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Recent Progress in Bioarchaeology: Approaches to the Osteological Paradox

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The publication of The Osteological Paradox (Wood et al., 1992, Current Anthropology, 33:343–370) a decade ago sparked debate about the methods and conclusions drawn from bioarchaeological research. Wood et al. (1992, Current Anthropology, 33:343–370) highlighted the problematic issues of selective mortality and hidden heterogeneity in frailty (susceptibility to illness), and argued that the interpretation of population health status from skeletal remains is not straightforward. Progress in bioarchaeology over the last few years has led to the development of tools that will help us grapple with the issues of this "osteological paradox." This paper provides a review of recent literature on age and sex estimation, paleodemography, biodistance, growth disruption, paleopathology, and paleodiet. We consider how these advances may help us address the implications of hidden heterogeneity in frailty and selective mortality for studies of health and adaptation in past societies.

KEY WORDS: skeletal biology; archaeology; human remains; frailty.

INTRODUCTION

Over the last thirty years, the study of human skeletal remains from archaeological sites has grown from a purely descriptive field to one that embraces hypothesis testing in the context of anthropological archaeology. Although the term bioarchaeology was first used to refer to the application of a broad variety of biological data found on archaeological sites that could be used to reconstruct ancient environments (Clark, 1972), it was soon adopted in North America in reference to populational studies of human remains (Buikstra, 1977, p. 69).

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With the exception of Britain, where the broader (nonhuman) usage continues at some academic programs, research on archaeological human remains is today described as bioarchaeology—to the exclusion of other paleoenvironmental research avenues—both in North America and around the world. The bioarchaeological perspective was influenced both by the development of the New Archaeology and of the biocultural approach to human biology. Bioarchaeology extends this biocultural research focus back in time and expands its scope to the origins of our modern world.

The bioarchaeological perspective can be considered distinct from the broader scope of research carried out on human remains, especially as compared to research often characterized as "skeletal biology." Chief among these differences is the extent to which culture and historical processes are central to the research interests of bioarchaeologists. Grounded in particular culture–historical contexts, bioarchaeology generates hypotheses for evaluation that draw together the reciprocal influences of culture on human biology and vice versa, and examines such biocultural themes as the adoption of agriculture (Cohen and Armelagos, 1984), the emergence of social complexity (Danforth, 1999), prehistoric population movements, and contact between distant cultures (Larsen and Milner, 1994). Indeed, the goals of research are often more solidly derived from questions of archaeological than of biological origin.

As Larson notes (1997, p. 3), a second key emphasis of bioarchaeology is a populational focus. Since we are interested in evaluating the implications of cultural and environmental changes on the lives of past peoples—or their "well-being" (see Wood, 1998)—we must focus on some aggregate-level measure of past societies, thus populations. Even as the presence of a skeleton showing a spectacular skeletal deformity tells us little about the overall health status of a prehistoric society, likewise the presence of a unique cusp pattern on a molar crown tells us little about population affinity. Our ability to make statements about past biological adaptation is thus dependent on the representativeness of archaeological sampling of ancient human remains and our ability to make representative statements about population success at an aggregate level.

In defining bioarchaeology, Larsen (2000, pp. 3–5) emphasizes its interdisciplinary nature, both in terms of its position at the nexus of physical anthropology and archaeology, as well as the technical specializations that provide the varied data with which bioarchaeological hypotheses must be tested. Because of this diversity of research methods and the varied culture–historical problems to which they are applied, most reviews of bioarchaeology emphasize method development more so than advances in interpretation of culture history and process. The present paper is no exception, although we endeavor to place recent work in context of the theoretical issues and problems that we see as the most critical and stimulating issues confronting the discipline today. In particular, we examine progress toward resolving a series of issues known as the "osteological paradox"

(Wood *et al.,* 1992). We focus our review and the accompanying bibliography on research published since the appearance of Larsen's detailed inventory of bioarchaeological research methods and findings (Larsen 1997). A more recent edited volume provides technical summaries of many of the methodological approaches considered here (Katzenberg and Saunders, 2000). Rather than repeating these reviews, we consider the development of bioarchaeological methods in light of the theoretical issues raised by Wood *et al.* (1992) and examine progress toward the populational and biocultural goals of bioarchaeology.

Challenges and Prospects

The publication of Wood *et al.*'s article "The Osteological Paradox" (Wood *et al.,* 1992) stimulated a period of introspection and debate that we believe has strengthened the discipline. Many of the concerns described in the paradox had been raised by other researchers, although they had never been so clearly articulated. The debate arising from this paper has strengthened intersample comparisons of health status by challenging scholars to think more deeply about the assumptions inherent in their research and the variety of interpretations that might account for the patterns they describe in sets of bioarchaeological data.

Wood *et al.* (1992) outlined three key issues that complicate bioarchaeological attempts to evaluate health status and/or adaptation at a populational level using archaeological samples of skeletons: (1) demographic nonstationarity, (2) selective mortality, and (3) hidden heterogeneity in risk. These issues are especially relevant to studies of skeletons that examine the biological costs of cultural behavior and disease-causing conditions. The first issue has been widely recognized in paleodemography for some time (Sattenspiel and Harpending, 1983) and has received a considerable degree of recent work. In brief, unless a population is stationary (of constant size), the age distribution of skeletons in a cemetery reveals more about fertility levels than it does about mortality patterns. The second issue articulates the self-evident observation that the skeletons we study are dead for a reason. Thus the abundance of lesions of a particular condition seen in a cemetery sample does not directly reflect its abundance in the living population at any given point in time. Rather, individuals have different experiences of health and illness, and this illness history contributes to their entry into the skeletal series at a given age. This "selective mortality" issue is evident in the previously recognized conundrum: Does a skeleton without evident lesions represent a healthy person or a weak individual who perished at the first exposure to a pathogen (Ortner, 1991; Stuart-Macadam, 1991)? The third issue articulates the less evident observation that individuals vary dramatically in susceptibility to illness, *i.e.* frailty, that this variation hinders aggregate measures of population health, and that the factors that contribute to this variation in frailty are generally not identifiable. Taken together, these issues reveal that differences in the abundance of stress indicators or pathological lesions between skeletal series may not always follow the common inference that better health makes for better skeletons.

Unlike Bocquet-Appel and Masset's "Farewell to Paleodemography," (Bocquet-Appel and Masset, 1982) Wood *et al.* did not dismiss bioarchaeology as a whole, although some early reactions to the article misinterpreted this intent. Most scholars agree that the article was an important contribution to the growth of the field, not its death knell. The strongest reactions have been to Wood *et al.*'s hypothetical reinterpretation of specific examples (Cohen, 1994; Goodman, 1993); there has been little suggestion that the theoretical issues raised by the article are not valid or important concerns to be explored. Ongoing work does address issues raised in this key paper and is gradually approaching some resolution of them.

Indeed, Wood *et al.* (1992, p. 357) outlined four areas where future research might contribute to a resolution of the paradox. First, they suggest a need for research on the underlying causes of heterogeneity in frailty in modern populations. Second, they indicate a need for demographic research on how frailty is related to risk of death. Third, they argue that we need a better understanding of pathological processes within the individual and how risk of death and frailty vary through the disease process. They then suggest that these tasks may be beyond the reach of bioarchaeology and that future contributions from bioarchaeology lie in exploring the role that culture plays in generating heterogeneity in frailty and how it interacts with selective mortality in the formation of skeletal series.

Although relatively few scholars have directly addressed the implications of the paradox using bioarchaeological data (Storey, 1997; Wright and Chew, 1998), we believe that bioarchaeology has taken some steps—however small—toward exploring heterogeneity in frailty and that new analytic methods will someday enable us to tackle the issues raised by Wood *et al.* (1992) more directly. In particular, bioarchaeology does have the ability to examine diverse dimensions that contribute to heterogeneity in frailty, many of which have been identified through human biological studies on living peoples. For instance, Wood *et al.* (1992, p. 345) indicate that heterogeneity "may arise from genetic causes, from socioeconomic differentials, from microenvironmental variation, or even from temporal trends in health." Although such sources of heterogeneity might at first appear to be "hidden," close consideration of archaeological context and the joint application of bioarchaeology's multidisciplinary strengths do provide avenues to explore past heterogeneity and selective mortality. Rather than a "nuisance" (Milner *et al.*, 2000, p. 486), this heterogeneity is itself a major focus of bioarchaeological research, especially on complex societies (Danforth, 1999; Goodman, 1998). By reference to mortuary context, we can study social differentials in diet and examine their implications for lesion abundance. New techniques permit us to evaluate the duration of breastfeeding and its implications for childhood morbidity and survival. Moreover, progress in genetic analysis and archaeological geochemistry may help us evaluate genetic differences between populations and their movement, factors that may also contribute to heterogeneity in frailty. Together, these techniques do have the potential to identify "measurable characteristics of skeletons . . . that are informative about an individual's frailty" (Milner *et al.*, 2000, p. 489). A decade after "The Osteological Paradox" was published, we examine recent progress in bioarchaeological research methods and highlight how new work raises the possibility of addressing these concerns.

RECENT PROGRESS IN BIOARCHAEOLOGY

We organize this review into five broad topical areas: demography, biodistance, paleodiet, growth disruption, and paleopathology. We define the scope of each area by the bioarchaeological questions that the methods may address instead of by a strict methodological classification, which would require a much more diverse topical list.

Demography

Age and sex data are the most fundamental variables in most bioarchaeological research questions, and so estimates of sex and age must be accurate. Unfortunately, poor preservation hampers the determination of sex and age-at-death in many archaeological contexts. Thus the estimators at hand must be diverse enough to encompass a variety of skeletal elements and differing degrees of preservation. This may lead, however, to a problematic situation in which age and sex are assessed by a very different set of criteria for each skeleton in a sample. Thus, errors in age and sex estimation may vary dramatically among individuals within a sample, and this variability may affect the overall age profile or sex ratio. Therefore continued research that improves existing techniques and develops new ones is always welcome.

As a fundamental component of osteological analysis, sex estimation continues to be an area of active research. Both forensic and bioarchaeological researchers have continued to seek out sexually dimorphic skeletal elements. This research has focused on metric dimensions of bony elements not previously explored in depth, such as the supero-inferior femoral neck diameter (Seidemann *et al.*, 1998; Stojanowski and Seidemann, 1999), hand and foot bones (Riepert *et al.*, 1996; Robling and Ubelaker, 1997; Wilbur, 1998), and other seldom studied bones. Population differences, however, are a key concern in the application of these metric techniques and should be kept in mind before applying these standards to disparate samples. Flexure of the mandibular ramus, a recently suggested morphological indicator (Loth and Henneberg, 1996), has not held up well in independent tests (Donnelly *et al.*, 1998; Hill, 2000; Koski, 1996; Loth and Henneberg, 1998).

Konigsberg and Hens (1998) have demonstrated the value of logistic and cumulative probit models for assessing sex using discrete dimorphic features of the cranium. When skeletal series are large, these statistical methods provide posterior probabilities for sex estimates of each skeleton, which permit assessment of the accuracy of the estimates.

Estimating the sex of subadult individuals has long been considered impossible using traditional osteological means. Recent attempts to sex infant skeletons from the sciatic notch (Schutkowski, 1993) do not appear to be reliable (Holcomb and Konigsberg, 1995), but features of the juvenile mandible and orbits may be of some use (Loth and Henneberg, 2001; Molleson *et al.*, 1998). More promising is identification of sex using DNA recovered from archaeological remains (Faerman *et al.*, 1998; Stone, 2000). These methods focus either on the amelogenin gene, which is found on both X and Y chromosomes, or use genes located on only one of the sex chromosomes. Although several studies have found that DNA sex estimates match skeletal sex estimates, preservation problems that might result in chromosome misidentification have not been entirely solved. These techniques are still experimental, destructive, and costly, and so their most promising applications are likely to be for subadult remains and to confirm the identity of important historically known individuals.

Techniques for age assessment that rely on frequently preserved skeletal elements, or that extend the applicability of existing techniques to other elements, are especially useful in that they allow age estimations to be obtained from a wider segment of the sample. For instance, Drusini *et al.* (1997) report a “coronal pulp cavity index,” a nondestructive method to estimate age using adult teeth, which follows from earlier work in dental histology (Burns and Maples, 1976). Histological analyses of bone have been used with considerable success (Aiello and Molleson, 1993; Dudar *et al.*, 1993). Sternal rib end morphology (Iscan *et al.*, 1984) is seldom used by bioarchaeologists to estimate age because of preservation and difficulty in identifying the fourth rib. Yet Yoder *et al.* (2001) have found that most ribs give age estimates similar to those of the right fourth rib, and that a composite score based on a number of ribs yields the same age as does the right fourth alone. This allows us to use all available ribs to estimate age. The accuracy of age estimation using existing techniques also continues to improve. Ongoing work evaluates age, sex, and population biases that complicate the application of such standards to other populations (Baccino *et al.*, 1999; Galera *et al.*, 1998; Hershkovitz *et al.*, 1997a).

In their famous critique, Bocquet-Appel and Masset (1982) argued that methods for estimating skeletal age result in age distributions for skeletal series that reflect the age structure of the reference samples on which the methods were devised. Considerable work has addressed this issue (e.g., Konigsberg *et al.*, 1997). The most promising new approach to age estimation is transition analysis, which focuses on the age correlates of the transition between discrete morphological stages of the pubic symphysis, cranial sutures, and auricular surface (Boldsen, 1997;

Boldsen *et al.*, 2002; Milner and Boldsen, 1997). They devised a new system for scoring individual components of these traditional age indicators. By iteration against a mortality model that is used as an informed prior distribution, logit or probit regression is used to estimate age from these scores. Hence, this method both combines multiple indicators into a single probabilistic estimate and results in an internally consistent age distribution for a complete skeletal series (Boldsen *et al.*, 2002). Preliminary presentations of the method indicate that it will find wide acceptance.

Paleodemographic research has moved beyond the issues raised in the critiques of the 1980s. Rather than a hindrance to study, the role of fertility in shaping paleodemographic profiles continues to be an active area of research in its own right (Paine and Harpending, 1998). Most crucially, paleodemography has moved from the calculation of life tables to the use of hazards models and maximum likelihood estimators to evaluate the possible effects of demographic change on the composition of archaeological death profiles (Hoppa and Vaupel, 2002; Konigsberg and Frankenberg, 2002; Paine, 1997, 2000). Since these methods have been reviewed in detail recently, we direct readers to those reviews (Jackes, 1992; Meindl and Russell, 1998; Milner *et al.*, 2000).

Clearly, resolution of the paradox depends on better integration of paleodemography and paleopathology. Accurate age-at-death estimates are critical for interpreting the impact of pathological lesions on well-being at the population level. Analysis of pathological lesion abundance by age-at-death cohorts may be a useful approach for evaluating the significance of lesions in terms of morbidity and mortality. Usher's research takes a promising first step toward integrating age-at-death distributions with the age-specific abundance of skeletal lesions into a multistate survival model of heterogeneity and frailty (Usher, 2000). Future work in this area may permit us to better evaluate the changing nature of frailty through the age distribution and its impact on lesion frequencies.

Biodistance and Population Movement

Research on biodistance is a key strategy by which hidden heterogeneity might be revealed, especially for biologically diverse prehistoric populations, such as those of ranked and complex societies and multiethnic tribal societies. Ongoing work continues to explore nonmetric traits of both the dentition (Corruccini and Shimada, 2002) and the skeleton (Christensen, 1998). Metric studies of cranial morphology have seen considerable attention recently, in part due to their role in the Kennewick Man controversy (Steele and Powell, 1999) and to ongoing assessment of ancestor–descendant relationships in the context of NAGPRA legislation. Such studies now incorporate population genetics modeling procedures to factor in the possible effects of selection and genetic drift on morphological variation, as well as to examine the role of effective population size in shaping genetic diversity through time (e.g., Powell and Neves, 1999). Such model-bound approaches have not yet been applied to nonmetric dental traits.

Ancient DNA research continues to be challenged by preservation issues in many environments, as well as by difficulties with contamination by modern DNA. Several recent reviews have examined the conditions for DNA preservation and methods for DNA extraction (Kolman and Tuross, 2000; Stone, 2000; Wayne *et al.*, 1999). Such studies have focused primarily on mitochondrial DNA (mtDNA) haplogroups. Chromosomal DNA studies that focus on highly polymorphic short tandem repeat sequences are less common. Although mtDNA studies are informative for investigations of population relationships on a broad scale, such as the peopling of the Americas (Stone and Stoneking, 1998), few have yet to look at variation in DNA on a smaller regional scale or have used DNA to test specific archaeological hypotheses about population relationships between neighboring sites, or indeed within sites. An important exception is Kaestle and Smith's study of the Numic expansion using mtDNA (Kaestle and Smith's, 2000). Such applications have been hindered by preservation, contamination, and cost. Should ancient DNA studies circumvent preservation and contamination problems to a greater degree (Burger *et al.*, 1999), large-scale studies may also be able to contribute to a picture of population structure in more recent archaeological contexts (Carlyle *et al.*, 2000).

Long the domain of biodistance research, migration is a key factor that may contribute to hidden biological heterogeneity within a skeletal series. Individual residential histories can now be more directly inferred from the oxygen and strontium isotopic composition of bone and tooth mineral. Oxygen isotope ratios in bone mineral depend largely on the δ^{18}O of imbibed water (Bryant and Froelich, 1995; Kohn, 1996), which in turn varies geographically due to Rayleigh distillation and climate patterns. Strontium isotopes are not fractionated in nature's food webs, but are passed from soils to plants and their consumers. Soil ^{87}Sr/^{86}Sr values vary with the geological age and rubidium content of the underlying rock from which soils are derived (Dasch, 1969). Because tooth enamel is not remodeled after it forms, teeth hold a record of childhood residential history. By comparison of enamel formed in early childhood with isotope values in bone that represent later adult life, it may be possible to identify the burials of migrants and thus evaluate the significance of migration between prehistoric groups. This may be an important way to evaluate at least one source of heterogeneity in frailty that is otherwise "hidden."

The potential for migration studies using these isotopes has been recognized for some time (Ericson, 1985; Schwarcz and Schoeninger, 1991), and there has been considerable progress in this area in recent years. First used to document U.S. soldiers buried in Canada (Schwarcz *et al.*, 1991), oxygen isotope ratios have been used both to identify migrants and to reject migration hypotheses at several Mesoamerican sites (White *et al.*, 1998, 2000). Recent studies of strontium isotope ratios have found that substantially more movement must have occurred than previously suspected in the Neolithic Bell Beaker culture (Price *et al.*, 1998), the prehistoric Southwest (Ezzo *et al.*, 1997), and in Classic period Mesoamerica (Price *et al.*, 2000). Lead isotopes may also aid identification of foreign migrants, but have received little work to date (Gulson *et al.*, 1997). Used together, such methods have considerable potential to identify individual movement in prehistory (Hoogewerff *et al.*, 2001). The success of these methods will depend on accurate mapping of geographic variation in isotope ratios and on detailed assessment of diagenetic change (Budd *et al.*, 2000).

Paleodiet

Stable isotope analyses have now become fairly routine for the general characterization of ancient diets, although significant issues regarding fractionation and the partitioning of macronutrients between phases of bone remain unclear (Schoeller, 1999; Schwarcz, 2000). The magnitude of fractionation in nitrogen isotopes in differing environments and under conditions of metabolic stress have been important components of recent research. Stable isotope research has been recently reviewed by Katzenberg (2000) and Katzenberg and Harrison (1997), and the fourth and fifth Advanced Seminar proceedings have now been published (Ambrose and Katzenberg, 2000; Bocherens *et al.*, 1999); thus we limit our observations here to new bioarchaeological approaches to stable isotope analysis.

Stable isotope research that contributes to a resolution of the osteological paradox may lie in work that attempts to study dietary change through the life span. Childhood nutritional status is a key variable that contributes to frailty and thus to survival through childhood (Dettwyler and Fishman, 1992; Stuart-Macadam and Dettwyler, 1995). In many societies, children are not given the same foods as their elders; indeed they may be the last to receive valued proteins that they most require (Dettwyler and Fishman, 1992). Studied in conjunction with nonspecific pathological conditions, childhood dietary data may help unravel the interaction between childhood nutrition, health, and survivorship. Until recently, such work was carried out through analysis of cortical bone samples from juvenile skeletons. Since diet may well have played a role in their premature demise, these analyses cannot inform us about the diet of children who did survive childhood. However, studies of deceased children may someday shed light on the role of diet in early childhood mortality. For instance, research by Schurr (1997) using recently formed trabecular bone is an innovative approach that allows us to examine diet on the short term, immediately prior to subadult death. Similarly, Bell *et al.* (2001) have used bone density fractionation to isolate recently formed bone from older bone in adult remains, thereby examining diet change during adulthood. Such strategies may be useful for identifying skeletons for whom a nutritionally compromised status contributed to mortality at a given age.

Childhood diet can also be studied through analysis of dentine collagen and enamel in teeth, which form at known ages (Fuller *et al.*, 2001; Wright and Schwarcz, 1999). In addition to childhood dietary composition, the duration of breastfeeding is a well-documented factor that contributes to frailty. To date, methods to examine breastfeeding in archaeological remains have emphasized nitrogen isotope studies of subadult skeletons (Fogel *et al.*, 1989; Katzenberg *et al.*, 1996). Certainly, measurement of nitrogen isotopes in tooth dentine would be one way to examine this process in the skeletons of individuals who survived childhood. Since nitrogen isotopes address breastfeeding by way of the trophic level effect, they are most useful for identifying the age at which breast milk is supplanted by solid sources of protein. If this is delayed much beyond 6 months, it may have significant implications for growth status and frailty (Dettwyler, 1991). Continuous-flow mass spectrometry can now handle very small samples of collagen, but there are still technical difficulties in isolating small samples of dentine in order to study this process with fine resolution. Alternately, oxygen isotopes in tooth enamel can shed light on the duration of breastfeeding, by focusing instead on the contribution of ^{18}O-enriched milk to total water intake (Wright and Schwarcz, 1998). Continued nursing after solid food supplementation provides an immune boost that is a well-documented factor contributing to health in later life. However, culinary practices may complicate interpretation of such dietary patterns (Bryant and Froelich, 1996).

For tooth enamel, age-related changes in diet can be inferred from drilling small samples of enamel for analysis (Wiedemann *et al.*, 1999) or by use of laser ablation mass spectrometry. Elemental analyses using laser ablation also show promise for reconstructing dietary changes through childhood, but have not yet been widely applied (Song and Goodman, 1999). Changes in strontium/calcium ratios in particular may shed light on the duration of breastfeeding and the timing of solid food supplementation. Considered together, these measures may provide a life history reconstruction of childhood diet that might help identify heterogeneity in frailty.

Growth Disruption

Skeletal growth continues to be a key area of bioarchaeological research (Hoppa and FitzGerald, 1999). Skeletal stature serves as a cumulative measure of childhood health that permits a comparison of average health between populations or subpopulations. Studies of subadult stature for age avoid the complication of catch-up growth that may confound adult stature patterning, but provide a different window into issues of mortality selection. Interpretation of growth faltering in subadult remains needs to be well grounded in an understanding of nutrition and heath compromises of the specific context (King and Ulijaszek, 1999), which might best be obtained through comparison of other forms of nutrition and health data. Wood *et al.* (1992, p. 351) envision a paradoxical scenario in which decreased stature in a subadult skeletal sample would be the result of reduced mortality, and taller stature would indicate a more stressed population. Byers (1994) suggests that the plausibility of this scenario can be tested via the skewness and kurtosis coefficients for the stature distribution, which help to evaluate the possibility of directional selection.

Konigsberg *et al.* (1998) compare Bayesian and maximum likelihood approaches to stature estimation. They note that regressing bone length on stature and then solving for stature is the better method when the estimated stature is an extrapolation beyond the limits of the reference sample. Boldsen (1998) looked at the relationship between stature and childhood health by correlating adult stature with enamel hypoplasias. He found that ill health in childhood (as indicated by hypoplastic dental enamel) did not affect adult stature but did affect body proportions.

Enamel hypoplasias continue to be among the most common means to evaluate childhood growth experience using skeletal remains. Dental defects are especially relevant to resolution of the osteological paradox because they provide a record of childhood illness experience that can be compared to morbidity and mortality at later ages by examining defect abundance among age-at-death groups (Storey, 1997). Studied together, dental defects and intracrown changes in stable isotope ratios provide a means to examine the role that nutrition may have played in childhood morbidity.

In addition to numerous case studies, recent research on enamel hypoplasias has emphasized refinement of methods to estimate the age of defect formation (FitzGerald and Rose, 2000; Goodman and Song, 1999; Reid and Dean, 2000), primarily through observation of incremental striae and perikymata. Through measurement of enamel microstructural features in a large series of teeth, FitzGerald (1998) has confirmed the regular periodicity of cross striations and striae of Retzius. There also has been renewed work on enamel microdefects. Simpson (1999) raises the possibility that pathological striae (Wilson bands) may result from short bouts of dehydration caused by weanling diarrhea. Since episodes of diarrhea typically begin with the introduction of solid (contaminated) foods, this hypothesis fits better with current views on the nature of the weaning process than did earlier hypotheses that attributed enamel defects narrowly to stress associated with “weaning” itself (Judkins and Baker, 1996; Katzenberg *et al.*, 1996). In his sophisticated analysis of microdefect frequencies in archaeological remains from northern Florida, Simpson (1999) ages the defects by reference to the distribution of striae of Retzius in the tooth crown and finds good correspondence between peak defect ages and the expected onset of weanling diarrhea.

Many scholars have studied enamel defects by generating a composite score for the complete dentition, or by scoring a single “representative” tooth such as the mandibular canine. Yet, differences in susceptibility to developmental insult between tooth positions (Goodman and Armelagos, 1985) provide a window into examining the distribution of stress insults of differing magnitude. Where the commonly studied “sensitive” teeth may not reveal differences in defect abundance between populations, less sensitive teeth may reveal changes in the stress experience (Wright, 1997). In her demographic analysis of skeletal lesions in medieval Danish remains, Usher (2000) found that hypoplasias on incisors (which have a low threshold for defect formation) were associated with a low risk of death, while hypoplasias on first molars (higher threshold) were associated with an increased risk of death. An additional factor may be the age at which these health insults occurred: hypoplasias provide an especially useful tool for examining the implications of health disturbance at specific ages on long-term survivorship (Storey, 1997).

Paleopathology

To better evaluate the implications of heterogeneity in frailty for lesion development, Wood *et al.* (1992, p. 357) suggest that more information is needed on the processes of lesion formation. Certainly, for paleopathology, a related issue is the more accurate identification of the specific pathogen responsible for a bony lesion. Recent advances in the identification of pathogen DNA lead us to be hopeful that future research will be able to draw on more direct inference between modern and prehistoric pathogens. To date, pathogen DNA has been identified in archaeological remains from leprosy (Spigelman and Donoghue, 2001), bubonic plague (Drancourt *et al.*, 1998), *Trypanosoma cruzi* (Guhl *et al.*, 1999), and tuberculosis (Haas *et al.*, 2000; Mays *et al.*, 2001). This advance is especially important when considering the possibility of pathogen evolution between past and present. For instance, skeletal lesions resembling tuberculosis in New World precolumbian remains have long been referred to as a “tuberculosis-like pathology” (Buikstra, 1981), and discrimination from other mycoses has been difficult (Kelley and Eisenberg, 1987). Identification of mycobacterial DNA resolves this issue significantly (Salo *et al.*, 1994). Should future work be able to identify evolving strains of pathogen DNA, we may be able to explore the implications of differences in strain virulence for paleoepidemiology. The identification of the β-thalassemia gene in ancient remains (Filon *et al.*, 1995) raises the possibility of discriminating between the varied causes of anemia for the first time in areas where porotic hyperostosis might be a result of both genetic and dietary/environmental causes. With continued progress in the identification of genes responsible for various diseases, there likely will be more developments of benefit to paleopathology. These advances also raise the possibility of identifying pathogen DNA in remains that do not show pathognomic lesions. Were it successful, such research would go a significant way toward resolving the question of whether apparently “healthy” skeletons represent those never infected, or the most frail individuals of a population.

The application of histological methods to ancient remains, or palaeohistology, has also gained attention in recent years (Pfeiffer, 2000; Schultz, 2001).

Although we believe that most conditions that cause significant bony response can be accurately diagnosed macroscopically, histological observation may be helpful in clarifying the nature of pathological bone changes. In terms of the paradox, histological analysis may be especially important for examining the degree of healing shown by diverse lesions, and in diagnosing pathology in cases where death occurred rapidly, with little skeletal response.

Because of the expense and destructive nature of both ancient DNA analysis and histology, paleopathological research will continue to emphasize skeletal lesion morphology and distribution for differential diagnosis. There has been considerable recent progress in delimiting the characteristics of skeletal lesions for a number of diseases, including rickets (Ortner and Mays, 1998), scurvy (Ortner *et al.*, 2001; Ortner and Ericksen, 1997), syphilis (Hutchinson and Weaver, 1998; Rothschild and Rothschild, 1997), leukemia (Rothschild *et al.*, 1997), sickle cell anemia (Hershkovitz *et al.*, 1997b), and tuberculosis (Santos and Roberts, 2001). For specific diseases that cause multiple pathognomic lesions, continuing study of the varied expression of these lesions may lead to a better understanding of frailty and the infection process. In the case of leprosy, individuals with a strong immune system manifest a less severe form of the disease, "tubercular" leprosy. The classic features of "lepromatous" leprosy develop only in those with compromised immune systems. Exploiting these differences, Boldsen (2001) has quantified the predictive value of seven common symptoms of leprosy. He attempts to examine leprosy pathogen loads at the population level among three medieval Danish samples. He concludes that one series, thought to be free of leprosy because it contains no severe cases, actually had a high frequency of lesions caused by the milder form of the disease.

Lesions of porotic hyperostosis were among the first to be interpreted in a paradoxical manner. Although Stuart-Macadam (1991, 1992) suggested that iron-withholding might be a response to infection that could contribute to the formation of anemic lesions, her arguments are sometimes misinterpreted as a "parasite model" (Holland and O'Brien, 1997). Since the direction of the arrows between anemia and infection is not conclusively demonstrated in the modern clinical context (Ryan, 1997; Walter *et al.*, 1997), it is perhaps more reasonable to conclude that infection contributes to dietary iron deficiency anemia, rather than that it is a primary cause. For children, nutritional insufficiency is the most likely cause of iron deficiency in many parts of the world, especially where bulky carbohydrates are the staple of children's diets. Hence, the presence of lesions on adult remains indicates low frailty and survival through a bout of childhood anemia. Elsewhere, the first author has suggested that the abundant healed porotic hyperostosis observed on ancient Maya remains may be a reflection of lower mortality than modern Maya children experience today (Wright and Chew, 1998). Clearly, integration of independent demographic data into such analyses is crucial to resolving the predictive value of such lesion abundance comparisons (Milner *et al.*, 2000).

DISCUSSION

Clearly bioarchaeology has not yet circumvented the issues outlined by Wood *et al.* (1992); we believe, however, that progress has been significant and that we do have the tools to approach the issues of selective mortality and hidden heterogeneity in frailty on several different fronts. Rather than dismissing the issue as unlikely to be significant or simply ignoring it, as many have done, explicit consideration of multiple alternate interpretations of bioarchaeological data is critical to arriving at an appropriate inference.

Many paleopathological studies focus on a single indicator of health, such as enamel defects, stature, or porotic hyperostosis. In part, this narrow focus is facilitated by the constraints of journal publishing formats, which encourage us to carve up large projects into manageable units. It also is due to the diverse technical specializations within the field. Yet, as Larsen (1997, 2000) notes, bioarchaeology's strength lies in its broad interdisciplinary scope. We have at our disposal a diversity of means to examine health, diet, and population affiliation at different stages of an individual's life history. Since these various methods focus on different angles of the frailty distribution, comparisons between them can help clarify the implications of lesion abundance with respect to each other. Many scholars reacted to Wood *et al.*, (1992) by suggesting that the study of multiple indicators of health has been a tradition in bioarchaeology and that it permits a more complete assessment of health change over time. Such views tend to emphasize concordance between indicator levels in multisample comparisons, for which the normative assumption—that lesions indicate poor health—is likely to be appropriate. For instance, studies of living populations have shown that malnourished children have higher abundance of hypoplasias in their permanent dentition than well-nourished ones (Goodman *et al.*, 1987). Hence, it is reasonable to infer that an abundance of dental defects is likely to indicate a state of poor "well-being," especially if other indicators of poor childhood health (e.g., anemia) show parallel trends. More meaningful information about relative frailty might be gleaned from apparently contradictory trends among the abundance of indicators across series. Although we believe that the traditional inferences drawn from bioarchaeological studies of major transitions—like the origins of agriculture—are probably correct, explicit consideration of possible paradoxical interpretations of each indicator is key to a sensitive interpretation of frailty and its change through time and space. Multivariate statistical analyses of diverse classes of data are challenging, but are clearly where these analyses must head if we hope to examine the varied dimensions of health over time and space.

A greater emphasis on comparison of lesion frequencies among age classes of skeletons also will be key for evaluating whether a paradoxical interpretation of pathology might be appropriate in a given context. Few studies to date have explicitly taken this approach, and most have focused on enamel hypoplasias

(Goodman and Armelagos, 1988; Storey, 1997). By considering the relationship between lesions indicative of morbidity during childhood and conditions representing health status in later adult life, for example, we may be able to evaluate the implications of such apparently contradictory trends for morbidity and mortality. Such analyses will be facilitated by the use of demographic modeling techniques in concert with pathological data (Usher, 2000) and by consideration of multiple lesion classes.

This focus on morbidity and its relationship to age-at-death can further benefit from a life history approach incorporating both pathological and dietary data. Since childhood nutrition is known to affect survival and morbidity in modern contexts, we may be able to identify the hidden factors that contribute to age-specific lesion abundance by focusing on the childhood diets of the skeletons of individuals who survived to adulthood. Isotope and elemental studies that microsample or scan across tooth enamel and dentine may soon bring into focus such heterogeneity in childhood diets. For instance, we might find that age-specific rates of stress indicators or infectious diseases differ among individuals who were weaned at a young age, versus those who benefited from longer-term breastfeeding. Since infant feeding practices are culturally determined, we should expect wide variability in prehistoric weaning age and motivations.

Social inequality is one fairly direct angle by which bioarchaeologists can address heterogeneity in frailty, although it can be examined with greatest success only in complex societies (Robb *et al.*, 2001). For instance, subgroups of a population may differ in the composition of their diets, in exposure to pathogens because of the characteristics of residential architecture, or in frailty due to genetic factors. By breaking a skeletal series into such social or kin groups, which may be identified through mortuary patterning, differences among the aggregate lesion frequencies of the subpopulations may shed light on the implications of pathological features at the broader population level. Characterization of dietary inequality and of differences in age-specific lesion abundance among social groups may further indicate whether the frequency of lesions in the subgroup, and in the population as a whole, should be interpreted in the normative manner (lesions indicate poor health) or in a paradoxical manner (lesions indicate low frailty). Likewise, foreign migrants to a prehistoric population constitute another identifiable component of heterogeneity that can be used to break up series into subgroups—using isotopic or biodistance methods—that may differ in frailty.

Inherently, bioarchaeology is a comparative exercise. Although paleopathology may focus on tracking the history of specific diseases, any populational study that aims to evaluate "well-being" must therefore have some comparative basis. A primary difficulty in drawing inference from lesion abundance is the fact that most diseases that affect the skeleton do so in nonspecific ways and, viewed in the deceased skeleton, represent a cumulative life experience of heath status. By contrast, epidemiological data is cross-sectional, and many of the lesions we study (e.g., periosteal reactions, porotic hyperostosis) are seldom documented in medical literature in a meaningful comparative way. Hence, most bioarchaeological work involves comparison between several archaeological series. Another strategy that may inform interpretation of archaeological skeletal series is comparison with modern skeletal data. Ongoing forensic analyses of modern war crimes have recently led to large skeletal databases that have the potential to contribute to a better understanding of lesion abundance in skeletal remains derived from populations with known demographic parameters and health status (Wright and Chew, 1998). Certainly there are ethical issues in such research, but many of the necessary data are collected in the process of routine forensic work and are of interest in the absence of personal information about the deceased.

To summarize, we believe that bioarchaeology has made progress toward developing a more sensitive toolkit for the study of ancient biocultural adaptation. These advances include both statistical and morphological refinements in methods of age and sex estimation, and the demographic modeling of skeletal age distributions. Skeletal biodistance and ancient DNA research now incorporate more sophisticated population genetics modeling procedures and will help evaluate the genetic basis of heterogeneity in past populations. Chemical analyses of residential history will help constrain the effects of migration for population heterogeneity in terms of both genetics and demographic modeling. Paleopathological studies are strengthened by progress in lesion diagnosis and by explicit consideration of the meaning of lesion frequencies among age-at-death groups. Paleodietary research is now exploring age-specific changes in diet that will allow reconstruction of individual nutritional life histories. Clearly, statistical modeling of morbidity and mortality has made us more sensitive to the complexity of interpreting health status in the past. The challenge confronting bioarchaeology today is to incorporate such models into analyses of data obtained from these varied tools. This integration may soon permit a more nuanced interpretation of health status and the costs and benefits of cultural and environmental change in past societies.

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