of long bone cortical geometry, and it is becoming clear that there are numerous genetic loci involved in producing

normal variation in skeletal structure and strength. Among these are loci involved in the regulation of the skeletal response to mechanical loading, as alluded to by Martin et al. (1998) above, and predicted by Frost (1986). Furthermore, there are often significant environment:gene interactions involved in phenotypic expression, whereby external environmental factors, such as mechanical loading, modify gene expression (Toma et al. 1997; Young and Dieudonné 2001). Environmentally responsive genes are involved in the biological processes of mechanosensation (the sensing of mechanical signals) and mechanotransduction (the processes involved in converting the mechanical signal into a cellular response). Therefore, genetic differences at both the individual and population levels could alter both mechanosensitivity and the efficiency of the adaptive processes (Nomura and Takano-Yamamoto 2000; Robling and Turner 2002; Volkman et al. 2003).

Genetic effects on bone structure in animals

A series of experiments involving two inbred breeds (strains) of mice designated C3H and B6 have revealed several apparently genetic-related differences in the response of bone to mechanical loading (Akhter et al. 1998; Amblard et al. 2003; Kodama et al. 2000; Pederson et al. 1999; Robling and Turner 2002). The C3H and B6 breeds differ with respect to bone density, exhibiting high density and low density, respectively (Akhter et al. 1998; Shultz et al. 2003). A study of bone accumulation in early postnatal, pubertal, and post-pubertal C3H and B6 mice (Richman et al. 2001) has demonstrated that the greater BMD of the C3H mice is apparent by 7 days of age. The mice do not differ in body size or weight and have similar external bone dimensions (Kodama et al. 2000). However, they exhibit breed-dependent differences in bone mass and cross-sectional geometry (Akhter et al. 1998; Kodama et al. 2000; Richman et al. 2001; Turner et al.

2000). Both total area and medullary area of lower limb bones are greater in the B6 mice, while cortical area is similar between the two, resulting in thinner cortices in the B6 mice. This explains the observed lower bone density in the B6 mice, but this structural arrangement also results in higher second moments of area, hence greater bending rigidity. Turner et al. (2000) report higher femoral bending strength in C3H mice due to their more mineralized and thicker cortices. Interestingly, these authors report that there was no difference in strength between B6 and C3H mice in their lumbar vertebrae. Within each breed, males exhibit thicker cortical bone than females (Richman et al. 2001). The high bone mass of C3H mice has been attributed to a reduction in bone cellular activity, while the low bone mass of B6 mice is a result of greater bone cell activity (i.e., higher levels of bone resorption and formation) (Amblard et al. 2003).

Several studies have identified differences between B6 and C3H in their response to mechanical loading and unloading prior to and after skeletal maturity (i.e., 16-weeks of age). Akhter et al. (1998) tested the effects of *in vivo* mechanical loading using a four-point bending device applied to the tibia of 16-week-old mice. Bending induced greater bone formation on both periosteal and endosteal surfaces in B6 mice but produced little periosteal bone formation and no endocortical response in the C3H mice prompting the authors to propose that the B6 mice are more sensitive to loading than the C3H mice. The authors suggested that the genes that regulate the adaptive response might differ from those that control peak bone density.

A study by Kodama et al. (2000) suggests a bone-specific, localized difference in response to identical mechanical loading between these two genetically distinct strains. A four-week jumping exercise regimen, begun when the mice were 9-weeks-old, produced an increase in tibial, but *not femoral*, dry weight in B6 mice. The jumping exercise

produced periosteal bone formation in the tibiae of B6 mice, but had no effect on the endocortical surface or medullary area in either strain. Kodama et al. (2000) attribute the differences in response to mechanical loading as a decreased sensitivity in the C3H mice. A study by Robling and Turner (2002) support this view. These authors performed mechanical loading experiments using the ulna, and observed that, unlike the tibia and femur for which the B6 mice exhibit a greater total cross-sectional area, the midshaft ulna of the C3H mice exhibited the larger total area. Thus, there seem to be bone specific differences in strength and geometry between these genetically distinct strains.

A study of 9-week-old C3H female mice (Pederson et al. 1999) revealed a load magnitude-dependent periosteal woven bone response in tibiae subjected to bending. Significant increases were observed in the loaded compared to the unloaded tibiae for total area, medullary area, and second moment of area. Interestingly, endocortical formation was opposite that of periosteal, with the nonloaded tibiae showing increased lamellar bone formation, resulting in a decreased medullary area. The behavior of the endocortical surface in the C3H strain is different from other animal models, which the authors interpret as suggesting “potential differences in the genetic control of bone adaptation” (Pederson et al. 1999).

The bones of B6 and C3H strains also respond differently to unloading (i.e., disuse). Kodama et al. (2000) report that immobilization by sciatic neurectomy led to a greater bone loss in B6 mice. Relative to the C3H mice, the tibiae of B6 mice showed an increase in endosteal bone resorption, and a decrease in bone formation as would be expected in disuse. Amblard et al. (2003) obtained similar results in an unloading experiment employing tail-suspension in 16-week-old B6 and C3H mice. Following 3 weeks of immobilization, B6 mice showed significant cancellous bone loss from the distal

femur due to thinning of the trabeculae, while the C3H mice did not. In contrast to the interpretation of Kodama et al. (2000) and Robling and Turner (2002), these authors do not interpret this as reduced sensitivity to unloading in C3H mice. Based on the presence of biochemical markers of bone activity in both strains, Amblard et al. (2003: 567) instead proposed that, “C3H mice...constitute a unique model in which genetic background overwhelmed the usual effects of reduced biomechanical usage in bone.” They conclude that their “results strongly suggested that susceptibility to bone loss is a genetically determined trait” (ibid: 567).

Findings by Turner et al. (2001b) suggest that inbred strains of rats also provide models with which to study the effects of genetics on skeletal structure and strength. Based on their evaluation of skeletal variability, these authors propose site-specific control of properties involved in skeletal strength, implying that, “no single gene regulates skeletal fragility at all sites” (ibid: 1532). Taken together these experiments on inbred strains of mice and rats suggest the possibility that individual or group differences in BMD, bone mass, and cortical bone geometry may be due to genetic differences. Furthermore, differences in the biological responses to mechanical loading and unloading may also have a genetic basis, and perhaps more significant in the context of this dissertation, genetic differences in adaptive response can potentially result in site-specific, localized skeletal effects.

Identifying the genes

Quantitative traits, such as body size, obesity, bone mineral density, and bone cortical geometry, are known as complex traits, controlled by multiple genetic loci, i.e., they are polygenic (Reis 2003; Robling and Turner 2002; Shultz et al. 2003; Volkman et

al. 2003). Complex traits are often analyzed using quantitative trait locus (QTL) analyses of inbred mice strains (Drake et al. 2001). In QTL analysis two strains with distinct phenotypic differences are crossed and successive generations are screened for the frequency of recombination between the phenotype under study and available markers. A statistically significant association of the phenotypic trait of interest with a series of markers at the same chromosomal locus indicates that at least one gene affecting the trait is likely to be physically linked with those markers, and therefore found at that locus.

Researchers have created a number of inbred strains of mice in order to estimate the heritability of skeletal phenotypes. QTL analysis of these strains is a first step towards identifying specific genes involved. Turner et al. (2001a) evaluated the heritability of “factors associated with bone strength” (e.g., volumetric BMD, cortical geometry, and microstructure) in femora and lumbar vertebrae from inbred strains of mice representing the progeny of crosses between B6 and C3H strains. Results of this study suggested site-specific regulation of bone strength by polymorphic genes. Findings of Yershov et al. (2001) and Klein et al. (2002) are similar. Both groups identified several chromosomal loci linked with skeletal properties associated with bone strength, including diaphyseal diameter and second moments of area.

Using a genetically heterogeneous mouse population derived from the progeny of crosses involving four inbred strains, including B6 and C3H, Volkman et al. (2003) detected significant associations between 14 genetic markers located on 13 different chromosomes and a number of geometric traits of the femur, including cortical area, cortical thickness and second moments of area. The authors found that the genetic markers accounted for only 8.2-21.7% of the observed variance in the geometric traits studied, but added that, “some of the variance could be attributed to genes whose effects

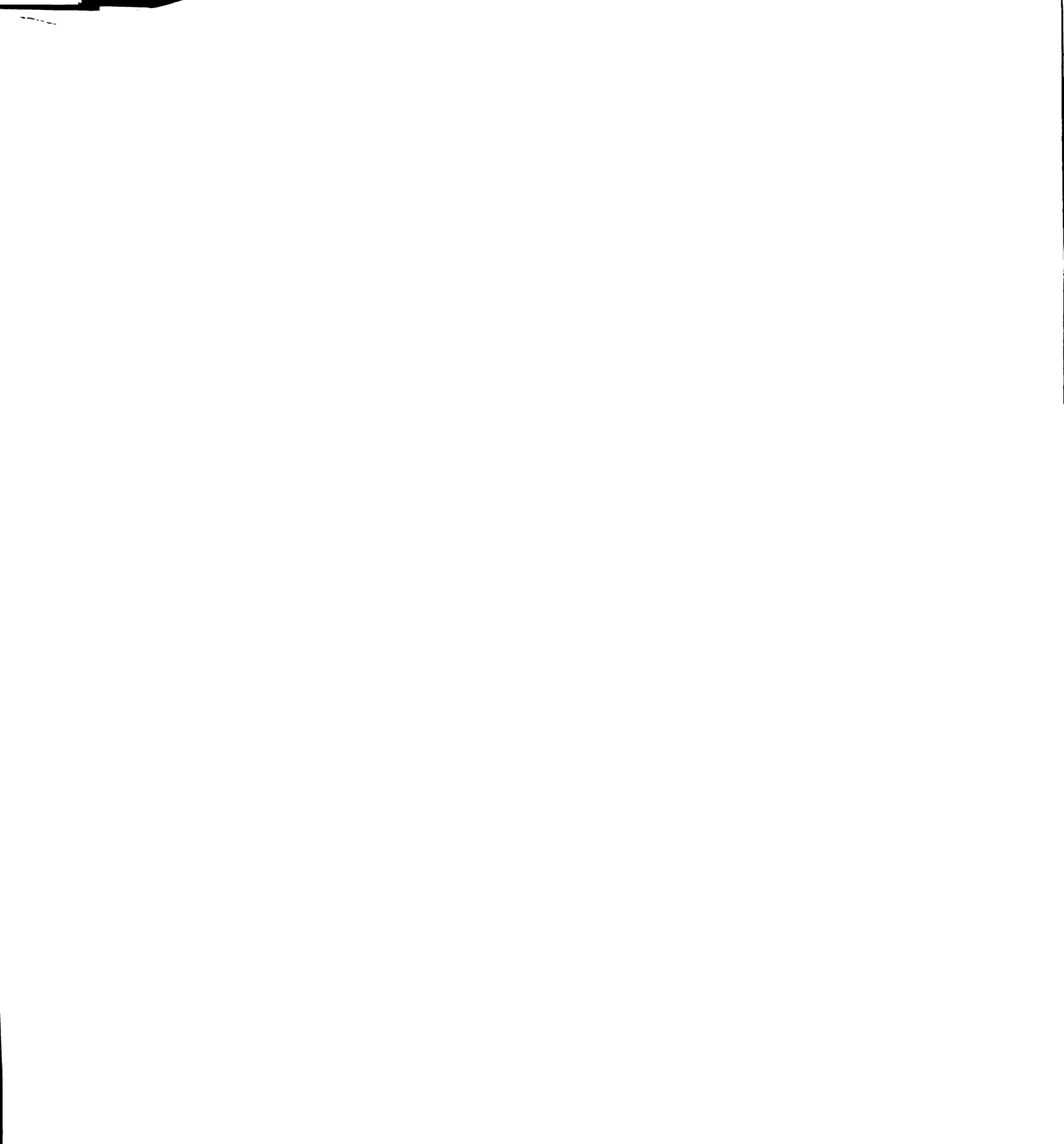
are too small to be measured in our survey” (ibid: 1502). In their discussion, the authors noted that in addition to genetics, bone geometry is influenced by a variety of factors including body weight, muscle strength, disease status, and nutritional levels. They pointed out that many of these other “nongenetic” factors, may in fact, “ultimately be regulated by genetic controls” (ibid: 1503). Volkman et al. concluded that, “the genetic control of cortical geometry is complex and that femoral size and shape may be influenced by different, although overlapping, groups of polymorphic loci” (ibid: 1502). However, they were also careful to state that their study could not distinguish among three possible mechanisms by which the genes could affect femoral geometry: 1) by directly influencing bone size and shape, 2) by indirectly influencing bone size and shape through primary affects on body weight, muscle strength, or activity level, or 3) by altering bone mechanosensitivity. The authors performed additional statistical analyses of covariance to account for variation in body weight, and were able to suggest that it was unlikely that the geometric effects of the genetic markers were due to a primary effect on body weight.

Drake et al. (2001) have identified seven chromosomal loci linked to femoral structural traits, including femoral length and multiple measurements of femoral width (e.g., width of the femoral head, intertrochanteric, mid-diaphyseal, and supracondylar regions). Three loci, located on different chromosomes, were found to be associated with the femoral width measures, suggesting the potential for site-specific effects within the femur. According to the authors, none of the identified loci controlling femoral width “influenced body weight or length, excluding these mechanical-related factors as mechanisms for these local effects” (ibid: 516).

Interestingly, one chromosomal locus involved in controlling femur width includes

genes for parathyroid hormone (PTH) and calcitonin. Hagino et al. (2001) found that PTH and mechanical loading have a synergistic effect on bone formation in rat tibiae, and suggest that, “PTH sensitizes bone cells to mechanical stimulation” (p. 249). In accordance with Frost’s mechanostat hypothesis, the authors explained their observations: “hormones act to adjust the skeletal ‘set point’ that regulates bone mass relative to customarily encountered loading stimuli. The observations in the present study indicate that intermittent PTH administration lowers this ‘set point’, such that identical loading stimuli are perceived as more intense...” (ibid: 249). The combined findings of Hagino et al. and Drake et al. are strongly suggestive that genetic control of hormone levels provides another source of normal variation in cross-sectional geometry. Perhaps not surprisingly, the two inbred strains of mice (C3H and B6) discussed earlier also exhibited differences in serum PTH levels (Akhter et al. 1998).

The creation of transgenic mice has allowed the study of gene function in vivo (Young and Xu 2001). As described by Young and Xu (2001) there are “two major types of transgenic mice”: 1) “Conventional” transgenic mice “overexpress” normal genes resulting in a gain in function. Conventional transgenic mice are created by inserting selected gene sequences into the host genome. The inserted genes can be transmitted to offspring thereby allowing the creation of strains of transgenic mice through selective breeding. 2) “Knockout” mice are created by “targeted deletions of specific genes” resulting in a loss of function for a single specific gene of interest. Subsequent breeding produces lineages that are homozygous for the normal allele, heterozygous, or homozygous for the mutant allele, i.e., “total knockouts.” Scientists are also working on creating “designer mice,” in which genes that have lethal consequences when “knocked out” at conception, can be knocked out at a specific developmental stage or within a



specific location, tissue, or cell type (Young and Xu 2001). These authors conclude with the optimistic proclamation, “anything is possible in creating transgenic mice; one is limited only by well-characterized genes and promoters and the proper analyses” (ibid: 4-13).

Both conventional transgenic and knockout mice strains have demonstrated numerous abnormal skeletal phenotypes, including structural anomalies (Young and Xu 2001). Conventional transgenic mice have revealed alterations in the activities of osteoblasts and osteoclasts leading to conditions of either too much or too little bone (e.g., Gardiner et al. 1998; van der Meulen and Huiskes 2002). Use of knockout mice has shown that, “different strains of mice vary in bone mass as a result of intrinsic differences in rates of bone formation” (Young and Xu 2001: 4-6). For example, in response to hind limb immobilization by way of tail suspension, osteopontin-knockout mice experienced no significant resorption of trabeculae in the tibial metaphysis, and no suppression of bone formation relative to wild-type mice (Ishijima et al. 2001). Osteopontin (OPN) is a noncollagenous bone protein that may facilitate attachment of osteoclasts during bone resorption (Ishijima et al. 2001). OPN is expressed in bone cells in response to mechanical loading, and is hypothesized to play a role in loading-induced changes in bone metabolism. Loss of OPN does not affect normal bone development or phenotype; however, loss of OPN function appears to reduce sensitivity to factors that would normally lead to bone loss during conditions of disuse. The authors conclude, “OPN may be involved in the mechanisms sensing the physical force that induces the increase in the number of osteoclasts...OPN directly modulates bone formation in response to mechanical stress” (ibid: 403).

Genetics effects on bone structure in humans

Studies of BMD in humans have revealed a high heritability with involvement of several chromosomes (Duncan et al. 2003). Evidence suggests that inheritance of BMD is site and gender specific (ibid). As discussed by Babij et al. (2003), QTL analysis has identified a specific region of chromosome 11 as the potential location of genes that “may contribute to the normal variation in BMD seen in the general population” (ibid: 961). The low-density lipoprotein 5 gene (LRP5 gene) is one candidate gene for which a variety of mutations are associated with variation in bone mass in humans (Babij et al. 2003; Koller et al. 1998). A particular mutation of this gene has already been identified in certain families with higher than normal bone mass, and Duncan et al. (2003) propose that LRP5 allelic variants play a role in normal population variation. A study of transgenic mice with this LRP5 allelic variant suggests the high bone mass results from increased numbers of active osteoblasts (Babij et al. 2003).

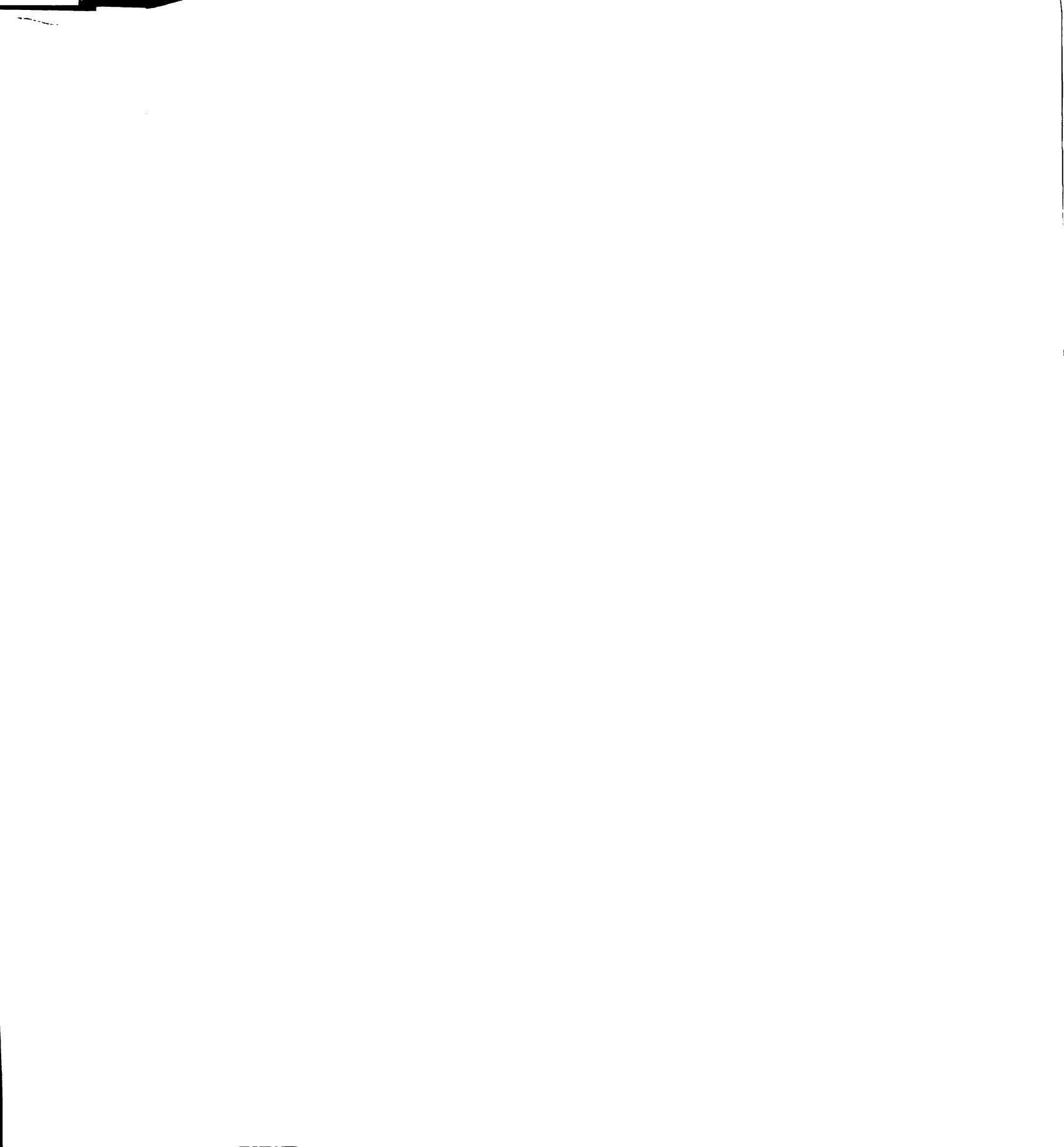
Researchers have also studied the genetics of proximal femoral structural variation in humans (Koller et al. 2001, 2003; Slemenda et al. 1996). Slemenda et al. (1996) focused on bone mineral content and geometric properties of the femoral neck, and found evidence for genetic influence on all properties except femoral neck length. Koller et al. (2001, 2003) have performed linkage analyses on large samples of sister-pairs to elucidate the location of potential genes involved in controlling femur neck axis length, midfemur width, femur head width, and pelvic axis length. In their first study of 309 sister-pairs they found linkage of structural variables with human chromosomes 3, 4, 5, 7, 9, 17, and 19. Their second, larger study (437 sister-pairs) confirmed linkage with chromosomes 3, 7, and 19, and identified a new locus on chromosome 8. Probable genes controlling femoral shaft width were restricted to chromosome 3 in this analysis, whereas

femoral head width showed significant linkage with regions on chromosomes 3, 7, and 8.

In summary, results of genetic analyses are not definitive. Moreover, it remains to be seen whether the effects seen in inbred and genetically engineered mice strains can be extrapolated to naturally occurring genetic variation in humans. Nevertheless, preliminary results are suggestive that genetics versus mechanical loading arguments need to be revisited. Cortical bone geometry is considered a complex trait under polygenic control. In mice, genes controlling cortical geometry are located on numerous chromosomes, and many traits appear to segregate independently. Studies on humans have also shown genetic control of femoral structure with associations at several loci located on different chromosomes. Furthermore, genes do not have to directly control the final form of the bone to play an important role in producing that form. Polymorphic genes can influence whether and to what degree exercise and mechanical loading will affect bone geometry. Genes can modify metabolism, developmental timing, and sensitivity to mechanical stimuli—all of which can subsequently affect cross-sectional geometry and produce localized (intraskkeletal) variation that might mask or mimic changes in external loading regimes. It is safe to conclude that, as an alternative explanation for group variation in cross-sectional geometry, genetic differences should not be ruled out a priori.

Nutrition effects on cross-sectional geometry

Nutritional status resulting from diet is thought to: 1) affect all bones equally (Bridges 1991), 2) affect stature via its effects on longitudinal growth (Larsen 1981; Ruff et al. 1984), 3) possibly affect the amount of bone (e.g., CA), but not its distribution (Ruff et al. 1984), and 4) affect bone quality (e.g., material properties) (Barondess 1998; Brock and



Ruff 1988). Dietary factors are not thought to influence the distribution of bone tissue, or have differential effects throughout the skeleton. Consequently, skeletally localized cross-sectional geometric variation is thought to primarily reflect differences in mechanical loading patterns (Ruff et al. 1984).

There are very few studies of the effects of nutrition on cross-sectional geometry. However, diet is considered a confounding variable in studies of functional adaptation (Forwood and Burr 1993), and is a risk factor for osteoporosis (Hernandez et al. 2000; Jiang et al. 1997; Wohl et al. 2000). Both macronutrients (protein and dietary fats) and micronutrients (vitamins A, C, and D, and minerals, e.g., calcium, magnesium, copper, iron) play important roles in skeletal physiology (Frost et al. 1998; Li et al. 1999). Dietary factors are likely to have indirect effects on skeletal structure, including cross-sectional geometry, through primary effects on body weight, muscle mass and strength, fat mass, hormone levels (e.g., estrogen, insulin, leptin, parathyroid hormone, calcitonin, glucocorticoids), and bone metabolism (Frost 1985, 1997c; Jiang et al. 1997; Li and Mühlbauer 1999; Orwoll 1992; Zernicke et al. 1995). In addition, the effects of diet, particularly nutritional deficiencies, on bone growth and maturation are likely to have consequences for cross-sectional geometry (Frost 1985). Significant changes in bone geometry are associated with growth spurts, developmental timing, and puberty, which can all be affected by nutritional status. Mosley and Lanyon (2002) have suggested that the response of bone to loading in growing animals is related to the rate of growth, i.e., increased physical activity during growth spurts is likely to produce a larger response. Therefore, factors that affect rate of growth, such as protein deficiency (Orwoll 1992), can affect the acquisition and potentially the distribution of bone mass.

Nutrition can affect body mass including the absolute amount, proportion, and

distribution of lean and fat mass. In a recent review article, Reid (2002) discussed the relationship among soft tissue mass, bone turnover, and bone mass. Studies have demonstrated a positive correlation between bone mineral density (BMD) and body mass. Although increased mechanical loading associated with increased body mass is a likely contributor to this relationship, the correlation exists for both weight-bearing (e.g., vertebrae, femora, and tibiae) and non-weight-bearing (e.g., radius and the metacarpals) skeletal elements (Reid 2002). Reid “cautiously” concluded “that both fat and lean masses impact positively on bone mass, although their *relative impacts may vary across populations*” (ibid: 550, emphasis added). Studies also point to male-female differences in the effects of soft tissue mass on bone mass, with the effects on males less significant (ibid). If true, this factor could potentially contribute to group differences in sexual dimorphism of cross-sectional geometry. Reid proposed that hormones “associated with nutrition are prime candidates” for the association between fat mass (adipose tissue) and bone mass citing “biochemical evidence that both food intake and weight change can impact on bone turnover” (p. 550). For example, fasting has been found to decrease osteoblast activity, hence reduce bone formation. Furthermore, insulin is osteogenic. Hyperinsulinemic conditions, such as obesity and type 2-diabetes, are associated with high bone density. Additionally, positive effects on bone density are linked to hormones secreted by adipocytes, such as estrogen and leptin.

While it is probable that the primary effects of nutrition are systemic, as has been asserted by Ruff and colleagues (Ruff et al. 1984) and Bridges (1989), diet and nutrition can affect bone metabolism, which could have more localized or site-specific effects by altering mechanical loading thresholds (e.g., MES setpoints). Researchers attempting to more accurately model bone adaptation (Hernandez et al. 2000) suggest that it is

important to consider metabolic factors (nutrition, drugs, disease state) because “metabolic factors can change the mechanical setpoint thereby modulating the mechanobiologic response” (p. 237). The authors suggest that metabolic factors, like mechanical factors, can influence relative osteoclast and osteoblast activity during remodeling. Resultant changes in bone density “caused by changes in activation frequency or bone balance ratio” can “[modify] the mechanical daily stress stimulus *even when the mechanical loading history remains constant*” (ibid: 242, emphasis added). By altering setpoints, nutrition and other metabolic factors would be capable of producing localized effects on cortical cross-sectional geometry, which could mimic the site-specific adaptations produced by differences in mechanical loading.

There is some experimental evidence to support this hypothesis. The magnitude of dietary effects on bone geometry and mechanical properties is often site-specific (Jiang et al. 1997; Parsons et al. 1997; Wohl et al. 2000). Bone-to-bone differences have been noted between axial and appendicular elements, as well as between bones of the lower limb. Li et al. (1990) and Zernicke et al. (1995) studied dietary effects on postnatal bone development in young rats. Li et al. (1990) fed young, rapidly growing rats a high fat-sucrose (HFS) diet for 10 weeks. Compared with the tibiae of control rats, fed a low fat, complex-carbohydrate diet, the tibiae of rats on the HFS diet exhibited no significant difference in cortical geometry, however, structural strength was lower. In contrast, the metatarsus bone exhibited increased cross-sectional area and reduced material properties, but no difference in strength. These authors concluded that, “adaptation of a bone to changes in diet can be bone specific” (ibid: 312). After a two-year experimental period Zernicke et al. (1995) found that compared with controls, rats on the HFS diet exhibited reduced architectural and mechanical properties of the sixth lumbar vertebra and femoral

neck. Changes to the femoral neck primarily involved a significant reduction in the percentage of cortical bone, which was most likely responsible for its reduced mechanical properties. The negative effects on the mechanical properties of these bones occurred in spite of significantly increased body mass in the rats on the HFS diet.

Many bone biologists recognize that nutrition plays a role in bone metabolism (Frost 1985; Frost et al. 1998; Rubin et al. 1990). Rubin et al. (1990) have stated that the physiology of functional adaptation is “(inextricably linked) to the organism’s systemic milieu” (p. 52). Furthermore, according to these authors, “Nutritional disorders...alter not only the manner in which the tissue responds, but also attenuate the ability of the tissue to react to osteogenic stimuli” (ibid: 48). They propose that the interaction of calcium deficiency and decreased loading is synergistic. Moreover, during systemic calcium deficiency, dynamic loading is insufficient to maintain bone mass. Specker and colleagues (Specker and Binkley 2003; Specker et al. 1999) evaluated the combined effects of calcium intake and increased gross motor activity in young children and infants. Decreased calcium intake during periods of rapid growth led to lower rates of bone accretion in infants engaged in gross motor activity as opposed to fine motor activity (Specker et al. 1999). Furthermore, Specker and Binkley (2003) found a significant interaction between calcium supplementation and physical activity with regard to cortical thickness and cortical area in young children; increased calcium intake resulted in greater tibial periosteal and endosteal dimensions. Iuliano-Burns et al. (2003) detected an interaction effect of physical activity and calcium intake on bone mass in prepubertal girls. Importantly, the effects were site-specific (i.e., they were not uniform throughout the skeletal sites evaluated). Among the exercise-loaded lower limb bones, a significant calcium-activity interaction effect was detected for the femur, but not the tibia-fibula site.

In addition, it was found that exercise, but not calcium supplementation, produced an increase in bone mass at the tibia-fibula site. However, at the non-loaded upper limb sites (humerus, and ulna-radius) there was no effect of exercise on bone mass; however, calcium supplementation alone resulted in increased bone mass. The researchers did not specifically evaluate the effects of calcium supplementation, if any, on cross-sectional geometry. Because of the interaction between mechanical loading and nutrition, Rubin et al. (1990: 48) proposed that, “exercise regimes prescribed for one given population may not be as effective (or generate completely different results) in another.”

Studies of the effects of specific nutrients and foods have demonstrated effects on bone metabolism, including altered bone cell activity, with consequent alterations in bone distribution. In a review of the effects of dietary protein on bone metabolism, Orwoll (1992) noted that protein deficiency not only leads to decreased longitudinal skeletal growth in children, but can also increase endosteal resorption. There are no reported negative effects of protein deficiency on periosteal growth. A similar observation was made for aged male rats; Bourrin et al. (2000) observed an association between dietary protein deficiency and decreased cortical bone BMD, cross-sectional geometry, and bone strength. In this study, a low protein diet led to an increased medullary area and decreased cortical thickness. The authors suggest that reduced dietary protein impairs bone formation creating a more negative bone balance on endocortical and trabecular surfaces undergoing remodeling. In addition, certain types of foods are associated with differences in bone cell activity. Consumption of a diet including onions, vegetables, leafy salad greens, and herbs was found to inhibit bone resorption and increase bone mass in rats (Mühlbauer et al. 2002). Sun et al. (2003) reported that the addition of fish oil to the diet might reduce bone loss through inhibition of osteoclast generation and activation.

Another potential indirect effect of nutrition on cross-sectional geometry is via its effect on bone material properties. For example, calcium deficiency decreases bone mineralization, which reduces the elastic modulus of bone tissue. Ruff has maintained that, “the primary response of long bone diaphyses to changes in mechanical loading during life is through alterations in diaphyseal geometry or structure, rather than material properties” (Ruff 2000b: 72). While most research on bone adaptation bears this out, it is also true that nonmechanical factors, including nutrition, affect material properties with potential secondary effects on geometry. It has been demonstrated that bone can compensate for reduced material properties by increasing cross-sectional area or changing cross-sectional shape (Akhter et al. 1999; Burr et al. 1981; Currey 2001, 2002; Li et al. 1990; Martin and Atkinson 1977; van der Meulen et al. 2001). As stated by Currey (2001: 19-13), “the architecture of the bones is rather precisely adapted to the loads placed on them *and* to the mechanical properties of the bone material.” A compensatory response may have been what occurred in the metatarsus bone of the rats fed the high-fat high-sucrose diet (Li et al. 1990); in this bone, the structural properties were similar to those of the control group in spite of reduced material properties, most likely because of the significant increase in cross-sectional area. Although this study showed no compensatory geometric response in the tibia, which also exhibited reduced material properties, it is possible that the time frame of the experiment (10 weeks) was not sufficient for such a response to occur in this bone.

Summary

A review of Wolff's Law reveals that its derivation is flawed, and it is largely unsupported. The contemporary usage of the phrase “Wolff's Law” is generally

understood to be synonymous with the concept of functional adaptation. However, functional adaptation may be an “umbrella term” for a variety of skeletal responses, not all of which are directly related to mechanical stimuli resulting from physical activity.

Research over the past century, and particularly within the last two decades, has increased the knowledge base regarding the biological processes involved in adaptation of the skeleton to mechanical loading; however, many facts remain unknown. To a large extent, the apparent variability in the results of functional adaptation experiments in both animals and humans, and among individuals of different ages may reflect the general lack of understanding of how and under what circumstances functional adaptation occurs, as well as the difficulty distinguishing the structural changes that result from adaptation to physical activity from those attributable to methodological variation and confounding factors. Furthermore, the adaptive response of bone is not always what would be predicted based on structural optimization hypotheses such as Wolff's Law, e.g., bone added to the endocortical rather than periosteal surface. Because of the age-dependent effects of activity on cross-sectional geometry, as well as the site-specific effects of non-mechanical factors such as genetics and nutrition, neither the level nor the type of activity need be different for two groups to exhibit localized differences in their long bone geometry. Therefore, while functional adaptation of bone may be a widely accepted phenomenon, the concept does not provide a coherent theory upon which to base interpretations of physical activity patterns from cross-sectional geometry.

CHAPTER 7—CONCLUSION

...plausibility alone does not prove an explanation is correct

Harold M. Frost

This dissertation presented a reconstruction and critical analysis of the argument underlying the following tenets in bioarchaeology: 1) Group variation in cross-sectional geometry reflects group differences in levels and types of physical activity. 2) Group variation in degree of sexual dimorphism of cross-sectional geometry is attributable to differences in sexual division of labor. 3) Group variation in degree of upper limb bilateral asymmetry reflects differential usage (e.g., unilateral versus bilateral activities).

It was shown in chapter 5 that the overall argument can be evaluated as two, separate but linked inductive arguments: 1) A 'theoretical' argument, the purpose of which is to establish a causal relationship between physical activity and cross-sectional geometric variation, and 2) An 'empirical' argument, which uses the conclusion of the theoretical argument to justify drawing specific behavioral conclusions from biomechanical data.

Evaluation of the theoretical argument revealed the following flaws: 1) Wolff's Law has little evidentiary value as the primary theoretical premise in the argument. 2) The argument does not make use of all available relevant evidence regarding the ability of bone to functionally adapt to its mechanical environment. The review of non-anthropological literature on skeletal mechanobiology presented in chapter 6 suggests that the concept of functional adaptation is not an adequate substitute for Wolff's Law as the primary theoretical premise. 3) The argument has failed to make a case for the ability to rule out or adequately control for a number of confounding variables, which could provide alternative explanations for the biomechanical findings. Consequently, the

conclusion of the theoretical argument, that group variation in cross-sectional geometry reflects differences in physical activity, does not follow from the premises.

The empirical argument is fundamentally flawed because its main premise, the conclusion of the theoretical argument, is not strongly supported. Furthermore, the second premise of the empirical argument, namely that group differences in cross-sectional geometric properties exist, is also frequently not supported by the specific findings of individual studies. Results of statistical analyses often failed to reject the null hypothesis for many of the cross-sectional properties ascertained (i.e., few statistically significant differences were found). In such instances, regardless of the strength of the theoretical argument, conclusions regarding group differences in physical activity are spurious.

Review of functional adaptation: a summary

The theoretical argument reconstructed in this dissertation represents a plausible line of reasoning relating cross-sectional geometry to physical activity patterns. In other words, if none of the premises was false, and there was no additional relevant evidence that could be brought to bear, then the conclusion of the argument would be at least as plausible as the least plausible premise. However, the review of the literature on skeletal biology and mechanobiology, presented in chapter 6, revealed a number of “facts,” which bear directly on the argument. This review revealed that what is missing from the argument put forth by Ruff and colleagues are all the caveats and contrary or equivocal evidence, which have the effect of rendering behavioral inferences based on long bone diaphyseal cross-sectional geometry *less* tenable. The following is a summary of this information.

Wolff's Law is cited as providing the primary theoretical premise linking cross-sectional geometry to behavior. However, Wolff's Law is based on a faulty argument from analogy, which compares two things that appear similar, but which actually differ in fundamental ways. Thus, the conclusion of the analogy proposed by Wolff, is not supported. Wolff's Law is not a scientific law, and is not generally accepted by skeletal biologists. The mathematical rules of bone construction predicted to exist by Wolff have not been identified. Therefore, current usage of the phrase "Wolff's Law" is suggested to be synonymous with the concept of functional adaptation, which asserts that bone has the ability to adapt to its mechanical environment via a cell-based biological feedback system.

Experimental studies of functional adaptation have revealed numerous problems that limit one's ability to directly link long bone cross-sectional geometry with physical activity. The biological processes involved in skeletal adaptation to mechanical stimuli are still poorly understood; indeed, the relevant characteristic of the mechanical stimulus responsible for initiating adaptation has not yet been identified. Research suggests the likely existence of a range of physical activities, which would not initiate an adaptive response. Furthermore, the actual in vivo loadings experienced by human bones during physical activity are mostly unknown, and cannot be accurately predicted using theoretical models or results of in vitro experiments. Consequently, association of levels or types of physical activities to specific patterns of cross-sectional variation is based on conjecture, not scientific evidence.

Experimental studies of functional adaptation in animals and humans have generated highly variable and equivocal results, which suggest the possibility that functional adaptation may be an "umbrella term" for a variety of effects, some systemic, and some due to local mechanical factors. The most dramatic examples of "functional

adaptation” have come from studies of extreme mechanical loading imposed by osteotomy and external loading devices in animals, or from studies of professional athletes who commenced their training while they were still young and growing (i.e., prior to skeletal maturity). It is questionable whether these extreme conditions apply to archaeological populations. To assume that they do presumes the very thing biomechanical studies are supposed to demonstrate.

Furthermore, studies of animals and humans have shown that the effects of mechanical usage are both age-dependent and envelope-specific. Prior to skeletal maturity, and particularly around puberty, bone seems to respond to mechanical loading by altering its geometry through modeling drifts on both periosteal and endocortical envelopes. In contrast, it is suggested that mature bone responds to mechanical loading by: 1) conserving existing bone mass via reduction of remodeling-dependent bone loss on endocortical and trabecular surfaces, or 2) increasing volumetric bone mineral density, a material property. Functional adaptation in mature bone does not seem to have primary effects on cross-sectional geometry.

Moderate to moderately intense exercise in animals and adolescent humans tends to primarily produce changes in endosteal dimensions, either through a reduction in bone loss or an increase in bone formation. Statistically significant changes to periosteal dimensions of lower limb bones are reported less frequently. However, changes in periosteal dimensions are necessary to affect the external shape of bones, e.g., the relative circularity of the femoral midshaft. Studies of extreme differential loading of upper limb in long-term players of racquet sports show significant bilateral asymmetry in cross-sectional properties, including cortical area and second moments of area. Changes usually involve both periosteal and endocortical envelopes, particularly in younger

players. Degree of bilateral asymmetry is indirectly correlated with starting age. Therefore, while on an individual level, bilateral asymmetry is at least partly due to differential mechanical loading, differences in degree of bilateral asymmetry among individuals or groups of individuals can be due to differences in the timing of the activity relative to puberty.

An additional difficulty in interpreting behavior from long bone cross-sectional geometry is the finding of counterintuitive effects of activity on these properties. Studies have demonstrated that reductions in cross-sectional geometric properties can occur following intense activity in both young animals and older women. Prolonged, intense activity may have detrimental effects on immature bone, including decreases in cross-sectional second moments of area. Furthermore, after skeletal maturity, increased mechanical usage may inhibit remodeling-dependent bone loss on the endocortical surface, and may therefore forestall the compensatory increase in periosteal diameter, thus resulting in relatively lower cross-sectional area and second moments of area. In contrast, reduced mechanical loading after skeletal maturity increases bone loss on the endocortical envelope, which could produce a compensatory increase in periosteal dimensions similar to, but potentially greater than that observed with age-related bone loss. These scenarios contradict standard interpretations of cross-sectional geometry, i.e., greater values indicate more activity and lower values indicate less activity. One common finding of most of the experimental research reviewed above is that activity-related functional adaptation appears to be both site- and bone-specific. Therefore, the bone location selected for analysis can affect the results, and therefore the conclusions of the study.

The review of the literature presented in chapter 6 also demonstrated that long bone cross-sectional geometry is influenced by non-mechanical factors. Consequently, just as Ruff and colleagues have presented a plausible line of reasoning linking group variation in cross-sectional geometry to physical activity, one could construct an equally plausible line of reasoning linking the same variation to group differences in genetics and diet. Genetic research provides substantial preliminary evidence that bone mass and cross-sectional geometry are complex traits influenced by multiple, polymorphic genes. Genes involved in controlling cross-sectional geometry have been identified in both mice and humans. Furthermore, genes controlling bone architecture appear to have site- and bone-specific effects. Genetic differences between groups could produce localized variations in skeletal structure by: 1) direct local control of bone cell activities during development, resulting in regional geometric size and shape differences among the different long bones of the skeleton, which persist into adulthood, 2) indirect effects on local geometry through primary effects on muscle mass and strength, body shape, body mass, or bone material properties, or 3) altering the sensitivity of bone to its mechanical environment, which could amplify or attenuate local mechanical stimuli. Studies have also demonstrated dietary effects, including site- and bone-specific effects, on cross-sectional geometric properties. The effects of nutrition on cross-sectional geometry are most likely due to primary effects on body mass and body composition, bone metabolism, and bone material properties.

Determining physical activity from cross-sectional geometry: an analogy

To better illustrate why the concept of functional adaptation is an inadequate theoretical foundation for relating physical activity to bone geometry, an analogy to the

relationship between exposure to sunlight and skin pigmentation is presented. In this analogy, amount of time spent in the sun is analogous to level of physical activity, and skin pigmentation, a measurable quantity, is analogous to cross-sectional geometry. The theory that skin “functionally adapts” to sunlight exposure by becoming more deeply pigmented is supported by scientific evidence. The underlying physiological mechanism involves the production of melanin (pigmentation molecules) by melanocytes, a type of skin cell, in response to ultraviolet (UV) radiation.

If a group of individuals with known biological characteristics (e.g., age, sex, nutrition, health status, hormonal status, melanocyte density, degree of initial skin coloration, genetic constitution, and ancestry) is exposed to a known amount of UV radiation for a specified amount of time, a researcher could probably predict the group’s changes in skin pigmentation. On the other hand, given skin samples from a population with *unknown* characteristics (apart from age and sex), could a researcher estimate the amount of time the individuals had spent in the sun? Given two such sample groups, one significantly darker than the other, would it be reasonable to conclude that the darker-skin group spent more time in the sun than the lighter-skin group?

Certainly, a plausible argument could be made, but it would be flawed in much the same way as the reconstructed argument presented in this dissertation. For example, there could be genetic differences between the groups. Perhaps genetic differences made the darker-skin group more sensitive to UV radiation resulting in ontogenetic differences in phenotype. Alternatively, the difference in skin pigmentation between the groups could reflect a difference in ancestry (phenotypic differences that are phylogenetic in origin). Perhaps the lighter-skin group used sunscreen, yet spent more time in the sun than the darker-skin group, or maybe the darker-skin group used a sunless tanning lotion,

but actually spent little time in the sun. Perhaps the skin samples were from regions of the body differentially exposed to sunlight, due to different types of apparel worn by two groups. There could be physiological differences between the groups, such as hormone levels, biochemical differences related to nutrition, or differences in melanocyte function.

Obviously there are numerous confounding factors that could potentially contribute to the observed difference in skin pigmentation between the two groups, and it would be impossible, without knowledge of the confounding factors, to determine with any degree of confidence which group spent more time in the sun, in spite of the fact that there is a known causal relationship between skin pigment and UV exposure. This admittedly imperfect analogy illustrates a significant obstacle to using cross-sectional properties to infer behavior, even given the general acceptance of the concept of functional adaptation.

Conclusion

The biomechanical model developed by Ruff and colleagues is based on the assumption that, because long bone cross-sectional geometric properties predict whole bone mechanical behavior (e.g., rigidity and strength) under known or approximated loading conditions (e.g., compression, tension, bending, and torsion), there is a direct causal relationship between the development of these properties and the mechanical forces they are capable of withstanding. The existence of the causal link is predicated on Wolff's Law. Users of this model suggest that by knowing a bone's cross-sectional geometry, one can infer the past mechanical loading patterns (i.e., the loading history), and sometimes the specific physical activities, which gave rise to that geometry.

In contrast, this dissertation has suggested two counterarguments to the current

biomechanical model, which are based on a review of the non-anthropological skeletal biology and mechanobiology literature spanning the past two decades. The first counterargument is that research on functional adaptation has shown the relationship between mechanical loading and bone architecture to be extremely complex and variable, for reasons that are not yet understood. Currently, there is no generally accepted model of functional adaptation that would allow predictions about behavior to be made from long bone cross-sectional geometry. Such predictions would entail answers to the following questions: 1) How do biological processes bring about site-specific adaptation to mechanical loads? 2) How are these processes affected by systemic factors? 3) What is the “goal” of adaptation, i.e., is it to minimize some strain-related variable, or maximize the predictability of the strain? 4) What are the circumstances under which an adaptive response is initiated, e.g., what is the nature of the stimulus? 5) What is the relationship between a specific activity and the resultant patterns of strain-related variables generated in the specific bone in question?

The second counterargument made in this dissertation is that the results of biomechanical analyses of archaeological skeletal remains can be potentially attributed to one or more of the following alternative explanations: 1) Group differences in the starting age of a particular physical activity, 2) Group differences in genes that directly or indirectly affect cross-sectional geometry, or 3) Group differences in metabolic factors (nutrition, health) that directly or indirectly affect cross-sectional geometry. It has also been suggested that there is no reason to assume *a priori* that all observed group variation in cross-sectional geometry is due to a single cause (physical activity *or* genetics *or* nutrition). Whole bone mechanical properties, estimated by cross-sectional geometry, reflect the cumulative effects of all these factors, but mechanical effects may have primacy

in one group, while nutritional factors or genetic differences may predominate in another. In fact, the “cause” of variation could be bone-specific, with some bones predominantly affected by their mechanical environment, others by nutrition, etc. Furthermore, there is no reason to assume that there are not complex, antagonistic or synergistic relationships among the various factors; certain combinations may be “good” for building bone, others may be particularly detrimental. In addition, observed group differences could be due to mechanical loading, but not as predicted. Increased mechanical loading can produce bones with reduced cross-sectional properties, and reduced mechanical loading can produce bones with larger cross-sectional properties, particularly second moments of area. In other words, the nature of the relationship between physical activity and bone structure could also differ among populations. Consequently, the conclusion of the theoretical argument presented in chapter 5 must be rejected, and one must therefore reject the three predictions of the biomechanical model: 1) Group variation in cross-sectional geometry reflects group differences in levels and types of physical activity. 2) Group variation in degree of sexual dimorphism of cross-sectional geometry is attributable to differences in sexual division of labor. 3) Group variation in degree of upper limb bilateral asymmetry reflects differential usage of the upper limb.

In conclusion, the strong likelihood that bones are capable of functionally adapting to their mechanical environment in no way implies that temporal or geographic differences in bone structure can be used to make reliable inferences (i.e., not purely conjectural) about changes in behavior, beyond what is already inferred from other, more traditional sources of evidence, e.g., archaeology. This is because there is ample preliminary evidence to suggest that long bone cross-sectional geometry is affected by a large number of factors, many of which cannot be known, and virtually none of which

can be adequately controlled for, particularly in archaeological contexts. It is hypothetically possible for two populations performing identical activities, in the same manner, and at the same frequency to demonstrate differences in their cross-sectional geometry, including skeletally localized differences, because of group differences unrelated to physical activity. If there is a story told by the skeleton, there is currently no “Rosetta stone” to decipher its language.

Suggestions for future bioarchaeological research

The method of critical analysis used in this dissertation, namely the application of techniques of critical reasoning in the analysis of a complex scientific argument, is a valuable tool for reflexive evaluation in research and academia. Reconstruction of the arguments used to support the fundamental tenets of any discipline can reveal critical logical flaws, weaknesses in the underlying theory, as well as dogmatic adherence to poorly supported assumptions and premises. As an interdisciplinary science, biological anthropology frequently borrows theories, models, and data from non-anthropological fields, such as medicine, epidemiology, evolutionary biology, biomechanics, physics, chemistry, ecology, etc. This is true for a number of related sub-disciplines of biological anthropology, including paleoanthropology, paleopathology, forensic anthropology, and bioarchaeology. Consequently, it is incumbent upon bioarchaeologists to revise their methods over time by continuing to review the non-anthropological literature and keeping abreast of changes and controversies in the relevant disciplines. The occasional reevaluation of core constructs can prevent the propagation of untenable conclusions, and reveal potential alternative explanations for research findings. For example, the critical analysis presented in this dissertation has shown that unquestioning acceptance of a

century old theory, namely Wolff's Law, resulted in scientifically unsupportable tenets regarding the primacy of the relationship between long bone cross-sectional geometry and physical activity.

In spite of the problems with the biomechanical model used to infer behavior, studies of past populations have contributed valuable data regarding group variation in cross-sectional geometric properties, and this type of research should continue.

Bioarchaeological research can *generate hypotheses*, which could potentially be tested under experimental (i.e., controlled) or quasi-experimental conditions in living populations. For example, based on the tentative conclusions of the bioarchaeological studies reviewed in chapter 3, one could construct a single-blind experiment in which the anthropologist-researcher would attempt to "predict" the behaviors of living people from cross-sectional geometric properties ascertained through radiological methods, such as peripheral quantitative computed tomography (pQCT). The experiment would entail recruiting individuals who had participated in known categories and levels of activity (e.g., running, swimming, walking, cycling, skiing, or sedentary activities). Many biological characteristics of the participants could be controlled for: body shape, body size, body mass, age, sex, ancestry, nutritional and health status, age of commencement of activity, length of time involved in the activity, etc. The researcher analyzing the cross-sectional geometric data would be unaware of which activity each individual was involved in, and would assign the individuals to predetermined groups based purely on their long bone cross-sectional geometry. Statistical analyses could be performed to determine if the resultant group assignments were better than what would be predicted by chance. Such an experiment could potentially assess the efficacy of using cross-sectional geometry to infer behavior under controlled conditions, in a population with known biological

characteristics and known behaviors. If under these conditions, predictive capability of the method was acceptably high, its use in archaeological populations might be justified.

However, being historical scientists, bioarchaeologists are in the particularly difficult position of never “knowing” whether their conclusions are correct (Waldron 2001) with the same level of confidence as scientists who are able to design replicable, controlled, prospective experiments in an attempt to *falsify* erroneous hypotheses. This is a problematic issue when studying archaeological populations, where numerous, untestable assumptions must be made (e.g., “the osteological paradox” Wood 1992), and points to the problems inherent in both developing *and* testing a model, such as the biomechanical model for inferring behavior, on archaeological skeletal collections. In bioarchaeology, research findings, *even those that are statistically significant*, should always be interpreted conservatively and cautiously. Bioarchaeologists must be especially cognizant of and explicit about the potential alternative explanations for their data, and must often accept that, at the present time, there may be no way to distinguish among them, i.e., no means of “differential diagnosis.” Tony Waldron (2001: 143) provided a positive view of this potential frustration that should serve as an inspiration to all bioarchaeologists: “There is no shame in not knowing and only when we admit that we don’t know, will we try to think up means by which we may be able to know in the future.”

Even if long bone cross-sectional geometry cannot be used to reconstruct the behavior of past populations (at this time or maybe ever), the continued study of group variation in geometric properties using archaeologically-derived skeletal collections can potentially contribute to an understanding of both skeletal biology and human adaptation. There is a great deal more to be learned about cross-sectional geometric variation, and it is important to do so. Understanding as much as possible about the

ctiology of “strong” bones is a paramount goal of osteoporosis research. The distribution of bone tissue within the cortex of a long bone is a primary determinant of whole bone mechanical behavior, including strength. However, future research must be conducted without the constraints of an activity-only perspective. For example, as discussed in this dissertation, it has been hypothesized that cross-sectional geometry and longitudinal bone curvature are architectural features of bone that control the direction of bending, thereby making loads more predictable (Bertram and Biewener 1988). It could therefore be informative to determine whether the relationship between cross-sectional geometry and bone curvature varies among different populations. In addition, Ohman and Lovejoy (2001) have suggested that the shape of the adult diaphyseal shaft is primarily a consequence of the shape of the developing physis. It would therefore be informative to study diaphyseal shape variation among prehistoric populations and its relationship to the shape of the growth plate.

The most striking result of all the bioarchaeological studies reviewed in this dissertation was the finding that so many of the differences among populations were non-significant. This, by itself, is interesting. Given the vast potential for differences in physical behaviors, nutrition, health, genetics, etc, one would *expect* there to be greater differences in long bone structure. It could be useful to reexamine the significant findings to see if a pattern emerges. Perhaps a meta-analysis of existing data would be informative. Because cross-sectional shape and cortical area are *generally similar* among widely divergent groups, it may be reasonable to ask: what is so different between the groups where significant differences in cross-sectional geometry are observed? It is possible that creative use of multivariate statistical methods could point future researchers in a new direction.

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