

## II

# It is Not Carved in Bone

## Development and Plasticity of the Aged Skeleton

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### Introduction

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The human skeleton is popularly characterized as a dry and inert material that acts primarily as a soft tissue scaffold and protector of the vital body. While the skeleton does indeed perform these roles dutifully, it is also a dynamic and living tissue that has the ability to grow, mold, and maintain itself over the life course. The dynamic nature of the skeleton resides in its basic biology – at its cellular level, bone tissue is able to respond to the physiological and biomechanical needs of the body. The fact that the skeleton can respond and adapt to the biological and cultural environment in which it resides forms the basis for the central tenets of bioarchaeology. The well-established biocultural approach in bioarchaeology emphasizes the importance of the interaction between humans and their larger social, cultural, and physical environments, recognizing that the skeleton is influenced by environmental variables (see Zuckerman and Armelagos this volume). This approach has been the cornerstone of bioarchaeology in investigating patterns of skeletal health and disease, and is particularly utilized in studies that seek to sort out the influences that may have affected bone aging and bone loss in past populations (Agarwal 2008; Agarwal and Grynpas 1996).

However, even within biocultural models, environmental and cultural effects on skeletal maintenance and bone loss are often viewed as only potential modifiers that are still tightly constrained by biology. For example, while lifestyle factors such as reproductive behavior (parity and/or breastfeeding) (Mays et al. 2006; Poulsen

et al. 2001; Turner-Walker et al. 2001) or diet (Martin 1981; Martin and Armelagos 1979, 1985) are considered to influence bone maintenance in the past, they are still only considered as isolated agents that exacerbate inevitable biological (hormonal or genetic) changes to bone loss. As such, indications of bone loss or osteoporosis in the past are generally regarded to reflect the irreversible course of menopause and aging (Macho et al. 2005; Mays 1996; Mays et al. 1998). Further, bioarchaeologists often hypothesize about the influence of environmental factors on bone morphology over a short period of time during the life of an individual(s) or during a distinct phase of the life cycle (typically the adult and post-menopause phase). This is in part due to the nature of archaeological samples that obviously do not permit looking at changes in morphology longitudinally over a given individual's life cycle. Skeletal samples permit only cross-sectional studies of bone loss and fragility and generally attract focus on individuals with unusual pathology, rather than lend themselves to life course approaches in the study of bone health. The result, however, is that while bone loss and fragility fracture have been widely reported and studied in bioarchaeology, they are regarded primarily as the result of skeletal degeneration that reflects senescence of the body (Agarwal 2008). In bioarchaeological studies the focus on bone maintenance and loss is at the end of the life cycle, particularly in females. The a priori assumption is that it is inevitable that women will lose bone and have more fragile skeletons (Agarwal 2008).

Where does this assumption about bone loss and maintenance in bioarchaeology come from, and is it really inevitable that women age into fragile skeletons? The assumption that bone maintenance and bone loss is tied entirely to menopause and old age is well perpetuated in popular biomedicine. While the level of sex steroids plays a vital role in bone maintenance across the life cycle in both sexes, particularly in old age, it is increasingly well known in clinical and epidemiological studies that there are many other biological and environmental influences on bone health that can change the outcome of bone loss and fragility. For example, biomechanical influences (physical activity), reproductive behaviors, diet and nutrition are just some of the factors now known to interact and potentially change the course of adult bone maintenance and loss (Sowers and Galuska 1993; Stevenson et al. 1989; Ward et al. 1995). While bioarchaeologists have strived to investigate environmental influences on bone health in past populations, it seems they are tied to the notion that the biological influences of menopause and senescence are primary. This may be related in part to the fact that bioarchaeological approaches to bone maintenance and aging are also shaped within, and struggle against, the larger framework of biological anthropology that gives primacy to biology and the gene in explaining bone morphology. In these developmental biological frameworks the morphology of the skeleton is seen as limited by regulatory mechanisms and a set range of possible responses in human tissue (Lovejoy et al. 2003). While insights from development biology have been revolutionary in our analyses of the evolution of the human primate skeleton, they should not overshadow the importance of postnatal influences on bone morphology during growth and aging. These nonpredetermined influences do not act in isolation, and often act synergistically with one another and with biological (genetic, hormonal) influences on bone morphology. More importantly, these influences act throughout the life course, beginning even in utero, to shape the skeleton (e.g. Cooper et al. 2006). The adult-aged skeleton, in both its

strength and frailty, is the creation of life history and trajectories taken during growth.

In this chapter we examine alternative perspectives on human morphology as the result of development and plasticity, and the specific history of these theories as applied to understanding growth and aging of the human skeleton. We then review some of the applications of developmental approaches in bioarchaeological studies of bone maintenance and loss in past populations. Finally, we explore the new directions in the study of maintenance and aging of the skeleton that are possible with the integration of ideas in both biological and social theory on the role of ontogenetic process and embodied lived experience in the construction of skeletal form.

## **Theoretical Understandings of Development and Plasticity**

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### *Definitions*

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Plasticity, growth, and development are essential concepts in anthropology as they form the foundation to understanding patterns of phenotypic variability. However, their meaning and use varies within the biological and archaeological literature. *Growth* is generally understood to reflect stepwise or progressive changes in size and morphology during the development of an individual (Scheuer and Black 2004). Growth is generally correlated with chronological age, however, differences in rates of growth are still common between individuals due to divergent life-history trajectories (Scheuer and Black 2004). As such, while growth in size is correlated with biological maturity, they diverge enough so that “individuals reach developmental milestones, or biological ages, along the maturity continuum at different chronological ages” (Scheuer and Black 2004:4). Growth can then be seen as the enlargement and differentiation of tissues advancing with chronological age, while development comprises the pathways of biological milestones along the life course, including for example embryogenesis and puberty. Rates of growth and timing of developmental changes differ between individuals, leading to considerable debate over normal growth and development trajectories (Bogin 1999; Worthman and Kuzara 2005), and the health (Clark et al. 1986; Klaus and Tam 2009; Mays et al. 2008), adaptation (Lasker 1969; Lewis 2007; Roberts 1995; Schell 1995; Worthman and Kuzara 2005) and evolutionary significance of growth rates (Ellison 2005; Nelson and Thompson 1999; Ruff et al. 1994). The complexity and debate on the role of growth and development is exciting as it allows us to explore how gene–environment relationships operate to produce a wide range of phenotypes at different stages of the life course.

*Plasticity* is a broader utilized concept that is much more difficult to grasp as there are inconsistencies in how the term is used to describe its role in the formation of the adult phenotype through developmental processes. Most of the confusion with the concept of plasticity resides in its conceptual link to adaptation (Lasker 1969; Roberts 1995; Schell 1995). Prior to the 1950s and 1960s the working definition of plasticity was simply an understanding that human morphology appeared to be malleable during growth and development (Bogin 1995). Yet

this vague conceptualization of plasticity was purely descriptive and was not amenable to hypothesis testing. Dobzhansky (1957) was one of the first to view plasticity as a form of adaptation. In this view natural selection produces genotypes “that permit their possessors to adjust themselves to a spectrum of environments by homeostatic modification of the phenotype” (Roberts 1995:2). Lasker (1976) is considered to have truly merged plasticity with adaptation and in the process redefine the plasticity concept altogether. Lasker’s (1969) view of plasticity operated within three modes of adaptation. The first of these was natural selection itself, where the selection of genotypes directly influences the genetic spectrum of the population (Roberts 1995). The second form of adaptive plasticity, acclimatization, is a nonpermanent physiological and behavioral response that adapts an individual to the immediate environment (Roberts 1995). The third and most important mode (in this discussion) is developmental or ontogenetic adaptation (Roberts 1995). The key features of ontogenetic modifications are that plastic responses operate through growth and development, and that the changes are not reversible and also not heritable (Schell 1995). Numerous others have studied variation in human phenotypes through the lens of plasticity and while they all have their own definition of plasticity, adaptation and a concern with trade-offs are central to most (see Worthman and Kuzara 2005 for an excellent review). While a concern for adaptation has been helpful in trying to fit plasticity into the framework of modern Darwinian thought (e.g. McDade et al. 2008), we believe a broadening of focus would offer a better understanding of the process of plasticity and its role in development.

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### *Plasticity in development*

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Understanding plasticity in the developmental context beyond a strictly adaptationist model has been put forward by a number of researchers (Cooper et al. 2006; Lewontin 2001; Oyama 2000a; Sofaer 2006; Worthman and Kuzara 2005) often using terms such as developmental plasticity, developmental systems theory or approach (DST/DSA), and developmental dynamics. All of these approaches share a general concern with the developmental processes in embryogenesis, fetal growth, early postnatal growth, and adolescence that give rise to variation through plastic responses. While these areas of research have much common ground, there are differences in nomenclature and conceptual divides about the limits of plasticity. Plasticity studies working primarily in fetal development (e.g. Hallgrímsson et al. 2002) are conceptualized differently than research that extends plasticity to include infancy, childhood, and adolescence (Fausto-Sterling 2005). In essence, this mirrors the larger tension between the two most prominent approaches, evolutionary developmental biology (EDB) and developmental systems theory (DST) (Table 11.1). Both are concerned with understanding how plasticity operates rather than solely looking at the products and evaluating their adaptive fitness and both give an alternative to reductionist approaches. However, the EDB perspective is limited primarily to embryology/fetal development and is less concerned with postbirth plastic and developmental changes (Hallgrímsson et al. 2002; Robert et al. 2001). Further, in EDB genes are given primacy during development as they are seen to supply the material needs of development (Robert et al. 2001); genes can exist without

**Table 11.1** Developmental approaches in biological and social theory that can be used specifically in the study of bone morphology, maintenance, and loss

<i>Theoretical approach</i>	<i>Primary concepts and interests</i>	<i>Some key references</i>
Evolutionary developmental biology (EDB)	– Interested in the evolution of development (ontogeny)– Focus is on the role of development (particularly embryonic/fetal) in phenotypic evolution– Interested in how developmental modifications effect evolutionary change– The gene is given primacy, and considered the primary unit of inheritance	Hall 1999, 2005 Roberts et al. 2001 Lovejoy et al. 2003
Developmental systems theory (DST)	– Development is considered contingent on context (broadly environment) and can extend well into postnatal growth– Interaction of developmental influences is key (and can include molecular, cellular, organismal, ecological, social, and biogeographical influences)– Developmental information is thought to reside in the interaction of genes and environment– Inheritance is extended to include non-gene factors such as ecological and social resources, and other epigenetic processes	Oyama 2000a, 2000b Oyama et al. 2001 Gray, 1992, 2001 Griffiths and Gray 1994
Life course approaches	– Emphasize the role of physical and social exposures during gestation, childhood, adolescence, young adulthood, and later adult life (e.g., the development and physical manifestations of disease risk)– Focus is on biological, social, and psychosocial pathways that operate over the life course, as well as across generations	Bengston and Allen 1993 Ben-Shlomo and Kuh 2002 Elder et al. 2003 Fausto-Sterling 2005
Embodiment	– As a concept, can be taken to refer to how beings literally biologically incorporate the world in which they exist, including social and ecological variables– Emphasizes the process of creation or transformation of beings and organisms over time as the product engagement with their world	Ingold 1998 Joyce 2005 Krieger 2001, 2009 Sofaer 2006

development, but there is no development without genes. EDB does emphasize the importance of variation, with the goal to observe patterns of variability to better understand underlying developmental systems that can ultimately be linked to how development intersects with natural selection and evolutionary change (Hallgrímsson et al. 2002). Perhaps most importantly, variation in developmental processes is studied in the context of conservation of form, where “individual variation is minimal and seemingly constrained” (Robert et al. 2001:959). The developmental systems theory (DST) or approach diverges from EDB in many ways. DST contrasts with EDB in that variation is primarily focused on in terms of plasticity rather than conservation of form. Developmental information is believed to reside neither in the genes nor the environment, but rather in the interaction of the two (Robert et al., 2001). As such, genes have no primacy in the DST model and plasticity is the defining feature of the development system that is defined as the interplay of all influences on development including the “molecular, cellular, organismal, ecological, social, and biogeographical” (Robert et al. 2001:954). As such development is seen to extend well into postnatal growth (Robert et al. 2001; Worthman and Kuzara 2005). There are a number of examples of this, including neurological growth (Kamm et al. 1990) and immune functions (Worthman 1995).

Common ground between EDB and DST approaches may be argued in the study of epigenetics (Robert et al. 2001). While there are many definitions of epigenetics, it can be broadly defined as the study of genetic and nongenetic interactions on development (Hallgrímsson et al. 2002; Robert et al. 2001). Robert et al. (2001) suggest that epigenetics may be the “practice of what DST proposes,” a place for scientific testing of DST. While both DST and EDB approaches advocate for both acceptance of genetic and nongenetic influence during developmental processes, DST goes one step further in suggesting that inheritance is also epigenetic (Robert et al. 2001). For DST theorists again the gene is not the only player in inheritance, and instead inheritance is extended to include ecological, social resources, or other interactants that influence development (Oyama 2000b). As such, epigenetic processes are seen as heritable and are constructed and reconstructed during each life cycle.

Whether nongenetic influences are heritable, particularly in skeletal morphology, continues to remain uncertain. This uncertainty, of whether or not nongenetic forces significantly shape postnatal and intergenerational skeletal morphology, has limited the theoretical explorations of plasticity and development in bioarchaeology. Moreover, EDB paradigms in biological anthropology essentially greatly minimize the role of environmental and postnatal influence on the plasticity of morphology (Lovejoy et al. 2003). The focus for studies of bone plasticity in biological anthropology has thus been primarily on evolutionary and adaptive change, rather than postnatal development over the life course. One thing that does unite all studies of plasticity is a desire to understand the roots of phenotypic diversity. Pritchard (1995) has noted that plastic responses in a given tissue or tissues not only react to external stimuli but also generate their own effects in other tissues. In this context plasticity during development is a generative force in shaping the body as much as a reactive one and should then be viewed as more than a side-note or byproduct of discussions on gene–environment dynamics. Furthermore it is unclear how plasticity can successfully modulate and affect existing genetic networks in widely

different developmental and environmental landscapes rather than relying on the evolution of novel genes or genetic pathways to produce phenotypic variation (Young and Badyaev 2007). The interdependency between genes, development, and environment are at the heart of the matter in understanding plasticity. We now turn to discuss how theoretical approaches to plasticity and development been applied in anthropology and bioarchaeology, and specifically how developmental approaches can help us better understand bone maintenance and aging across the life course.

### **The Concept of Plasticity in Skeletal Growth and Morphology**

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The formal history of the study of plasticity in anthropology can arguably be said to have begun with Boas (1912), although earlier studies do exist that similarly observed generational changes in growth in migrants (Baxter 1875; Bowditch 1879). Through detailed anthropometric measurements of body size and shape Boas (1912) observed that the children of new immigrants (of European descent) to the United States displayed different growth patterns than their parents. Moreover, he noted the change was accentuated with each generation (Boas 1912). In an earlier work commissioned by the U.S. Congress, Boas (1910:53) remarked “we must speak of plasticity (as opposed to permanence) of types.” Boas’s 1912 article was pivotal as it presented solid evidence that environmental changes, which included changing cultural milieus, could produce changes in body size and shape in future generations. Growth and adult stature was seen as more than the sole product of genetic heritability. Boas’s work was supported by Shapiro’s (1939) often-cited growth study of Japanese children in Japan and Hawaii that also showed significant differences in growth, stature, and development, which he also attributed to environmental triggers. Numerous migrant studies have repeatedly confirmed the correlation of changing environments to changes in growth and development (Baker et al. 1986; Bogin 1995; Bogin and Rios 2003; Goldstein 1943; Kasl and Berkman 1983; Lasker and Evans 1961). Plasticity studies were not limited to migrants only; plasticity was studied within cultures as well to account for the fact that those who stayed behind might have differed in some important ways (e.g. Mascie-Taylor 1984). Plasticity was also studied through observation of so-called natural experiments (Roberts 1995). For example, Roberts and Bainbridge (1963) observed a population of three Nilotic tribes living in the same environment but with slight cultural differences. Somatotype and anthropometric measures demonstrated small but significant differences between the three tribes (Roberts 1977). Roberts (1977) concluded that these differences were environmentally based through ways of life and dietary differences in particular. Similar studies among Polynesian and other traditional cultures have observed similar results in cases of changing or differing socioeconomic conditions between two closely related migrant/sedante groups (Baker et al. 1986; Kasl and Berkman 1983).

Schell (1995) has argued that by 1954 with Kaplan’s review of migrant-sedante studies in *American Anthropologist* that plasticity was firmly established as a recognized phenomenon of growth and development. Research into plasticity has faced numerous challenges since Boas first set out to develop a new model for how phe-

notypes vary. A dominant challenge, as noted previously, has been defining the concept of plasticity itself. This appears to have become an interpretive problem only after Lasker (1969) permanently tied plasticity to adaptation. There is much we do not know about the adaptiveness or relative benefit of plastic modifications made during growth and development, in part because of the difficulty of interpreting growth patterns (Humphrey 2000; Lewis 2007; Saunders 2000; Schell 1995; Worthman and Kuzara 2005). Two general interpretations have been put forward in attempts to understand variation in growth and development. Both models address the issue of morphological variation and compare stress and health among and between cultures from an adaptationist perspective, but from very different theoretical positions. The first of these interpretations is the “medical model” common in public health policies, pediatrics, and nutritional science (Schell 1995). The medical model views growth as a reflection of health, and with this it literally becomes a measure of health and consequently, of adaptation (Schell 1995). Growth to the full extent of an individual’s genetic potential is interpreted as good health while slow or stunted growth signifies ill health (Schell 1995). The implicit assumption is that the body will always reach its full genetic potential if no boundaries are presented. Determining this with archaeological skeletons is difficult given that retarded growth and development may not show clear outward signs (Humphrey 2000). The opposing model is termed the human adaptability paradigm (HAP) (Schell 1995). The HAP views growth and development as the mechanism of plasticity (Schell 1995). In other words, “growth patterns can be a mode of adaptation” and in “this context growth is a means of achieving an adapted state rather than a result of that adaptation” (Schell 1995:223 emphasis in original). The problem here is that the modifications that reduce stress/strain can be seen as adaptive but they cannot be proven so in a strict sense (Bogin 1995; Schell 1995). Further, the medical and HAP models conflict because growth cannot be both a measure and a means of adaptation (Schell 1995). As such, the models are mutually exclusive. Clearly this poses a problem for which model to use in bioarchaeology. To some degree this may depend on what influences or stressors are being considered as causes for the observed plastic changes. Schell (1995) has offered that the medical model may be better suited to interpreting plasticity as a feature of human-made environmental changes, such as slums, where nutrition is poor and disease load high, while the HAP may be beneficial for interpreting plastic responses induced by the physical environment. However, it is unclear how to structure bioarchaeological research questions and analyses when typically both human-made and naturally occurring environmental factors are at play. While both these models have contributed significantly to studies of growth and development, neither works fully when applied to bioarchaeological analyses, particularly to the interpretation of patterns of bone maintenance and loss.

Considering development as a generative force (Oyama 2000a), rather than a “reading out” of genetic material during key periods of growth, may help us better understand how the human body and skeleton is shaped and reformed throughout life. Recent biomedical and epidemiological studies have specifically explored how plasticity during growth and development can influence aspects of lifelong bone health, such as bone mineral density and loss. For example, infant and adolescent growth spurts seem to be highly influential in defining bone quality and quantity



at later life stages (Cooper et al. 2001, 2006; Javaid and Cooper 2002; Javaid et al. 2006; Miller 2005). Peak bone mass (the maximal amount of bony tissue accrued during growth) is generally thought to be mostly inherited (Duncan et al. 2003), but Cooper et al. (2002:391) remark that “only a small proportion of the variation in individual bone mass” is accounted by genetic markers. Seeman (1999:91) has also noted that the contribution of heritability in bone health is not a constant proportion, and that statements claiming “80 percent of areal BMD (bone mineral density) is genetically determined leaving only 20 percent to modify” is flawed. Heritability is a complex, fluid measure based on a relationship between population and environment variance (Seeman 1999). As age, height, gender, and body composition vary, so do heritability measures of bone mass or density (Seeman 1999). Cooper et al. (2006) posit that environmental cues early in life interact with the genome to create the boundaries of growth and development for a given individual. It has been hypothesized that these types of developmental boundaries or trajectories may originate in expectation of future environmental conditions and serve as predictive adaptive responses (or PARS, Gluckman and Hanson 2005). For example, fetal programming by maternal under-nutrition is a risk factor for low birth weight (Cooper et al., 2002). Low birth weight is strongly correlated with lower levels of basal level growth hormones, even during adult life, placing the individual at risk for lower peak bone mass, reduced mineralization, and an elevated rate of bone loss later in life (Cooper et al. 2002; Dennison et al. 2005). Numerous epidemiological studies have shown that impaired fetal and childhood growth place individuals at risk for fragility fractures later in life (Cameron and Demerath, 2002; Cooper et al. 1995, 1997, 2001; Dennison et al. 2004; Dennison et al. 2005; Gale et al. 2001). These studies emphasize the dramatic role of environmental influences on phenotypic plasticity in early life, and more importantly underscore how this early exposure can change the trajectory of development and aging of skeletal morphology throughout life.

### **Studies of Plasticity in Bone Development and Maintenance in Bioarchaeology**

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The general concept of skeletal plasticity is fundamental in bioarchaeology, particularly in the study of temporal and spatial differences in skeletal morphology as related to influences such as nutrition, activity or disease (Bogin 1999; Hind and Burrows 2007; Knüssel 2000; Larsen 1999; Lewis and Gowland 2007; Lloyd and Cusatis 1999; Mcdade et al. 2008; Prentice et al. 2006; Rauch 2005; Ruff et al. 2006; Saggese et al. 2002; Schwartz et al. 2003; Skerry 2006). However, studies of plasticity in growth and development in past populations have largely followed approaches developed in studies of living human biology. Most notably, patterns of long bone growth in archaeological skeletal samples have been widely used as a proxy for comparing health and stress statuses between and among populations (Humphrey 2000; Kemkes-Grottenthaler 2005; Lewis 2007; Mays et al. 2008; Saunders 2000). In studies of bone maintenance and loss in bioarchaeology the focus has been primarily on the influence of nutrition and levels of physical activity in either encouraging, or protecting against, the onset of age- and sex-related bone

loss and fragility (Agarwal 2008; Agarwal and Glencross in press). There has been some study of the affect of early growth and development on the maintenance of the mature skeleton in archaeological samples. For example, the classic studies of bone loss in prehistoric Sudanese Nubia were some of the first studies to consider and compare bone growth and maintenance in both juvenile and adult skeletons. Armelagos et al. (1972) suggested that the significant cortical bone loss in the femur found in young-aged female Nubians, as compared to males, was likely due to early growth disturbance and stress as young adults during pregnancy and lactation. Similarly, a study of cortical bone growth maintenance in prehistoric juvenile Nubians from the Kulubnarti site found that while bone mineral content increases after birth, processes of modeling combined with likely periods of nutritional stress, cause a reduction in percent cortical area during early and late childhood (Van Gerven et al. 1985), although this study does not comment on the role of early bone maintenance on later femoral bone loss. Two recent studies have focused on the structural variation of trabecular bone during ontogeny. Kneissel et al. (1997) examined the ontogeny and aging patterns of vertebral trabecular bone in a juvenile and adult skeletal sample from Medieval Lower Egyptian Nubia. The authors found the largest bone trabecular volume during adolescence when the rod-like trabeculae of childhood begin to change to plate-like structures. In addition, age-related loss of trabecular structure was observed in adults, with changes occurring earlier than those seen in modern populations (Kneissel et al. 1997). Gosman and Ketcham (2009) also examined patterns of ontogeny in trabecular bone in their study of tibial bones from the prehistoric Ohio Valley, particularly noting changes in trabecular structure and connectivity from growth to skeletal maturity and with increasing ambulatory activities.

More recent studies have attempted to more directly correlate growth patterns and developmental stress, with variation in skeletal morphology and bone loss. For example, a study by Rewekant (2001) examined the correlation of adult cortical bone loss with indicators of growth disturbance (specifically compression of the skull base and vertebral stenosis) in two Polish medieval populations with differing socioeconomic status. Rewekant (2001) found greater adult age-related cortical bone loss in the metacarpal in the population that also showed greater disturbance of bone growth during childhood. Interestingly, lower sexual dimorphism in measurements of metacarpal cortical bone and skull base height were also found in the population that appeared to have suffered greater environmental stress during growth. This study suggests a relationship between the disturbance of growth and the achievement of peak bone mass, as well as the age- and sex-related patterns of bone loss later in life. Similarly, McEwan et al. (2005) examined the correlation of bone quantity in the radius to overall growth patterns and indicators of growth disturbances typically attributed to poor nutrition (specifically Harris lines, and cribra orbitalia) in juvenile skeletons in a medieval British sample. The authors found that while bone mineral density (BMD) was well correlated to overall growth, cortical index (a measure of total cortical bone) was not (McEwan et al. 2005). This again suggests that some aspects of bone maintenance such as the overall amount of cortical bone may be compromised during development under the influence of environmental (nutritional) stress with a lasting effect on cortical bone content and morphology well into adulthood (Mays 1999; McEwan et al. 2005).

There has also been focus on influences after childhood, into young adulthood that may play a significant role in later bone fragility. For example, several bioarchaeological studies within and between skeletal populations suggest that physical activity during adulthood can result in a conservation of bone quantity during life and offer protection against the affects of bone loss in old age (Ekenman et al. 1995; Lees et al. 1993). The opposite has also been noted, with observations of decline in bone quantity and strength in more sedentary agricultural populations as compared to physically active hunter-gatherer groups (Larsen 2003; Ruff et al. 1984; Ruff et al. 2006), although this observation is not universal as workloads were likely variable in agriculturalists depending on region and local terrain (Larsen 2003; Nelson et al. 2002). While it is known that bone tissue responds to mechanical loading, the biomedical literature is unclear on what type and level of physical activity or exercise is needed to affect bone mass and more importantly bone strength into adulthood. There may be an ideal “window of opportunity” for physical activity to contribute to the growth and robusticity of the skeleton during the acquisition of peak bone mass (Pearson and Lieberman 2004), but it seems likely that some high strain stress activity may still be effective at older ages (Rittweger 2006). Reproductive behavior is another factor that may influence the trajectory of bone maintenance and loss in older age. Several studies have suggested that young age females in the archaeological record show evidence of bone loss that is result of physiological stress on the skeleton due to pregnancy and/or breastfeeding (Martin and Armelagos 1979, 1985; Martin et al. 1985, 1984; Mays et al. 2006; Poulsen et al. 2001; Turner-Walker et al. 2001). However, it can be argued that the loss of bone in reproductive-age women in the past was transitory, and that bone loss during reproduction would have little or no affect on long-term bone fragility in women who would have survived to old age (Agarwal 2008; Agarwal and Grynepas 2009; Agarwal et al. 2004; Agarwal and Stuart-Macadam 2003). In fact, high parity and prolonged breastfeeding in some past populations would have provided women in the past with a very different hormonal milieu and steroid exposure that could have offered protection against the sudden postmenopausal drop of hormones experienced by modern women (Agarwal et al. 2004; Agarwal 2008; Weaver 1998).

All of these studies take the first step in exploring the role of development in bone morphology and maintenance, and emphasize the importance of earlier life experiences on the strength and fragility of the aged skeleton. While influences such as nutrition, physical activity, and reproduction are critical to understanding bone growth and maintenance, it is increasingly evident that what is really important is how these influences are played out over the life course, and the cumulative effect that they may have on the skeleton at the end of life.

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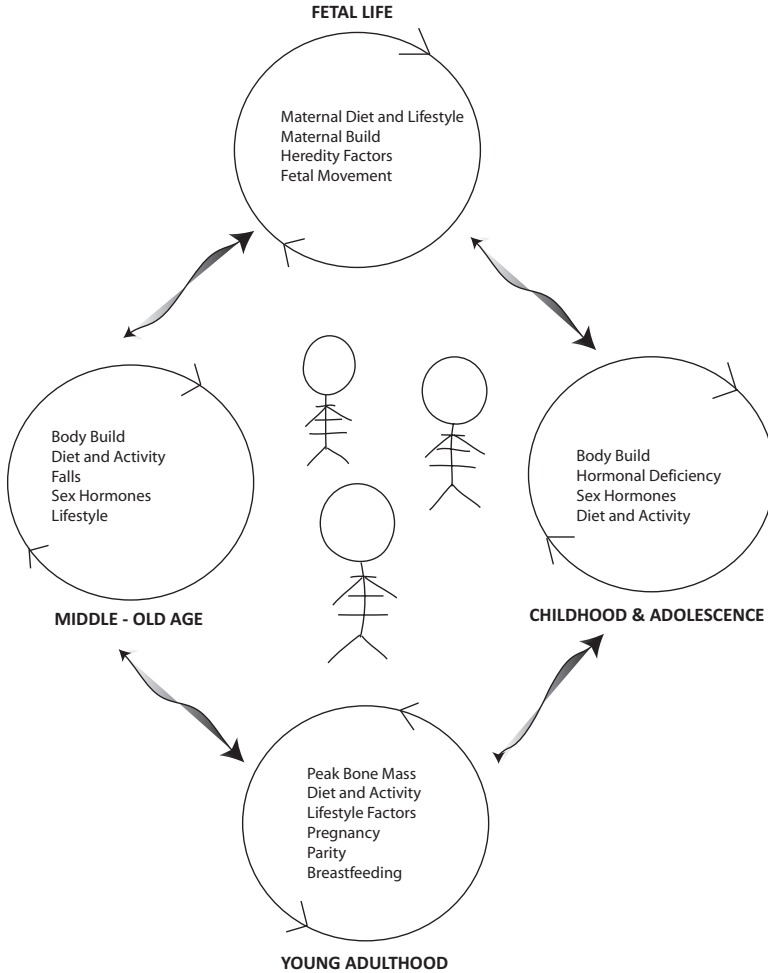
### **Pushing Beyond Plasticity and Adaptation: The (Re)construction of the Skeleton Through Time**

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Despite the numerous studies of bone aging and osteoporosis in bioarchaeology, the etiology of bone loss in the past remains unclear (Agarwal 2008; Agarwal and Grynepas 1996, 2009). Paleo-populations of similar temporal or spatial origin show

similar patterns of bone loss, while others do not, and most differ from the typical age- and sex-related patterns of bone loss and fragility observed in modern Western populations (Agarwal 2008). For example, bone loss is often seen in young age and equal in both males and females, and there is a low prevalence of fragility fracture in comparison to modern populations (Agarwal 2008; Agarwal and Grynpas 1996, 2009; Brickley and Agarwal 2008). The explanation for these observed patterns in the bioarchaeological record is complex, and the use of often incomplete and biased skeletal samples is an ongoing issue in the analysis of any indicator of health and disease in the past (see also Jackes this volume). However, the variable patterns of bone maintenance fragility in the past are also not surprising given that groups in the past would have had very different biosocial histories from our own. The fact that human skeletons in the archaeological record vary in overall morphology and indicators of skeletal health, such as bone maintenance and loss, perfectly illustrates the plasticity and development of the body. Yet, recent bioarchaeological studies have used familiar patterns of bone loss in the past to ratify traditional paradigms of aging in the female skeleton, while discounting patterns that simply do not fit a *priori* expectations. How then can we begin to make more meaningful interpretations of bone maintenance, loss, and aging in the past?

More comprehensive explanations for the observed patterns of bone loss may be gained through the appreciation of the cumulative nature of bone maintenance over the life cycle. For example, a second look at the patterns of bone loss and fragility in the British medieval skeletal sample, Wharram Percy, discussed earlier, from a life course perspective offers new insights on bone health. The Wharram Percy sample shows evidence for age- and sex-related cortical bone loss at multiple bone sites typical of modern populations, and has been used to illustrate how despite historic lifestyle practices, human females are inevitably subject to menopausal and age-related bone loss (Mays 1996; Mays et al. 1998). However, the same population also shows evidence for stress-related reduction of bone mass during growth (Mays 1999; McEwan et al. 2005) that would have changed the trajectory of bone maintenance later in life regardless of expected changes with senescence or menopause, and little or no evidence for typical fragility fracture (Agarwal and Grynpas 2009; McEwan et al. 2005). Further, study of bone loss in the trabecular bone tissue of the vertebrae shows atypical patterns of bone loss in females that suggests that other factors such as reproductive behavior may have played a role in bone loss in young adulthood. This may have conserved and strengthened bone post-menopause (Agarwal et al. 2004; Agarwal and Grynpas 2009). While there are many hypotheses that can be suggested from the patterns of bone maintenance and loss at Wharram Percy, none support the notion that bone loss in the rural medieval population was solely an outcome of aging and menopause. What is evident is that bone maintenance and loss is the result of ontogenetic processes over the life course, with trajectories of bone maintenance laid out in early growth, refined during adulthood, and played out and modified within the everyday individual and generational choices of behavior and life experience (Figure 11.1). Observing one snapshot of bone maintenance at one scale (such as bone loss only in adulthood; one area of the skeleton, or using one methodology) will give a skewed perspective on the complex and unique path that has created the observed bone morphology.



**Figure 11.1** Diagrammatic model of the plasticity in development and maintenance of the skeleton over the life course.

Figure 11.1 shows a diagrammatic model of the plasticity in development and maintenance of the skeleton over the life course. Circles represent major periods of the biological life cycle (fetal life, childhood and adolescence, young adulthood, and middle/old age) each containing examples of some of the major influences within each life stage in human skeletal development. Influences within each stage are interdependent (represented with arrows around each circle), and influences in each stage are cumulative and dependent on influences in earlier life stages (represented as arrows between circles). Cumulative influences shape skeletal morphology, and affect bone maintenance and bone loss. These influences account for the variation in skeletal morphology and maintenance observed over an individual's life course, as well as within communities/populations (represented by varied skeletal figures in middle of model). Note, interdependent arrows are shown even between

middle/old age and the fetal life stage, as representation of the potential intergenerational effect of individual and population life history to skeletal morphology in subsequent generations.

This life course perspective of plasticity and development of the skeleton is suitably grounded in the DST approach to the development of organisms discussed earlier. DST approaches emphasize the interaction of both environmental and biological influences on the development of the organism that occur over the entire life cycle (Oyama 2000a). Fausto-Sterling (2005) has applied this model specifically to understanding skeletal morphology and osteoporosis in modern humans. Borrowing from life course approaches that have been used in the study of chronic diseases, Fausto-Sterling (2005) highlights the cumulative nature that influences have on bone health, and suggests that prior events during life can alter the trajectory of bone development in later points of the life cycle. Life course approaches extend this model of “critical periods” in fetal development (Ben-Shlomo and Kuh 2002), and suggest there could also be modifiers on bone form and health later in life (Table 11.1).

The concept of the body as a product of developmental context (both biological and social) is not limited to DST and life course approaches, and is also found in archaeological perspectives on embodied life experience (Table 11.1). Ingold (1998) has argued that the body is a developmental system that is contextually dependent, and that more importantly humans grow and are active in their development through engagement with the social world. This engagement with the world in which bodies are situated can be both conscious (with agency) or unconscious (Krieger 2001, 2009), and dilutes the belief that organisms are primarily passively built by their genetic code. In her discussion of skeletal markers of gendered behavior in archaeological skeletons, Sofaer (2006:161) notes that while it may be difficult to directly correlate skeletal markers with distinct activities or lifeways in the past, “plasticity of the body means that the body is never pre-social and is contextually dependent”. There is no pristine bodily state that is outside of the environmental and cultural context in which it operates (Oyama 2000a). This is not to say that the plasticity and development of organisms are limitless (Oyama 2000a; Sofaer 2006). Bone’s ability to shape itself is bound by, among other things, genetics, environment, age, and sex (Oyama 2000a; Hallgrímsson et al. 2002, Lovejoy et al. 2003; Pearson and Lieberman 2004; Ruff et al. 2006; Sofaer 2006). For example, processes such as canalization and developmental stability tightly control fetal skeletal development (Hallgrímsson et al. 2002). However, novel or stressful environments can reduce the ability of these processes from limiting variation (Young and Badyev 2007). While the traditional view gives the gene formative power as keeper of the plan or code, the developmental perspective sees the gene not as an information-containing device, but as an information-generating device that depends on immediate environment (Oyama 2000a). While bioarchaeologists do not dismiss the notion that genes and the environment interact, it is that the flow of information in development is thought to move outwards in one direction from the genome, which then interacts with the environment (see Oyama 2000b). This leads to the idea that there are “two kinds of developmental processes, one controlled primarily from the inside and another more open to external forces” (Oyama 2000b:21). What this means for our discussion, is that while the coded forces of bone

physiology and senescence play vital roles in bone growth and maintenance, they need to be viewed as interwoven in a larger developmental process driven by cumulative life experience. While it may be suggested that the focus on life experience limits the exploration of bone morphology and health to the individual context, these theoretical approaches to the body and development over the life course are inherently intergenerational. For example, epidemiological life course approaches contextualize early life exposure in structures that include the role of parents, grandparents, households, and communities (Ben-Shlomo and Kuh 2002). Here biological and social risk is seen as playing across entire generations. DST approaches go one step further, extending what we traditional think of as heredity. Inheritance is seen as more than the passing of a trait or blueprint, but instead the transmission of entire developmental contexts, which can include genes, cellular machinery as well as social and ecological systems (Oyama et al., 2001; Robert et al. 2001). Social and environment context are seen as potential intergenerational influences on the phenotypic variation of the skeleton. As such, skeletal variation in bone maintenance and loss potentially could be the result of developmental processes that have acted at the level of the individual, generations, or entire communities. This has great relevance for how bioarchaeologists observe variation in not only bone maintenance but all aspects of bone morphology.

Lived experiences over the entire life cycle build the final skeleton observed in the archaeological record. In this sense plasticity is viewed as more than adaptation to specific environmental context. Instead through a developmental process, plasticity constructs and reconstructs the body and skeleton again and again over the life course, and potentially over generations of multiple life cycles. The quantity and quality of bone tissue is an exceptional bony indicator in the analyses of past life as it literally reflects the lived experience of the body crafted at the cellular level through bone remodeling. The trajectory of skeletal development is not “carved in stone,” and similarly the fate of degeneration with aging and menopause is not inevitably carved onto the bony tissue at birth. The fact that patterns of bone maintenance, loss, and fragility are different among and between human populations provides an opportunity to go beyond biological reductionism toward hypotheses of biosocial development of whole beings and populations.

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