

Phenotypic Approaches for Understanding Patterns of Intracemetery Biological Variation

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ABSTRACT This paper reviews studies of phenotypic inheritance and microevolutionary processes in archaeological populations using data on cranial and dental phenotypic variation, often referred to as paleogenetics or biodistance analysis. The estimation of biological distances between populations, or among individuals within populations, is one component of bioarchaeological research on past populations. In this overview, five approaches that focus on morphological variation within cemeteries are summarized: kinship and cemetery structure analysis, postmarital residence analysis, sample aggregate phenotypic variability, temporal microchronology, and age-structured phenotypic variation. Previous research, theoretical justifications, and methods are outlined for each topic. Case studies are presented that illustrate these theoretical and methodological bases, as well as demonstrate the kinds of inferences possible using these approaches. Kinship and cemetery structure analysis seeks to identify the members of family groups

within larger cemeteries or determine whether cemeteries were kin-structured. Analysis of sex-specific phenotypic variation allows estimation of postmarital residence practices, which is important for understanding other aspects of prehistoric social organization. Analysis of aggregate phenotypic variability can be used to infer site formation processes or cemetery catchment area. The study of temporal microchronologies can be used to evaluate provisional archaeological chronologies or study microevolutionary processes such as adaptive selection or changing patterns of gene flow. Finally, age-structured phenotypic variation can be reflective of selection processes within populations or it can be used as a measure of morbidity, growth arrest, and early mortality within past populations. Use of phenotypic data as a genotypic proxy is theoretically sound, even at small scales of analysis. *Yrbk Phys Anthropol* 49:49–88, 2006. © 2006 Wiley-Liss, Inc.

Bioarchaeology is the contextual study of the biology, culture, and human evolution of human populations using skeletal remains interpreted within archaeological, historical, and contemporary problem orientations. This immensely popular field emerged during the 1970s in the wake of the New Archaeology and the subsequent adoption of regional, population-based research (Buikstra, 1977). Focus on skeletal data allies bioarchaeology with skeletal biology and forensic anthropology disciplines, which experienced concurrent rises in popularity over the last three decades. The field is most visibly associated with paleopathology and demography, particularly for its contribution to studies of the agricultural transition and the health implications of sedentary village farming economies (Cohen and Armelagos, 1984; Larsen, 1997, 2001; Steckel and Rose, 2002). In addition to pathology and demography, bioarchaeologists study dental anthropology, bone chemistry, diet, long bone cross-sectional geometry, mortuary ritual, and genetic variation (including biological distances) within and among populations (Larsen, 1997; Katzenberg and Saunders, 2000). Bioarchaeologists are united in their use of biological data from archaeological contexts to investigate social and cultural adaptations of past societies, including subsistence and activity patterns, as well as the effects of disease and nutrition on population health.

The focus of the present review is biological distance analysis (hereafter, biodistance). Biodistance analyses use phenotypic data from the cranium or dentition to estimate genetic similarity among regional or continen-

tal populations to reconstruct patterns of gene flow, population origins, or long-distance migration (Buikstra et al., 1990; Larsen, 1997). However, despite emphasis on inter-population approaches, genetic comparisons are also possible among individuals within a sample. Such “intracemetery” analyses are less visible in the discipline but nonetheless provide unique inferences about past peoples that are not available using other methods. In this paper, we review the various intracemetery biodistance analytical approaches, focusing particularly on the identification of relatives within skeletal series (kinship analysis or cemetery structure analysis) and on the inference of postmarital residence practices. We also outline other types of intracemetery analyses that are less common or unique in the literature such as the study of general levels of phenotypic variability, temporal microchronology, and age structured phenotypic variability

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(see Konigsberg, 1987). These five topics can be grouped into two broad categories: the study of structure within a cemetery based on spatial (kinship analysis), temporal (temporal microchronology), or demographic (age structure) variables; or the study of variability that is sex-specific (postmarital residence) or aggregate (total phenotypic variability). We assume a broad definition of “cemetery” to mean any aggregate of human remains whose accumulation is intentional or unintentional (see discussion in Rugg, 2000; Janeva, 2001, for example), which is sufficiently general to include the full range of human burial environments (e.g., a shipwreck - During, 1997).

Our goals are three-fold:

1. To demonstrate the complete range of inferences available from an intracemetery analysis.
2. To provide examples demonstrating how to perform intracemetery analyses and the unique inferences they offer, and
3. To counter prevailing wisdom that phenotypic data are too environmentally plastic or too insensitive to be used to infer relationships of such small scale.

In accomplishing these goals this overview demonstrates how to move beyond the simple “case study” that typifies osteological site reports, which include observations on age, sex, and pathology. By focusing on the site as a unit of investigation we demonstrate how to complement descriptive reports with additional analyses that only require data from that specific site. In other words, non-specialists can, and should, do more than simply describe a skeletal sample. They can infer a range of behavioral and evolutionary processes not possible through other techniques:

1. If kin groups can be identified, family-specific social and demographic composition can be outlined, pathology and mortality can be compared within and among family units, and archaeological markers of status can be related to specific family groups within a larger population.
2. Reconstruction of postmarital residence can be used to infer other aspects of social structure based on extrapolation from comparative ethnographic research. If the natal and non-natal components of a population can be separated, regional migration patterns can be identified.
3. Identification of micro-temporal units within a cemetery can provide information on short-term microevolutionary processes that can be related to broader archaeological or historical issues of migration, population replacement, or genetic admixture. Micro-temporal units allow finer-grained consideration of health and diet, how each changed between generations, and their relationship to demographic trends. Natural selection can be evaluated by comparing phenotypic distributions between generations and can be related to biological and cultural adaptation.
4. Comparison of adult and subadult dental phenotypes can also be used to infer natural selection or provide evidence of morbidity associated with reduced longevity.

Re-focusing attention on site-specific research is also consistent with recent theoretical and critical developments from within anthropology. For example, focusing on small-scale relationships uses information on the

genetic variability that exists within local populations. Based on three decades of research using multiple genetic loci (e.g., Lewontin, 1972; Nei and Roychoudhury, 1982; Excoffier et al., 1992; Jorde et al., 1995; Barbujani et al., 1997) and phenotypic traits (e.g., Relethford, 1994, 2001, 2002), a significant amount of human genetic variation is found within local populations. Concentration on broad, taxonomic phenotypic comparisons ignores this variation by treating the site as a unit of analysis instead of a unit of investigation. As Calcagno noted, “. . . large data sets based on skeletal samples are often melted down into a single summary statistic, and that “centroid” is then typologically and erroneously used to represent the entire population (Calcagno, 2003).” While not meant to supplant phenotypic comparisons of global scale, we feel as much can be learned about the human past by studying the “local” and extrapolating to the “regional.” Finally, we note that intracemetery research counters recent critiques of biodistance analysis in general (Houghton, 1996; Armelagos and VanGerven, 2003; but see Stojanowski and Buikstra, 2004), which claim that typological modeling still dominates bioanthropology and that descriptive historical research is antithetical to processual anthropological inference. Intracemetery research certainly falls within the purview of biodistance analysis and, as this review demonstrates, there is no typological undertone.

The structure of this review provides non-specialists with a broad introduction to biodistance analysis generally, and intracemetery approaches specifically. We begin by presenting a general overview of biodistance analysis with focus on the different scales of inference (global and regional). Summarizing global and regional scales of analysis provides an appropriate contrast to the site-specific approaches highlighted in this review. We then discuss the traits used for biodistance research and provide several demonstrative visual examples. However, the primary focus of this paper is discussing kinship and cemetery structure analysis and postmarital residence analysis. Secondary types of intracemetery approaches that are less common in the literature (temporal microchronology, variance comparisons, and age structured phenotypic differences) are also summarized. As appropriate, we maintain the same structure for each section, beginning with introductory comments and then discussing historical foundations and previous bioanthropological research. The theoretical basis for each analysis is then outlined followed by brief comments about previous methods used. Finally, a case study is presented for each section that highlights the anthropological utility of that approach. For kinship analysis and postmarital residence we present new research. For the former, a kinship analysis of Windover Pond, an early Archaic period mortuary pond in Florida with preserved brains and textiles, is presented (Doran, 2002). For the postmarital residence section, additional research on matrilocality at Pueblo Bonito is discussed in the context of Chacoan culture and Southwestern prehistory (Schillaci and Stojanowski, 2002). For the three additional approaches, case studies are selected from the previous literature and no new data are presented.

BIODISTANCE ANALYSIS

The underlying theoretical model of all biodistance analyses is relatively straightforward. Populations that exchange mates become more phenotypically similar over time and those that do not become more dissimilar

at a rate determined by their effective population size. That is, biological distance analysis studies the effects of gene flow (or migration) and genetic drift, which are more important evolutionary mechanisms over the shorter time periods typically sampled by archaeological sites of the recent past. Because phenotypic data are used, similarity is measured in terms of means and frequencies and evolutionary processes are measured in terms of phenotypic variation. Mate exchange between two populations result in increasingly similar means for metric traits and similar trait frequencies for non-metric traits. Between-sample phenotypic variability decreases as a result. The primary assumptions of biodistance analysis are: 1) holding mutation rates and selection effects constant, genetic drift and gene flow affect allele frequencies within and between geographically proximate populations sharing similar environments, 2) populations are accurately represented by samples of archaeological human skeletons that accumulated over an extended period of time, in other words, the samples used are not natural biological populations but temporal aggregates or lineages, 3) that changes in allele frequencies result in measurable changes in skeletal traits (phenotypes) that can be characterized in a mathematical manner, 4) environmental effects on phenotypic variation within populations are minimal or randomly distributed among the samples being studied, and 5) inheritance of phenotypic variation is additive (due to the action of multiple genes each with a small effect on the phenotype) and resemblance among relatives is strong.

In general, biological distance analysis has goals identical to anthropological genetics, studying patterns of microevolution and inheritance within our species. The particular research orientation depends on the scale of geographical comparison and the amount of time that separates the archaeological samples (Buikstra et al., 1990). Analysis at the inter-regional, continental, or global scale (Fig. 1a) reconstructs broad patterns of modern human emergence, subsequent migration and colonization patterns, population origins, and models of population replacement versus *in situ* microevolution across large geographic regions. Interest in these types of research questions predates anthropology itself (e.g., Morton, 1839). The work of Howells (1969, 1973, 1989, 1995) and Turner, (1985, 1986) are the most notable examples of inter-regional comparison of human populations that explain broad patterns of affinity and population origins. Inter-regional biological distance analyses complement those based on genotypic data. The primary benefits of phenotypic approaches are the availability of larger sample sizes, methodological and analytical efficiency, non-destructive sampling, and the ability to include ancient populations. On the other hand, these analyses are often based simply on phenetic similarity, lack testable underlying evolutionary models, and are taxonomic in orientation. Recent incorporation of population genetic modeling (see Relethford and Lees, 1982) addresses some of these concerns (González-José et al., 2001, 2002; Relethford, 2001, 2004a,b; Hanihara and Ishida, 2005). Nonetheless, critics still argue inter-regional cranial or dental comparisons are essentialist and based on racial models of human prehistory and that the questions addressed by these studies have not changed in over 100 years (Houghton, 1996; Armelagos and Van Gerven, 2003). While we disagree that inter-regional biodistance analyses are typological, primarily because analyses are now based on phenotypic variance rather

than just means, Armelagos and Van Gerven (2003) are correct that the fundamental question posed by inter-regional comparisons have not changed in over 100 years and remain fundamentally descriptive and historical. We, however, find nothing particularly wrong with this.

In contrast to inter-regional comparison of human populations, others have focused on temporally and geographically restricted samples (Fig. 1b). Biodistance research at the regional scale is not concerned with population origins or broad patterns of affinity but with local demographic variables such as population size, migration patterns, population turnover or replacement, and population aggregation, and their effect on the distribution of alleles within a mating network. A primary focus of regional biodistance analysis is describing the relationship between cultural and linguistic variation and the distribution of genetic variation. Mating preferences, social organization, ethnic group boundaries, residential mobility, patterns of conflict, and subsistence economies all affect the degree to which human populations are biologically integrated. To what extent do cultural and biological variation co-vary? The literature addressing this topic is extensive and largely descriptive. However, examining the relationship between biology and culture can be re-defined in more informative ways. For example: 1) under what conditions do language, culture, and biology correspond to one another, or 2) what role does microevolutionary process have in affecting patterns of cultural and linguistic variation? The first is also descriptive but adopts a comparative orientation. The second is the most promising because a multi-variable process is being modeled.

Regional biodistance analyses have been widely applied throughout the Americas: in Oaxaca, Mexico (Christensen, 1997, 1998a,b, 2001); in the Lower Illinois Valley (Buikstra, 1972, 1977, 1980; Droessler, 1981; Conner, 1984; Konigsberg, 1987, 1988; Konigsberg and Buikstra, 1995; Steadman, 1998, 2001), in colonial La Florida (Griffin et al., 2001; Stojanowski, 2001, 2003a,b, 2004), in the American Southwest (Schillaci et al., 2001; Schillaci, 2003), for prehistoric Ontario populations (Molto, 1983), and in the Great Lakes region (Ossenbeger, 1974), for example. Konigsberg and Buikstra (1995) is exemplary in its use of spatial statistics to generate maps of genetic boundaries among Illinois valley populations. We are surprised their approach has not been used elsewhere. Recent work in anthropological quantitative genetics (Williams-Blangero 1987, 1989a,b; Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990; Relethford, 1991, 1996, 2003; Relethford et al., 1997) has completely re-defined the methodological orientation of biodistance research and implemented calculation of population genetic statistics such as phenotypic F_{ST} , a measure of regional genetic diversity. Estimation of relationship (R) matrices provides genetic distances and allows estimation of extra-local gene flow patterns (Relethford and Blangero, 1990; Relethford et al., 1997; Relethford, 2003), see examples in (Steadman, 1998, 2001; Tatarek and Sciuilli, 2000; Schillaci, 2003; Stojanowski, 2004, 2005a,b).

Inter-regional biodistance analyses remain visible in the literature because they examine broad issues of human evolution. They are, however, based on a weaker theoretical foundation than regional approaches. For regional analyses, the shorter time frames of comparison and the smaller geographical areas sampled minimize the effects of between-population environmental variance

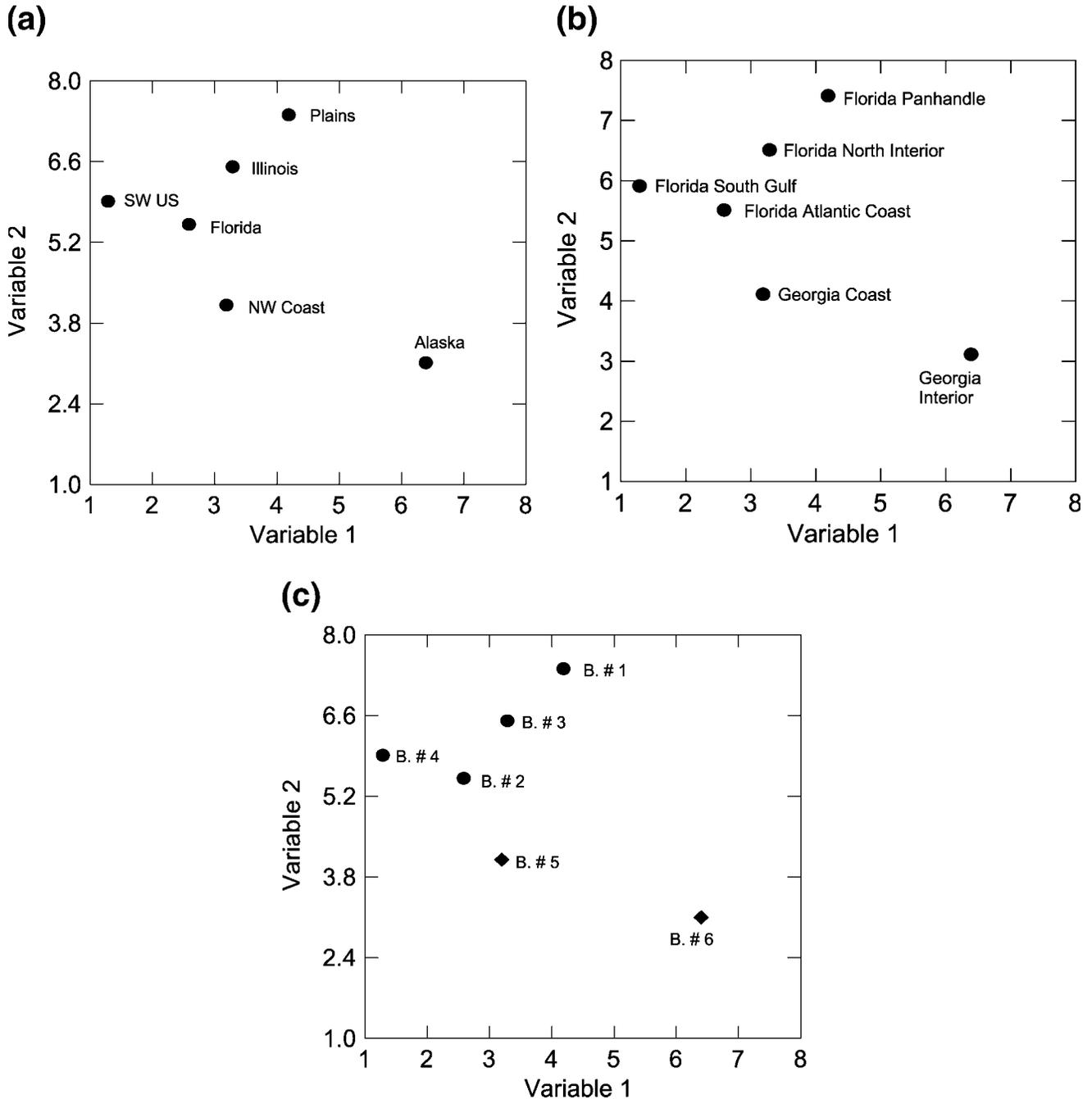


Fig. 1. (a–c) Demonstration of the different scales of biodistance analysis based on comparison of two phenotypic variables. In Figure 1a comparisons are made between populations on a continental scale using broad geographic aggregation of regional samples. For example, as demonstrated in Figure 1b, the “Florida” sample represents an average of six different sites from the southeastern US (Florida and southern Georgia, or La Florida). In Figure 1b, individual sites are compared using the same two variables. In both Figure 1a and b a geographical structure (isolation-by-distance) is evident. Figure 1c represents biological distance among individuals from one of the Florida sites where circles represent burials from one internal subgrouping and diamonds represent burials from a second internal subgrouping.

and selection effects on patterns of phenotypic variation. Although more theoretically justified, regional biodistance research is also more local in orientation and therefore less accessible to a broader audience. Nonetheless, we feel that regional research will continue to advance a holistic bioarchaeological perspective that integrates both cultural and evolutionary principles.

Inter-regional and regional biodistance research uses the site, or cemetery, as a unit of analysis. While justified in many cases, not all cemeteries are appropriate for comparison, a fact that is rarely evaluated. This caveat reflects the variability of cemeteries in size, temporal scope, and representative nature of the living population that created them. Cemeteries are foremost a biological

lineage not a population sampled at a single point in time (except for mass fatality sites) (see Cadien et al., 1974; Konigsberg, 1987, 1990a,b). Sex and age biases are a common concern as is the treatment of culturally atypical individuals. However, most problematic are differences in cemetery “catchment area,” that is, the portion of a broad mating network represented by any single cemetery. Obviously comparing family household cemeteries with large aggregate village cemeteries will introduce significant bias into analyses at the regional or inter-regional scale. One of the strengths of intracemetery approaches (Fig. 1c) is the ability to evaluate these concerns.

BIODISTANCE ANALYSIS: DESCRIPTION OF THE DATA

Biodistance analyses use metric and non-metric observations of the cranium and dentition as proxies for genotypic data. Postcranial traits are used less frequently. Justifications for phenotypic analysis almost always appeal to heritability studies, which are numerous for craniometric variables (Susanne, 1975, 1977; Cheverud et al., 1979; Sjøvold, 1984; Devor, 1987; Cheverud, 1988; Konigsberg and Ousley, 1995; Sparks and Jantz, 2002; Carson, 2006), cranial non-metric traits (most recently summarized in Sjøvold, 1984; Hauser and DeStefano, 1989), dental metrics (most recently summarized in Kieser, 1990; Stojanowski, 2001, 2005c), and dental morphological variables (most recently summarized in Scott and Turner, 1997). Although considerable variability exists among the study samples, most phenotypic heritabilities cluster around $h^2 = 0.55$ (but see Carson, 2006). Over- and misinterpretation of the meaning of heritability is common (see concise discussion in Konigsberg, 2000). Scott and Turner (1997) and Stojanowski (2005c) provide descriptions of the concept directed at a bioarchaeological audience. Vitzthum (2003) is a more general, yet accessible, critique of the heritability concept.

Metric analyses use measurements of continuous variables and standard descriptive (mean, standard deviation) and inferential statistics to estimate similarity between populations or individuals. Although standard multivariate statistical analyses are most common (Pietruszewsky, 2000), three-dimensional analyses via the “new morphometry” are becoming more prevalent (Richtsmeier et al., 1992). Cranial metrics are most common and have the longest history in comparative human research because of early scholarship’s fascination with “capacity for civilization,” brain size, and its archaeologically observable correlate, cranial capacity (Gould, 1996). Data recording is based on inter-landmark distances and several measurement definition sets have been used (see Martin, 1928; Howells, 1989; Buikstra and Ubelaker, 1994; Bass, 1995). Dental metrics have also been used for biodistance analysis and, as with craniometric data, several different measurement definitions have been proposed (see Kieser, 1990; Buikstra and Ubelaker, 1994; Hillson, 1996 for discussion). Most commonly used are mesiodistal (front to back) and buccolingual (cheek/lips to tongue) dimensions of the dental crown. Similar measurements of the cervical region (where the enamel meets the root) have been proposed and are promising because they reflect a similar genetic signal as crown data but their presence within a sample is less affected by dental wear (Hillson et al., 2005; Stojanowski, in press). Although postcranial measurements are part of standard osteological descriptions (Buikstra and Ubelaker, 1994)

they are not used for biodistance research. This may reflect the prevailing view that weight-bearing postcranial bones are primarily functional and therefore not preferable for genetic comparison because they either are subject to selective mechanisms or do not display enough inter-individual variability. Case (2003) is an exception in its use of metacarpal and phalangeal bone lengths for kinship analysis.

Non-metric traits are discontinuous in phenotypic expression but are assumed to have an underlying continuous polygenic mode of inheritance (Hauser and DeStefano, 1989). Because these data are not recorded on a continuous scale, trait presence or sample frequency is the primary descriptive statistic. Inter-observer error is more problematic for non-metric phenotypic variation and analysis is complicated by the discontinuous mode of expression. Dental morphological (Scott and Turner, 1997) and cranial non-metric (Anderson, 1968; Finnegan, 1978; Saunders, 1978, 1989; Hauser and DeStefano, 1989) data have been identified and incorporated into standard data collection protocol (Buikstra and Ubelaker, 1994). Traits that are polymorphic, i.e., those found in moderate frequencies in several populations, are preferred for regional or global analyses. Examples of dental morphological traits include shovel-shaped incisors, variations in molar cusp morphology, cingulum projections, and root variations. Many of these traits are subtle and not easily depicted in pictures. Interested researchers should consult the Arizona State University dental plaques and compare variation among several geographically distinct samples to appreciate the full range of variation. Examples of cranial non-metric traits include hyper-(excess) or hypo-(dearth) static bone variants, variation in cranial foramen number, and accessory sutural bones (ossicles) (Ossenberg, 1969). Postcranial non-metric traits are not used as polymorphic traits in regional or global comparisons.

At the within-site level, rare traits or those considered genetically anomalous are more useful than commonly occurring traits for identifying closely related individuals (Alt and Vach, 1998). The rarity of these traits precludes using their joint absence in different populations as an indicator of gene flow between them. Alt (1997) has presented an entire catalog of dental anomalies suitable for intra-population analysis, for example incisor germination (twinning), talon cusps, or premolar odontomes (Fig. 2a–c). Malocclusion includes information on tooth rotations, displacements, false eruption directions, diastema, tooth transpositions, and occlusal plane Angle classes (Fig. 3a,b). Postcranial anomalies are most useful at this scale of analysis, for example, sacralization of lumbar vertebrae, humerus supracondylar processes (Fig. 4a) and os intermetatarsium (Fig. 4b). Accurate reporting of skeletal and dental anomalies requires extensive knowledge of the human skeleton and there are few sources that summarize this range of variation (see Barnes, 1994). In addition, recording anomalies is not typical of basic descriptive analysis.

KINSHIP ANALYSIS AND CEMETERY STRUCTURE

In a kinship analysis, the goal is to identify members of family groups based on the shared presence of rare or anomalous phenotypic traits, or on greater metric similarity among presumed relatives in comparison to a reference standard. In the more general consideration of cemetery structure, the goal is to identify social or politi-

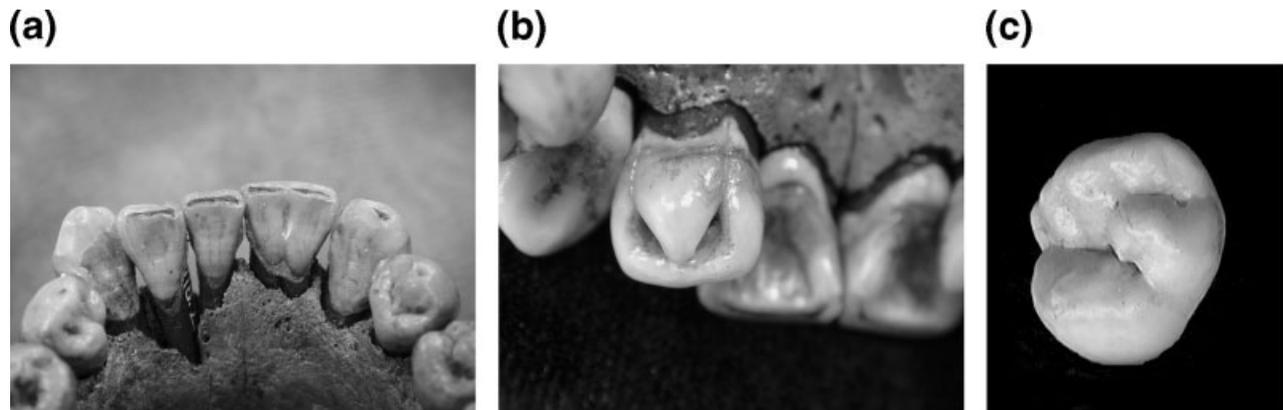


Fig. 2. (a–c). Three examples of rare tooth anomalies: a) twinning or germination on mandibular right incisor 1 and 2, b) talon cusp on maxillary left incisor 2, c) Uto-Aztecan premolar.

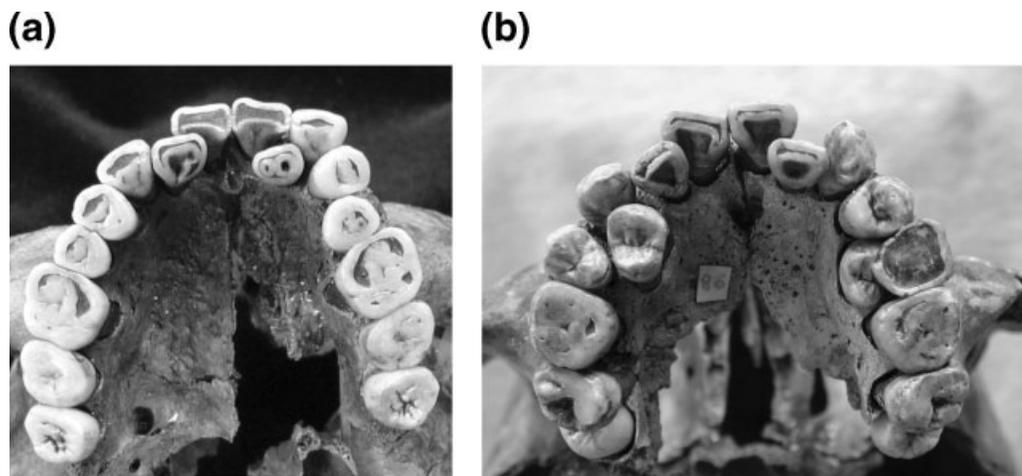


Fig. 3. (a–b) Malocclusion in the maxillary dentition: a) moderate malocclusion with complete palatal displacement of the lateral I^2 s and left P^4 , note the unusual morphology of the left I^2 , b) extreme malocclusion with palatal displacement of both I^2 s and both P^4 s, the premolars are rotated 90 degrees and the canines (particularly the left) are likewise rotated slightly. Note the large distal accessory ridge on the left canine.

cal groups above the family level such as clans, moieties, or bands. Examples of the latter, which are less common include works by Birkby (1982) and Byrd and Jantz (1994) which differ little methodologically from the study of temporal microchronology discussed below. We center our discussion on the more prevalent kinship analysis literature which, to this point, has focused on two topics despite the grander potential often stated. The most prevalent research focus is methodological. Researchers are concerned with determining which types of traits are most useful for kinship reconstruction and defining methods best suited to this task. The second focus is related to the archaeological context, for example, reconstructing site-formation processes, determining whether a cemetery is kin-structured or whether graves with multiple skeletons contain closely related individuals. These analyses have greatest significance when interpreted in reference to regionally-contextualized archaeological data. Despite the narrow range of application more significant goals are often stated, which reflect the potential of kinship analysis within bioarchaeology. According to Alt and Vach (1998) kinship analyses are

useful for delineating burial practices, reconstructing mating patterns, defining the manner in which social families were constituted, and reconstructing the nature of ascribed inequality in reference to social positions. (Case, 2003) noted the potential of kinship reconstruction for implementing finer-grained levels of analysis, for example cross-referencing the distribution of economic and political resources within and among specific lineages within a population. Much of this potential remains unrealized. It is important to note that, unlike postmarital residence analysis which engages social theory directly, bioarchaeological kinship analysis does not reconstruct kinship systems in past societies. Recent molecular contributions have been more successful in this regard, identifying spatial patterns of genetic variability consistent with patri- or matrilineal burial structure (Usher and Weets, 2001; Usher et al., 2002, 2003; Dudar et al., 2003; Usher, 2005; Usher and Allen, 2005). However, this is far removed from the degree of social complexity documented in modern human populations. In addition, mechanisms of phenotypic inheritance limit the specificity of kinship reconstructions. The “fuzzy” limits

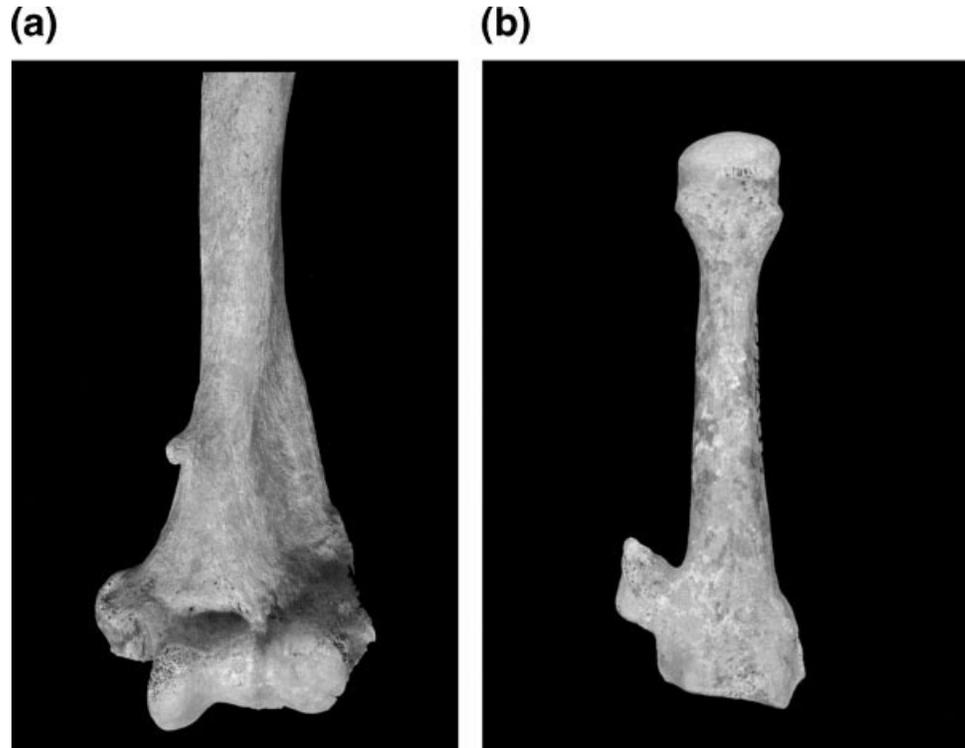


Fig. 4. (a–b) Two examples of postcranial anomalies: a) humerus supracondylar process; b) os intermetatarsaleum, an accessory bone found between metatarsal 1, metatarsal 2 and the first cuneiform; fused in this example. Photographs are courtesy of D. Troy Case.

of a family group make exact enumeration of relationships difficult for even moderately-sized burial series. As noted by Thompson (1986), “each generation is only a particular realization of all the events that could have occurred in the segregation of genes from parents to offspring. Even if, on average, the characteristics of offspring were those of their parents, over a period of time random fluctuations would occur. If the same genealogical process occurred again . . . one would not expect to see the same alleles present in descendant individuals.” For this reason, kinship analyses, with rare exception (see Alt and Vach, 1992, 1995a; Spence, 1996), do not specify the exact nature of genetic relationships among individuals, which requires a priori knowledge of the genealogical or demographic structure of graves often only available in historic contexts. Here again, recent genetic contributions have been more successful (Gill et al., 1994; Hummel and Hermann, 1997; Gerstenberger et al., 1999; Shinoda and Kanai, 1999). In summary, bioarchaeological kinship analysis identifies individuals who are likely to be closely related but rarely specifies the exact genealogical nature of this relationship.

Previous research by bioanthropologists

Sjøvold (1976–77) attributes the origins of bioarchaeological kinship analysis to the work of Acsadi and Nemeskéri (Acsadi and Nemeskéri, 1957; Ullrich, 1962, 1969a,b). However, informal observations of rare anomalies within site-specific reports were, and remain, commonplace (e.g., Gejvall and Henschen, 1968; Kazachenko, 1979) such that tracking the origins of kinship analysis remains difficult. As with much else in bioarchaeology, the 1970s witnessed the rise in popularity of kinship studies. (Sjøvold, 1975, 1976–77) delineated several critical issues such as the difficulty of defining fami-

lies within large, homogeneously distributed cemeteries (subsequently addressed by Vach and Alt, 1993; Alt and Vach, 1994), the importance of minor, non-metric traits for identifying kin groups, and the near impossibility of pedigree reconstruction.

Methodological concerns continued to center research throughout the 1980s, reflecting the emergence of dental discrete trait variation in bioarchaeology. While both Hanihara et al. (1983) and Doi et al. (1986) presented successful uses of metric-based kinship analyses, the shift to a “pseudo-cladistic” approach whereby specific families (lineages) are identified by accumulations of alleles for rare phenotypic variants, was further promoted by Rösing’s influential writings (Rösing, 1982, 1986a,b,c, 1995; but see Case, 2003; Corruccini and Shimada, 2002; Adachi et al., 2003; Stojanowski, 2005d for recent examples of metric applications). Based on his analysis of two Egyptian X period elite tombs, Rösing (1986a) found metric traits were too susceptible to environmental variation and difficult to operationalize because the degree of phenetic similarity between kin is relative, a criticism which applies to polymorphic non-metric traits as well. Emphasis on discrete trait variation was clearly demonstrated in Rösing’s (1986b) group report: Kaufman analyzed kinship within cemeteries at Stein aum Rhein, Germany using abnormalities of chin morphology, Szilvássy (1982, 1986) reported on the potential of frontal sinus morphology for kinship analysis, and Nemeskéri documented high frequencies of six-segmented sacra in the royal Hungarian tomb of Szekesfehervár. The multiplicity of traits used, all of which are infrequently recorded, highlights the utility of rare anomalous morphology in kinship reconstruction. These papers, among others from the mid-1980s (e.g., Breitinger, 1980; Stuchlíková et al., 1985), are similar in their focus on small grave contexts or samples of known pedigree, which belies

TABLE 1. Kinship analysis studies by type of data

| | |
|-------------------------|---|
| Dental metric | Adachi et al. (2003), Bondioli et al. (1984), Bondioli et al. (1984, 1986), Matsumura and Nishimoto (1996), Stojanowski (2001, 2003a,b, 2005c,d), Strouhal, (1992) |
| Dental morphology | Alt and Vach (1991, 1992, 1994, 1995a,b), Alt et al. (1992, 1993, 1995a,b,c, 1996a,b, 1997, 1998), Bondioli et al. (1984), Bondioli et al. (1986), Christensen (1998a,b), Corruccini and Shimada (2002), Corruccini et al. (2002), Hammond et al. (1975), Howell and Kintigh (1996), Jacobi (1996, 1997, 2000), Kelley (1989), McClelland (2003), Pietrusewsky and Douglas (1992), Spence (1996), Strouhal (1992), Strouhal and Jungwirth, (1979) |
| Cranial metric | Bartel (1979, 1981), Bondioli et al. (1986), Byrd and Jantz (1994), Kelley (1989), Strouhal (1992) |
| Cranial non-metric | Alt and Vach (1992), Alt et al. (1995a,b), 1996 (1997), Bondioli et al. (1986), Larsen et al. (1995), Rubini (1996), Spence (1996), Strouhal (1992), Strouhal and Jungwirth (1979), Veleminský and Dobisiková (2005) |
| Postcranial traits | Bondioli et al. (1986), Veleminský and Dobisiková (2005), Gejvall and Henschen (1968), Pietrusewsky and Douglas (1992), Strouhal and Jungwirth (1979) |
| Postcranial anomalies | Case et al. (1998), Kelley (1989), Regan et al. (1999) |
| Digital pattern profile | Case, (2003) |
| Frontal sinus | Szilvássy (1986), Vliék (1995) |
| Paleoserology | Bodor (1974), Derrish et al., 1987, Salamon and Lengyel (1980), Stuchlíková et al. (1985) |
| Ancient DNA | Adachi et al. (2003), Corruccini et al. (2002), Clisson et al. (2002), Delefosse and Hänni (1997), Doi et al. (1985), Dudar et al. (2003), Fily et al. (1998), Gerstenberger et al. (1999), Hummel and Herrmann (1996), Oota et al. (1995), Ricaut et al. (2004a,b), Scholz et al. (2001), Schultes et al. (2000), Shimada et al. (2004), Shinoda and Kanai (1999), Shinoda and Kunisada (1994), Williams et al. (2002) |

their exploratory and methodological nature. This attention to discrete variation was paralleled in North America where a more regionally-contextualized orientation was adopted (Buikstra, 1980; Mackey, 1980; Molto, 1983; Konigsberg, 1987).

This emerging approach based on discontinuous morphology was subsequently adopted and most fully developed by Alt, Vach, and coworkers in a series of publications beginning in the late 1980s. Although Alt published several works on kinship analysis through 1991 (Alt, 1989, 1990, 1991; Vach and Alt, 1990), publication in German may have prevented widespread recognition in North American bioarchaeological research programs. This changed with Alt and Vach (1991), and this article, and those that followed, remain the most current and complete exposition on bioarchaeological kinship analysis. Alt's research methods and case studies have been the subject of recent review (Alt, 1997; Alt and Vach, 1998) and we refer the reader to these excellent sources for additional details. Building on earlier work by Ullrich (1969a,b), Sjøvold (1976-77), and Rösing (1982, 1986a,b), Alt and Vach fully develop the prerequisites for an archaeological kinship analysis: traits must be rare, heritable, genetically independent, easily observed, and independent of age and sex. The issue of independence was addressed by the microsymptom concept. A microsymptom is one phenotypic manifestation of a trait with a single genetic basis. For example, dental agenesis, peg/reduced forms, impacted or falsely erupted teeth, delayed eruptions, and microdontic cusp formations are all considered microsymptoms of dental hypoplasia (Alt, 1991, 1997). Alt and Vach have been most prolific in the use of kinship analysis in biological anthropology and their work (Alt, 1989, 1990, 1991, 1997; Alt and Vach, 1991, 1992, 1994, 1995a,b, 1998; Alt et al., 1992, 1993, 1995a,b,c, 1996a,b, 1997, 1998) which is mostly methodological, most visibly promotes the approach. Although their research continues to impact the field, the advent of molecular anthropology and improved ancient DNA extraction methods has added a genotypic component to archaeological kinship analysis.

Stone's work at Norris Farms in central Illinois pioneered this approach (Stone, 1996; Stone and Stoneking, 1993, 1999) and the extent of this analysis has not been duplicated. The work of Usher and colleagues is exemplary in its use of computer modeling to infer kinship structure within cemeteries (Usher and Weets, 2001; Usher et al., 2002, 2003; Usher and Allen, 2005; Usher, 2005) while Japanese scholars have focused on methodological issues in small grave contexts (Oota et al., 1995, 2001; Adachi et al., 2003, 2005).

The full range of phenotypic traits has been used for kinship analysis (Table 1). Presentation of this literature in table form provides a concise summary, which the reader can access. We are unable to comment on the historically precedent serology literature (Lengyel and Nemeskéri, 1963, 1964; Lengyel, 1964, 1968, 1975; Nemeskéri and Lengyel, 1965) or its replacement, ancient DNA. The latter has been the subject of recent review and we refer the reader here for additional methodological details (Hummel and Hermann, 1996; Schultes et al., 2000; Kaestle and Horsburgh, 2002).

A more useful structure for this overview is to consider differences in analytical context, which influence the methods used and the questions addressed. Three basic types of kinship analysis have been presented in the literature (Fig. 5a-c): 1) small grave analyses such as isolated double burials or small (less than ten individuals) burial environments such as tumuli, wells, and mounds, 2) large cemeteries that contain distinct burial areas, and 3) large cemeteries that do not contain distinct burial areas and are homogenous in spatial distribution of graves (Alt and Vach, 1998). The last garners the most potential for providing important bioarchaeological inferences, whereas the first two provide important case studies for developing appropriate methodologies.

Small grave contexts. In small grave contexts, the goal is to determine the degree of relatedness among individuals buried within a well-defined environment. These analyses are non-spatial in orientation and use comparative frequencies or measures of variability to draw con-

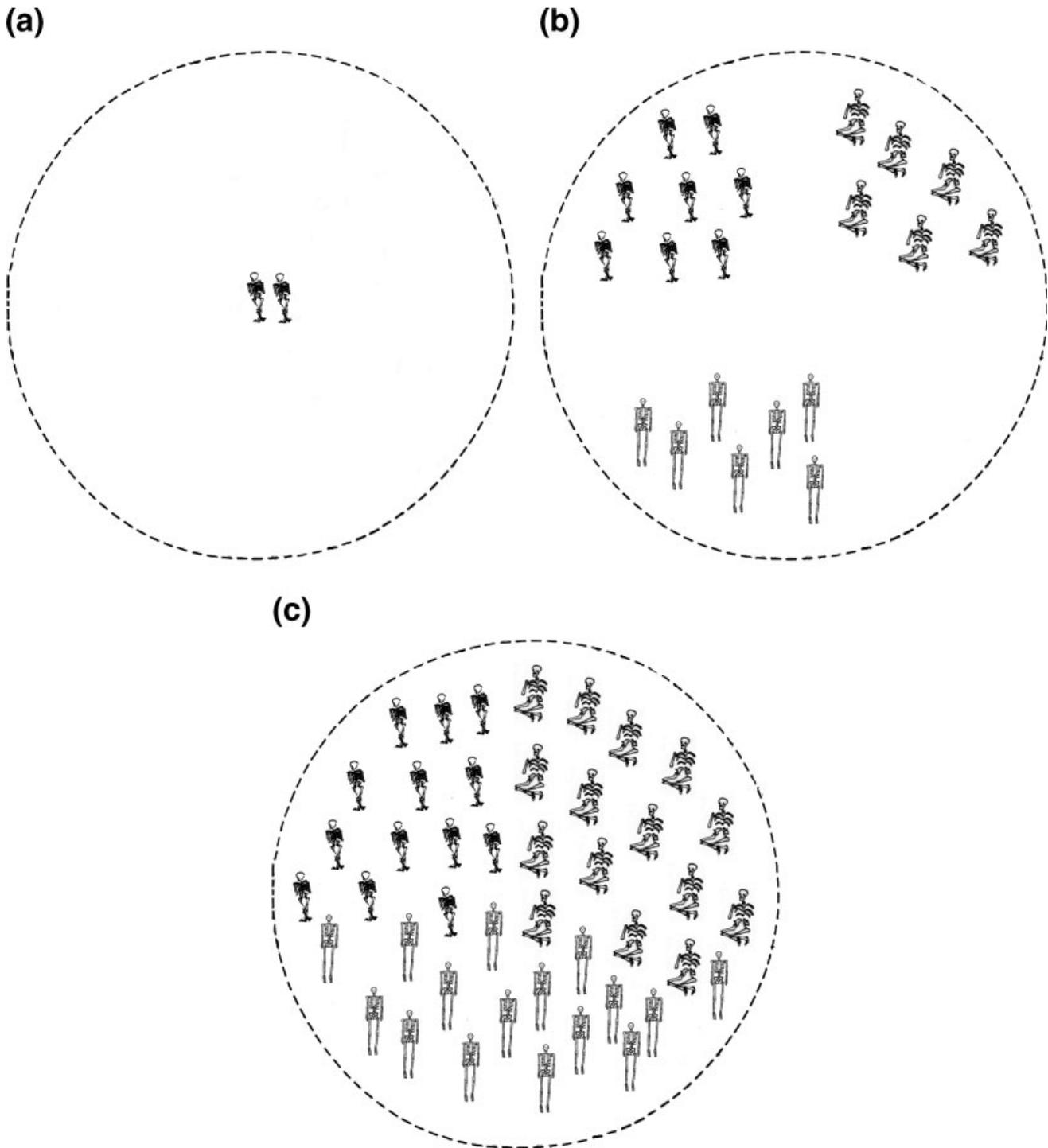


Fig. 5. (a–c). Different types of cemeteries pose different questions and methodological challenges for kinship analysis: a) small grave analysis, double burial, b) cemetery with spatial subdivisions clearly defined, c) cemetery with spatial subdivisions present but not visible to the observer. The different skeleton icons represent different family groups buried within each cemetery.

clusions about similarity and familiarity (e.g., Alt and Vach, 1992). Previous literature has three foci: 1) evaluating the performance of phenotypic or biochemical methods on samples of known pedigree (Rösing, 1986a,c; Spence, 1996; Velemínský and Dobisiková, 2005), 2) informal observations or case reports on anomalous or generally low frequency traits co-occurring within a

small grave environment (Gejvall and Henschen, 1968; Hammond et al., 1975; Pietrusewsky and Douglas, 1992; Larsen et al., 1995; Christensen, 1998b; Duncan, 2005), and 3) formal testing of the relatedness among individuals in a small grave environment (Stuchlíková et al., 1985; Vlíek, 1991, 1995; Alt and Vach, 1995a,b; Alt et al., 1995b, 1996a,b, 1997).

Within this literature, several studies are significant. Formal probabilistic methods for morphological kinship analysis were developed by Alt and Vach (discussed further below). Duncan's (2005) research on the dental morphology of skulls placed in rows and pairs within a temple at the Maya site of El Petén, Guatemala is also noteworthy because the kinship analysis was interpreted in the broadest context of ritualized ethnic violence and Maya worldview. Such anthropological contextualization is rare in the kinship analysis literature. Finally, the work of (Rösing, 1986a,b,c), Spence (1996), and Velemínský and Dobisiková (2005) is important because it demonstrates that phenotypic data can be used as a proxy for genetic relatedness in archaeological samples where pedigrees are wholly or partially known. For example, Spence (1996) used cranial and postcranial non-metric features to infer relationships among the multi-generational Wise family cemetery in Canada. He concluded that these types of traits performed well in kinship reconstruction despite their unknown genetic etiology. In this particular case, familial status was indicated by well-known features (accessory supraorbital foramina, palatine tori, missing zygomatico-facial foramina, patent spinosum foramina) as well as less commonly recorded variations (superior squamous foramina, sutura mendosa, talar facet reduction, and accessory posterior talar facet). Velemínský and Dobisiková (2005) reported moderate success in reconstructing the historical genealogy of eight individuals from Sweets-Sporck's family tomb in the Czech Republic. Using over 170 postcranial and cranial non-metric features, they demonstrated high trait concordance among fathers and sons, and among cousins of both sexes but not among siblings. In-marrying females were also morphologically discernible. As with Spence (1996), both commonly recorded (palatine torus, costal facets of C7) and uncommonly recorded (sella turcica variation and ponticuli basales ossis sphenoidalis) variants were indicative of generational relationships. Both studies, therefore, highlighted the importance of observer knowledge in kinship analysis and the required presence of "private traits" (sensu Rösing, 1986a) for familial diagnosis. Reliance on rare anatomical variants, while the hallmark of the German school (Rösing, 1986a; Alt and Vach, 1991, 1998) does limit the range of application to only those contexts in which rare traits have, by chance, manifest within a particular lineage.

In addition to morphological analyses, paleoserological methods have been presented in Bodor (1974), Salamon and Lengyel (1980), and Strouhal (1992) while mtDNA sequencing has been used to affirm (Gill et al., 1994; Hummel and Herrmann, 1997; Gerstenberger et al., 1999; Scholz et al., 2001) or deny (Shinoda and Kunisada, 1994; Delefosse and Hänni, 1997; Fily et al., 1998; Shinoda and Kanai, 1999; Clisson et al., 2002; Adachi et al., 2003, 2005; Ricaut et al., 2004a,b) close genetic relationships within graves. Of the genetic studies, several deserve further discussion. Shinoda and Kanai (1999), Shinoda et al. (1998), and Matsumura and Nishimoto (1996) examined genetic and odontometric diversity at the Jomon period Nakazuma site, Japan. Both sources of data suggested a non kin-based interment pattern. That tooth sizes produced results consistent with mitochondrial DNA sequences affirms their utility in intracemetery approaches. In fact, Adachi et al. (2003) found

dental metrics more useful than mitochondrial DNA in confirming a close genetic relationship between two burials from Usu-Moshiri, Japan (see also Adachi et al., 2006). Genetic researchers have primarily used sequencing of autosomal STRs and mtDNA HV region I and II and control region comparisons in their assessment of genealogical structures. Y chromosome haplotype comparisons (e.g., Gerstenberger et al., 1999) and comparative haplotype diversity methods (Shinoda and Kanai, 1999; Adachi et al., 2003, 2006) have been more limited in application. Despite use of more formal genetic analyses, anthropological interpretation is generally minimized, indicative of the methodological focus of small grave kinship analyses in general.

Spatially structured cemeteries. The second type of kinship analysis seeks to identify families or social groups such as clans or bands within a cemetery that has physically distinct burial areas, interment types or archaeological indicators of social divisions that can be used to generate hypotheses about social structure (Alt and Vach, 1995a). In most cases, the sample size determines whether inferences are at the family level (smaller sample sizes) or at some level of social or political organization above the level of the individual family (e.g., Birkby, 1982; Byrd and Jantz, 1994). The majority of these analyses rely on archaeological evidence to define suspected social groupings within the larger mortuary complex (Bartel, 1979, 1981; Strouhal and Jungwirth, 1979; Zhongpei, 1981, 1985; Birkby, 1982; Corruccini et al., 1982, 2002; Bondioli and Macchiarelli, 1984; Bondioli et al., 1984, 1986; Bentley, 1986; Byrd and Jantz, 1994; Alt et al., 1995c; Howell and Kintigh, 1996; Rubini, 1996; Corruccini, 1998; Corruccini and Shimada, 2002; McClelland, 2003; Shimada et al., 2004) such as spatially distinct burial areas, mound interments at multi-mound complexes, or distinctive grave goods. Others have used more informal spatial definitions such as center versus periphery (Underwood, 1969; Tainter, 1976) quadrant areas designations (Saunders, 1990), sections of architectural features such inside/outside or front/back (Jacobi, 1996, 1997, 2000), or burial rows (Gao and Lee, 1993; Stojanowski, 2005d).

Within this literature several studies deserve mention. Shinoda and Kunisada (1994) and Oota et al. (1995) presented genetic and morphological analyses and documented a high degree of concordance between these data sets. This further supports our view that morphology can be used to infer relationships between individuals at such a small scale. Dudar et al. (2003) is also noteworthy for the extent to which the kinship analysis was incorporated with broader issues of pioneer history in 19th and early 20th century Canada. Finally, Shimada, Corruccini and Shinoda discuss the biological structure of graves at the elite tomb at Huaca Loro, Peru (Corruccini and Shimada, 2002; Corruccini et al., 2002; Shimada et al., 2004). Using both dental metric and morphological data and ancient DNA, the authors generated a highly contextualized picture of social structure and identity at this Sicán period tomb. As with other morpho-genetic analyses, both phenotypic and genotypic data produced relatively concordant results and acted in complementary fashion to further illuminate the relationships among burials in the tomb.

Uniformly distributed cemeteries. The third type of analysis identifies closely related individuals within large cemeteries that lack clearly-defined subgroupings.

The analytical difficulties presented by a non-structured cemetery have resulted in a primary focus on methodology. Alt and Vach have been most prolific in morphological research (Alt and Vach, 1991, 1994, 1995a,b; Alt et al., 1993; Vach and Alt, 1993) and have presented several different methods for ascertaining groups of relatives within large cemeteries (discussed below). Case (2003) developed a methodology based on metacarpophalangeal pattern profile analysis that differs considerably from that of Alt and Vach. Despite primary focus on methods, others have used kinship analysis within anthropologically contextualized case studies. Most notable is the work of Gamble et al., (2001) who presented a multi-faceted analysis of the Chumash Malibu cemetery in California. In this paper, kinship analysis was one component of a broad bioarchaeological study of postcontact social change within a California tribal population. Finally, Usher and colleagues presented a novel clustering method for detecting kinship structure and postmarital residence within cemeteries (Usher and Weets, 2001; Usher et al., 2002, 2003; Usher, 2005; Usher and Allen, 2005). The analysis uses Y chromosome and mtDNA lineage distributions within cemeteries to detect patterns of lineage density consistent with patrilineal or matrilineal spatial segregation. Application on historic period Amish cemeteries indicated a patrilocal and patrilineal social organization for these communities (Usher and Weets, 2001; Usher et al., 2002, 2003; Usher, 2005; Usher and Allen, 2005).

Theoretical basis for kinship analysis

Kinship analysis is based on a simple and familiar premise: members of a family are more phenotypically similar to each than to contemporary unrelated individuals. In terms of metric variation this manifests as similarity in size and shape, and in terms of morphological variation this manifests as the joint presence of morphological anomalies or variants. Phenotypic similarity results from family members sharing genes that are identical by descent, and close relatives are more likely to do so, as opposed to spurious situations in which alleles are identical by state (the alleles are the same) but not by descent (inherited from a recent common ancestor) (Thompson, 1986; Konigsberg, 2000). Kinship coefficients (Ψ) represent the probability that an autosomal gene chosen randomly from one individual is identical to a homologous gene chosen randomly from a second individual, and this term is mathematically linked to the coefficient of relatedness (Blouin, 2003). The coefficient of relatedness (r) is the, "expected fraction of alleles that are shared identical by descent (Blouin, 2003)." Coefficients of gene identity (k_0, k_1, k_2) represent the probabilities of particular relationships sharing 0, 1, or 2 alleles in common that are identical by descent.

There are many categories of relationship that have the same expected identity by descent coefficients and/or coefficients of relatedness. Thompson (1986) identified four categories of relationship that can be distinguished genotypically from one another, although she was working at a time when genetic technologies were less developed: 1) nuclear family relationships between parents and offspring and between siblings, 2) close relationships (first cousins, half sibs, double first cousins), 3) more remote cousins, and 4) unrelated individuals. This is similar to, although not identical to, the categories presented by Blouin (2003: Table 1). One should note that

advances in genome scanning technologies have improved pedigree analysis, although large numbers of unlinked loci are typically needed to differentiate relationship categories that share similar coefficients of gene identity. The crude parceling of genealogies reflects the multitude of factors that affect our ability to infer the relationship between any two skeletal individuals: 1) the number of generations that separate them; 2) trait linkage and linkage disequilibrium; 3) effective population size; 4) assortative mating and inbreeding in the current generation; 5) homozygosity in the founding lineage; 6) allele frequencies for traits (the genetic diversity present); and 7) within-family versus between-family environmental variation. Much of this information is unknowable for archaeological populations and in most cases pedigree analyses based on alleles are not possible. As a result, the conceptual frame of reference of archaeological kinship analyses differ from those based on modern populations.

Most studies of kinship in archaeological contexts highlight the importance of using traits with high narrow-sense heritability. While heritability is central to the field of quantitative genetics (Konigsberg, 2000), bioarchaeologists are increasingly accepting the limitations of this concept for modeling relationships within prehistoric populations (see, for example, Eades and Desideri, 2003). Vitzthum (2003) provides a historical overview of heritability studies and should be consulted by bioarchaeologists with interests in phenotypic variation. Definitions of narrow-sense heritability are ubiquitous but do little to clarify the true purpose and utility of the statistic: predicting phenotypic response to artificial selection, and not resolving the nature-nurture debate (Vitzthum, 2003). Narrow-sense heritabilities are statistical estimates of the ratio of additive genetic to total phenotypic variation within a population. Appeals to heritability are based on the false assumption that these statistics tell us how "genetic" a trait is, its penetrance within families, or its degree of epigenetic canalization, a suite of trait properties Eades and Desideri (2003) refer to as "familiality." Narrow-sense heritabilities also do not consider the effects of dominance which could affect kinship analyses, particularly if lineages are highly inbred. Narrow-sense heritabilities also ignore the potential operational contribution of between-family environmental variation and cultural transmission. Common family environmental effects could result in similar within-family phenotypes and divergent between-family phenotypes, but for non-genetic reasons.

With these caveats in mind, some further comment on narrow-sense heritability is warranted. First, traits with high heritability are useful for kinship analysis. High heritabilities indicate high additive genetic variability in comparison to environmental variability. However, it is impossible to know trait heritabilities for an archaeological population unless the genealogical structure of individuals has previously been established. Extrapolation beyond the population for which a heritability was estimated is problematic. Second, traits with low heritability are not necessarily poor markers of kinship. There are many reasons why a trait has low heritability. While it is tempting to focus on the environmental variance component being too high, low heritability can also reflect a lack of additive genetic variance in the population. Natural selection, inbreeding and genetic drift all reduce additive genetic variance (Hartl and Clark, 1997) and traits related to fitness also have low heritabilities but

this does indicate a lack of genetic involvement in their expression (Konigsberg, 2000). Whether or not low heritability affects within-family patterns of inheritance, and the ability to identify family members within a cemetery, is difficult to generalize and depends in large part on the genealogical structure of the cemetery. Finally, dual emphasis on rare or anomalous traits and those with high heritability is counter-intuitive because rare variants, by definition, are uncommon in a population, likely to have very low additive genetic variance components, and therefore low heritability, and may not be identical by descent. Their presence within a family is due to chance. As Rösing noted, "there is no method which allows kinship reconstruction in any given ancient skeleton pair. Only in the very rare cases of private traits a reconstruction is sufficiently reliable (Rösing, 1986a)." Therefore, despite the veneer of formality by appealing to quantitative genetic theory, archaeological kinship analyses must remain organic and flexible in practice. Desirable traits are those that are highly variable in populations, thus allowing for segregation into different states within families, and also determined primarily by genetic factors. Narrow-sense heritability does not measure these factors.

Methods

The methodology adopted for kinship analysis depends on two factors: the measurement scale of the traits used for analysis (metric or non-metric) and the size and internal spatial structure of the cemetery being investigated. The latter is the primary determinant of methodology and we discuss previous research using this as a guide.

Small grave analyses. In small grave analyses, the goal is to determine whether individuals buried in the cemetery are closely related. There are two different phenotypic approaches to this question, one for metric traits and the other for non-metric traits. Neither considers spatial relationships.

The metric approach was developed by Japanese scholars and first presented by Hanihara et al. (1983). Hanihara et al. (1983) proposed using Q-mode correlation coefficients calculated between all pair-wise individuals based on dental metrics to determine whether individuals within a small grave are closely related (see Sokal and Sneath, 1963). Similar methods were adopted by Doi et al., 1985, 1986, Matsumura and Nishimoto (1996), Shinoda and Kanai (1999), Shinoda et al. (1998), and Adachi et al. (2003, 2006). What is interesting about these studies is their use of modern Japanese standards to estimate ranges of Q-mode correlation coefficients associated with specific degrees of relatedness, from monozygotic twins to full and half sibs. Hanihara et al. (1983) and Doi et al., (1985, 1986) compared the Q-mode scores among individuals within their study populations to known pedigree ranges based on modern Japanese dental casts to determine the degree of genetic affinity. Craniometrics can be evaluated in a similar manner, however, comparative modern dental data are more prevalent and preferred for this reason.

The second approach is based on the presence of rare non-metric features and the probability of these features co-occurring among individuals in a small grave environment by chance. Such methods were first proposed by Acsadi and Nemeskéri (1957) and by Ullrich (1962, 1969a,b). These methods and their limitations, primarily factor weighting, were discussed by Sjøvold (1976-77) who presented an alternative model that uses reference

sample data to determine the trait rarity and the probability of finding multiple examples of that trait in a sample of a specific size. Sjøvold (1975) provides probability calculations, which are relatively straightforward but complicated by missing data and bilateral trait scoring. Alt and Vach (1992) presented a similar model based on binomial probabilities and trait frequencies in a reference population. Given a subset of individuals suspected to be a family, the null hypothesis tests whether the particular density of traits within that suspected family group are likely to co-occur at random given the frequency of those traits in a reference population (Alt et al., 1997). More complex formulae that consider missing data and trait symmetry are presented in Alt and Vach (1992). Univariate techniques must consider family-wise error. Alt et al. (1997) suggest a Bonferroni correction in which the global *P*-value for multiple univariate tests is determined by dividing the desired alpha level by the total number of tests. What is most critical for these approaches, however, is the selection of a suitable reference population. This is exceedingly difficult for archaeological samples (see examples in Alt and Vach, 1995a,b; Alt et al., 1995b, 1996a,b, 1997). Sjøvold (1976-77) suggested that trait frequencies in a suspected family group within a larger cemetery (with some spatial structure) can be compared against the overall trait frequency in that cemetery. This ameliorates concerns with reference sample representativeness. This reasoning, however, seems circular.

Spatially structured cemetery analyses. Cemeteries in which spatially discrete subdivisions are present provide fewer methodological challenges and most have used standard inferential or discriminatory statistical methods. The assumption is that social groups such as families are more phenotypically similar to each other than to non-related individuals. Variation within a family is, therefore, lower and if the archaeological groupings represent family plots then biological affinity should be greater within plots than between plots. Because the suspected social groups are defined a priori, standard statistical tests are used to verify the null model. A variety of different techniques have been used. For non-metric traits, frequency differences between burial groupings can be tested using standard Fisher's Exact or chi-square tests (Strouhal and Jungwirth, 1979; Corruccini et al. 1982; Alt et al., 1995c; Howell and Kintigh, 1996; Rubini, 1996). For metric traits, ANOVA (Bondioli and Macchiarelli, 1984; Bondioli et al., 1984, 1986) and discriminant function analysis have been used (Bartel, 1979, 1981; Gao and Lee, 1993; Byrd and Jantz, 1994; Jacobi, 1996, 1997, 2000; Stojanowski 2005d). It is important to consider the distributional and methodological assumptions associated with each of these analyses.

Others have used biological distances to determine the pattern of inter-individual similarity. Examples of previous measures include the mean measure of divergence (MMD) (e.g., Birkby, 1982) and Euclidean distances (e.g., Corruccini and Shimada 2002; Corruccini et al., 2002). Because biological distances are not independent, their statistical significance cannot be assessed using standard inferential statistics. Bondioli et al. (1986) first presented a novel test statistic based on the rank order of phenotypic distances in reference to hypothesized burial structure. The method compares the rank of the within-subgroup distances to the between-subgroup distances and tests for significant count differences using a chi-

square analysis. This method was also used by Corruccini and Shimada (2002) and Corruccini et al. (2002). Finally, (Stojanowski, 2005d) used bootstrap resampling to analyze the pattern of phenotypic variances among burial subgroupings. In this case, bootstrapping was used to equalize sample sizes and provide *P*-values for variance differences within- and between hypothesized lineage groupings.

Uniformly distributed cemetery analyses. In the absence of internal spatial divisions, kinship analysis is more challenging because suspected family groups must be identified without reference to internal spatial distinctions. Three approaches have been used. The first is spatial correlation analysis which tests for overall correspondence between phenotypic and spatial distances, the second is a nearest neighbor count method that tests for spatial clustering of traits, and the third is a non-spatial block search procedure that simultaneously identifies suspected relatives and the traits indicative of their degree of relatedness.

Spatial correlation analysis tests for a significant correlation between a spatial distance matrix and a phenotypic distance matrix. If the cemetery is kin-structured then closely related individuals are buried closer together and there is a positive correlation between the distance matrices. Because the cells within each matrix are not independent, a permutation method is needed to generate significance values. Mantel's (1967) test has been used widely in a number of contexts (see Smouse and Long, 1992; Manly, 1998). The choice of a phenotypic distance statistic is complex and dependent on the data scale and the number of missing observations. Defrise-Gussenhoven (1967) and Defrise-Gussenhoven and Orban-Segebarth (1984) provide an inter-individual estimate of the Mahalanobis generalized distance for metric traits. Missing data are not permitted, however. Alt et al. (1995a) present a simple matching coefficient for non-metric data that is more flexible. For each pair-wise comparison (*i*, *j*) the number of traits that are found in both individuals (*i* and *j*) is divided by the number of traits observable for both (*i* and *j*) and present in at least one (*i* or *j*). Many other types of ordinal distance statistics are discussed in general qualitative statistics texts (see also Constandse-Westermann, 1972). McClelland (2003) and Gamble et al. (2001) used Gower similarity coefficients which are most flexible because they incorporate metric and non-metric variables and missing data are not a problem (see Wishart, 2004 for computational details; also www.clustan.com).

Although use of matrix correlation analysis is valid computationally, a phenetic approach will not be satisfactory because families are typically indicated by only a few traits that will be swamped in the distance statistics unless variables are weighted (Alt and Vach, 1995a). One solution is to weigh the relative merit of each variable by its sample frequency, with rare traits afforded greatest value. Obviously metric traits must be treated differently. Another problem with the matrix correlation approach is its insensitivity to internal spatial structure within the data matrices. If multiple lineages are buried within a larger cemetery, and within each lineage there is kin-structured burial, the matrix correlation method may not detect this internal spatial structure. The result is an insignificant *P*-value. This concern was discussed by Stojanowski (2001, 2003b) and a model was presented to estimate the number of distinct lineages within a cem-

etry, assuming kin-structured burial did occur within each lineage.

The second approach for kinship analysis in cemeteries without spatial subdivisions uses count methods to test for non-random trait clustering. In Alt and Vach (1991) a univariate method to test whether a phenotypic trait is spatially clustered and indicative of family-oriented burial within a larger, homogeneously distributed cemetery was presented. These authors used a spatial autocorrelation model based on counts of positive trait expressions within an arbitrarily defined section of a larger cemetery (called a neighborhood). Neighborhoods can be defined based on a specified distance from each positive expression of the trait (preferred if the overall grave distribution is uniform) or on a standardized count of nearest neighbors (preferred if density differs throughout the cemetery). For each individual demonstrating the trait in question, the numbers of other individuals within the neighborhood that also express the trait are counted. These individual scores are summed for all positive expressions of the trait. With this method one begins with a large cemetery without spatial structure. By scoring a battery of non-metric traits, the observer finds some that appear to occur in distinct spatial clusters. The method presented in Alt and Vach (1991) formally tests whether the observed clustering of the trait is expected by chance alone, given the frequency of the trait within the cemetery, the number of individuals expressing the trait, and the number of individuals not expressing the trait. Details of statistical computation are fairly complex and presented in Alt and Vach (1991). A similar nearest neighbor approach (Orton, 1982) was used by Stone and Stoneking (Stone and Stoneking, 1993; Stone, 1996) in their analysis of the Norris Farms cemetery in Illinois. Many other options are available for testing for spatial auto-correlation, for example, unit-area randomization tests (Mead, 1974 and see Manly, 1998), join counts analysis (Rosenberg, 2001), and proximity-based clustering algorithms (see applications in Usher and Weets, 2001; Usher et al., 2002, 2003; Usher, 2005; Usher and Allen, 2005). Many analyses are provided in PASSAGE (Pattern Analysis, Spatial Statistics, and Geographic Exegesis) available at www.passagesoftware.net. Choosing an appropriate test is highly dependent on the circumstances of burial and the general structure of the cemetery being investigated.

The third approach for kinship analysis in cemeteries without spatial subdivisions uses computer searches for blocks of related individuals and identifies the phenotypic traits that indicate their family status (Alt and Vach, 1993, 1995a,b, 1998; Vach and Alt, 1993). This methodology is unique to kinship analysis and differs considerably from other approaches. Whereas spatial autocorrelation analyses begin with a distribution of variants and test for non-random spatial patterning, this approach does not use any spatial information. The assumption is that rare traits are indicative of familial status, regardless of their spatial distribution within the larger cemetery. The purpose of the method is to identify these traits and those individuals that express them. In contrast to the nearest neighbor approach of Alt and Vach (1991), this method is less sensitive to the presence of affinal or completely unrelated individuals such as servants within the burial environment. The computational details of this model are extremely complex (see Alt and Vach, 1993) and the agglomerative search strategy is time consuming and not tractable without a computer search algorithm. The test statistic is the probability of



Fig. 6. Map of the United States with locations of samples used in case study indicated. CC = Chaco Canyon, M = Mobridge, P = Patale, S = Sully, SL = San Luis de Apalachee, SCDG = Santa Catalina de Guale, SCDG-SM-Santa Catalina de Guale de Santa Maria, W = Windover.

observing a set of T independent traits in s individuals given the rarity of the traits. Alt and Vach (1993, 1995a,b) stress that this method only produces a hypothesized family unit that must be evaluated using subsidiary archaeological and demographic data. We know of no independent use of this method. This is unfortunate because it offers the most potential for making significant anthropological inferences within past populations.

Case study: Death and burial at Windover Pond, Florida

Although cemeteries are not uniquely associated with sedentary horticultural societies, they are uncommon in hunter-gatherer populations, particularly of the size discovered at Windover Pond, Florida (Fig. 6). The site was excavated in the mid-1980s and over 160 well-preserved individuals were recovered as well as numerous artifacts made from perishable materials (Doran, 2002). Burial in an anaerobic, aqueous, peat environment allowed the preservation of antler and bone tools (Penders, 2002), floral remains such as bottle gourds and gut contents (Newsom, 2002), woven textiles (Andrews et al., 2002), and the wooden burial stakes that were used to secure the deceased to the pond bottom (Adovasio et al., 2002). The preservation of 91 human brains was also noteworthy (Doran, 2002). Analysis of cemetery structure and the identification of kin groups at this Early Archaic period (ca. 6,980–8,120 ybp) mortuary pond provides important information on site formation processes, hunter-gatherer mortuary practices, and aspects of early Holocene social and political structure in Florida.

Burial at Windover occurred on the shallow margins of a pond with differential burial density around the perimeter. Our analysis focuses on material from Pond C which has the highest burial density, the best preservation, and the least amount of post-depositional disturbance (see Doran, 2002: map 1.5 for information on the excavation strategy). Preservation of perishable artifacts provides a unique perspective on hunter-gatherer burial practices that help inform our analysis. First, the wooden stakes that secured burials to the pond bottom

were two distinct sizes. Those with a smaller diameter were clearly functional and found penetrating the burial shrouds of several individuals. The larger stakes, however, had taphonomic signatures suggesting they were visible above the water line and it is proposed they marked burial plots within the pond (Adovasio et al., 2002; Andrews et al., 2002; Dickel, 2002). Because of the difficult logistics of burying a body under water, and the annual variation of water level within the pond, we propose pie-shaped segments were demarcated using wooden stakes and these segments were used by specific social groups within the broader Archaic population. That distinct social groups used the pond for burial is also suggested by differences in raw material size of the woven burial shrouds. Andrews et al. (2002) documented six different textile weaving patterns, but there was no spatial patterning. However, differences in thread size used to weave the fabrics suggest an east-west division within Pond C, which we confirmed using cluster analysis of inter-grave distances (Fig. 7). This central division is our null model for the general structure of the cemetery. Within each half (Pond C east and Pond C west) we expect to find evidence for kin-structured burial.

Data were collected for 23 craniometric, 80 dental morphological, 83 cranial non-metric, and 128 odontometric variables. In addition, 12 malocclusion variables and 30 dental anomalies were observed. We used a number of different analytical methods. To compare phenotypic similarity between Pond C east and west we used cluster analysis of Gower similarity coefficients estimated from 97 variables (10 odontometric, 15 dental morphological, 57 cranial non-metric, and 15 craniometric). We also compared non-metric trait frequencies between the burial units. Kinship analysis was complicated by the unique burial environment which we propose precluded burying kin in predictable clusters. Therefore, we plotted each non-metric variable and visually assessed the patterns. We propose two patterns should reflect kin-structured burial: 1) proximity clustering indicates relatives who were buried when the water level in the pond was at the same height; 2) perpendicular orientation of traits in relationship to the pond margin indicates relatives who were buried within a designated section of the pond at times when the water level was different. We also used a

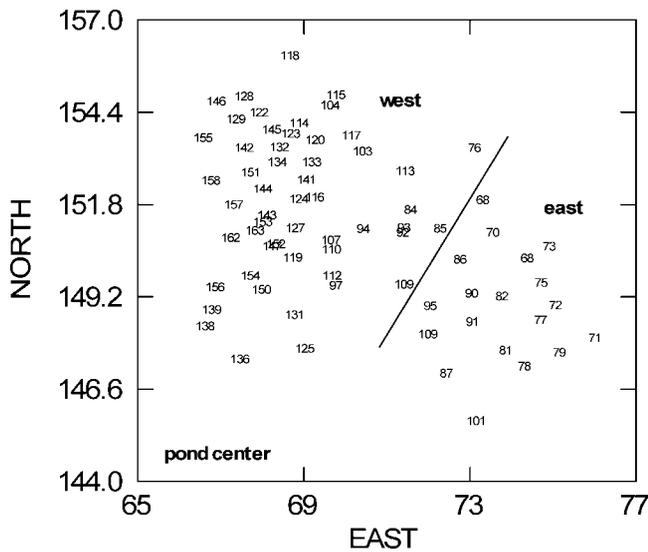


Fig. 7. Division of Windover pond C based on cluster analysis of burial densities. Burial numbers indicate grave locations. The pond center and the division between East and West subgroups are indicated. Axes are burial coordinates measured in meters.

resampling method to compare average spatial distances between genetic nearest neighbors.

The cluster ordination (Fig. 8) indicates burials were divided into east (a) and west (b) burial cohorts. East burials form a tight cluster located within branches a_1 and a_2 . The former contains Pond C east individuals only, whereas the latter has two subsidiary branches (a_{2a1} and a_{2a2}) with one representing only Pond C east burials and the other burials from Pond C west that were buried near the hypothesized central division. The three Pond C east outlier burials (95, 101, and 109) are located at the lowest elevations within Pond C east and are buried in an orientation parallel to the pond margin, suggesting a near contemporaneous interment. It is interesting that the three Pond C east outliers are all located at the lowest vertical level within this section of the cemetery. The primary branch b contains only Pond C west burials. The hypothesized division of Pond C into two halves based on spatial and fabric construction analyses (Andrews et al. 2002) is well supported by this multi-trait analysis of phenotypic similarity.

The univariate analyses of non-metric trait distributions supported this result. Approximately 41% of cranial and dental discrete traits were differentially present in Pond C east and west, although significance tests of these associations were hindered by small sample sizes. Trait frequency differences are easy to generalize. Individuals buried in the western half of the pond had more complex maxillary crown morphologies such as shoveling and double shoveling, tubercula dentale, interproximal grooves, and extra molar cusps. Malocclusion was not common in Pond C west while maxillary trema (midline diastema) were. On the other hand, Pond C east burials had simpler maxillary crown morphologies with more limited evidence for mandibular crown complexity in the form of M_1 protoconids and three-cusped premolars. Maxillary crowding and malocclusion was common and often severe in Pond C east (see for example Fig. 4b). These data suggest a significant social division is represented within the cemetery.

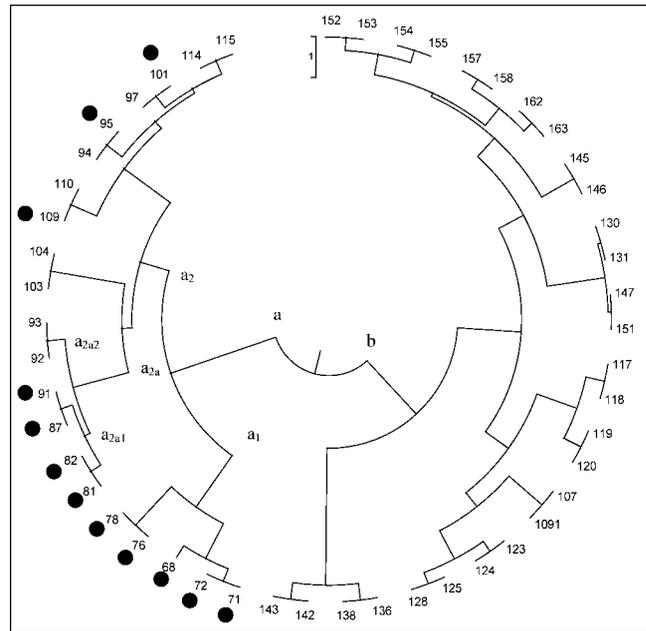


Fig. 8. Cluster analysis of inter-individual Gower similarity coefficients for Windover burials. Pond C east burials are indicated by circles.

To explore further biological patterning within the cemetery, we adopted a nearest-neighbor randomization approach that considers the average spatial distance between genetic nearest neighbors for given ranks of similarity (Table 2). Each individual has a genetic nearest neighbor, a second nearest neighbor, etc. If burial was kin-structured then the spatial distance between genetic nearest neighbors should be smaller than between individuals at lower positions within the genetic ranking. For example, for all individuals at Windover the average spatial distance between genetic nearest neighbors was 5.21 units, whereas the average spatial distance between genetic furthest neighbors was 9 units. Statistical significance was based on random sampling of spatial distances and designed to test whether using information on genetic similarity produces lower average spatial distances than expected by chance. Data in Table 2 indicate that genetic nearest neighbors are significantly spatially clustered. Using a more liberal alpha level of 0.10, these data suggest that on average only three individuals (ego plus two genetic nearest neighbors) could be buried in spatial proximity.

Finally, analysis of non-metric trait spatial distributions supported the hypothesis of kin-structured burial perpendicular to the pond margin. Numerous traits demonstrated a perpendicular spatial orientation suggestive of division of the pond by kin groups using the same segment of the pond over several generations. Two examples are presented in Figure 9a,b. As water level fluctuated, burials were placed at different depths within the pond, but within the appropriate section.

Analysis of cemetery and kinship structure at Windover highlights the dynamic nature of this burial environment. Results suggest use of the pond by at least two genetically distinct subpopulations which we assume to be bands. That the biological data were patterned similar to differences in textile manufacturing techniques is also intriguing and may suggest a matrifocal aspect

(assuming females did the weaving) of hunter-gatherer mortuary practice not previously documented. Kinship analysis provides insight into the manner in which the site was used, likely by the same groups of people over extended periods of time in which water level fluctuation within the pond was significant. Use of marker stakes reflects concern with lineage boundaries that existed in death and likely in life as well. The lack of proximity burying suggests that mortality was low in relationship to the rate of change of water level in the pond. Future research on health, demography and mortuary patterning will, therefore, be better informed by considering these internal spatial and biological differences.

POSTMARITAL RESIDENCE AND SEX-SPECIFIC MIGRATION

Historically, the concept of social integration has been important in the development of anthropological theory. Understanding how individuals or groups are integrated into a cohesive system is essential to the study of the evolution of sociopolitical and economic complexity in prehistoric societies. Social structure, which refers to the static rules that govern or guide social relations within a society (Barrett, 1976), is an essential component to integration, as is social organization which refers to the

ordering of social relations through dynamic processes (Green, 1976a). Although the terms “social structure” and “social organization” are often used synonymously (e.g. Eggan, 1950), some scholars, including Firth (1951) and Radcliffe-Brown (1952), distinguish between these two important concepts (see discussion in Sarana, 1991).

We have chosen to use the term “social organization” here because the rules that comprise social structure in prehistoric societies are not amenable to study by archaeologists and biological anthropologists. The dynamic ordering of social relations through individual or collective choice or action, on the other hand, may have consequences with respect to the distribution of material culture, architecture, and biological variation. For example, within the present-day Hopi community of Orayvi in Arizona, although the extended matrilineal family is the ideal condition determined by cultural rules or norms of Hopi social structure, the majority of households represent neolocal nuclear families (see Cameron, 1999). Similarly, with respect to the matrilineal Hopi kinship system, kin terms and relations are determined by social recognition not necessarily by genealogical relations (Eggan, 1950). While a kin relationship is recognized between the ego and the mother’s mother’s brother’s son, no such recognition is given to the relationship with the father’s father’s brother’s son, despite the similarity in genealogical relationships (Eggan, 1950). In both of these examples, discrepancies between the static rules or ideals of social structure and the dynamic process of social organization are not observable in the archaeological record (see Hill, 1970 for a similar discussion).

Postmarital residence, as one aspect of social organization, is an important component to social integration in prehistoric societies. Residence rules provide a culturally defined system for incorporating outside members into a community. As such, postmarital residence can play an essential role in regional integration or aggregation by

TABLE 2. Average genetic and spatial distances by genetic neighbor rank at Windover Pond

| | Ranks | | | | | N |
|---------|-------|-------|-------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | |
| Genetic | 1.06 | 1.47 | 1.75 | 1.96 | 2.20 | 13.68 |
| Spatial | 5.21 | 5.65 | 7.41 | 6.47 | 5.77 | 9.00 |
| P-value | 0.028 | 0.086 | 0.595 | 0.263 | 0.106 | 0.071 |

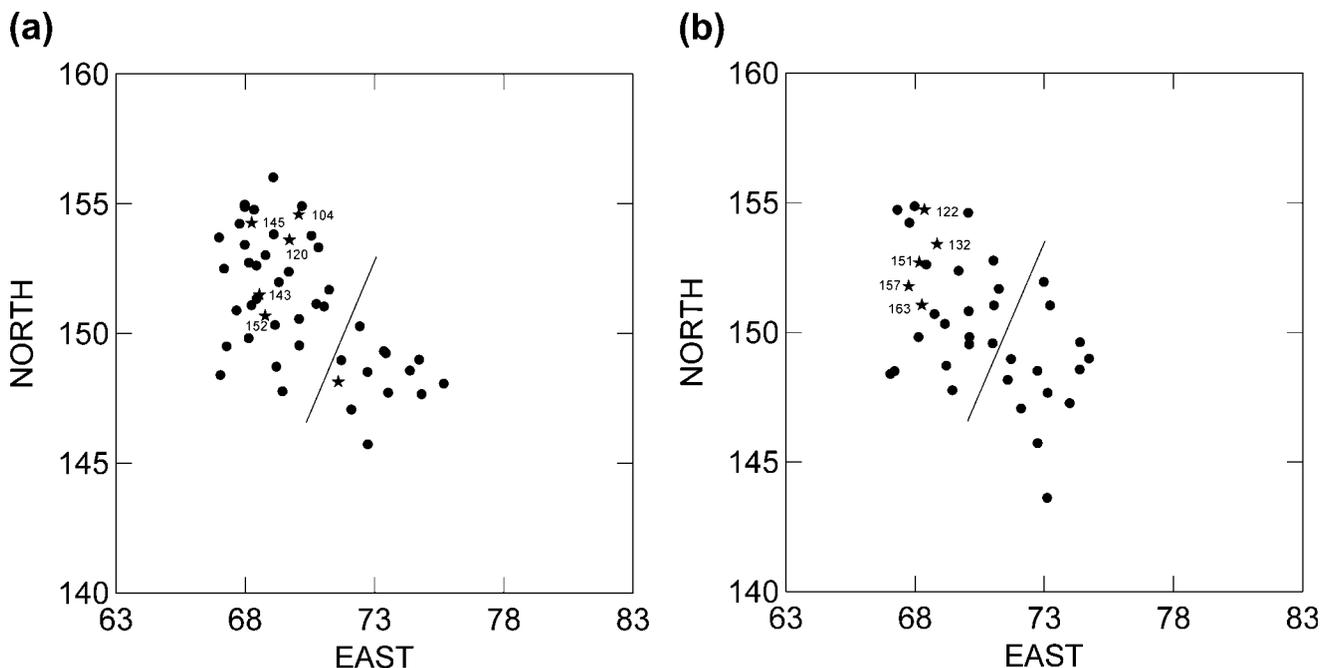


Fig. 9. Two examples of the perpendicular distribution of a non-metric trait at Windover: **a)** M³ peg-shaped molars, **b)** incomplete foramen ovale. Stars indicate positive occurrence of the trait and circles indicate negative occurrence of the trait. Burial ID numbers are provided for those individuals demonstrating the trait in Pond C west. The hypothesized pond division is also represented by the line dividing the burials. Axes are burial coordinates measured in meters.

promoting the development of trade networks, defense alliances, and solidarity within and among ethnically or linguistically diverse communities through intermarriage (Schillaci and Stojanowski, 2002). Integration within and among communities also establishes the foundation for developing sociopolitical influence or power by establishing bonds among individuals, families and regional communities. Because of the obvious significance of social integration in the development of complex societies, postmarital residence and other aspects of social organization are of considerable interest to anthropologists, particularly archaeologists.

There are five primary patterns of postmarital residence that are most commonly recognized in the literature: uxorilocal, virilocal, neolocal, bilocal, and duolocal. Uxorilocal and virilocal refer to female- and male-based residence patterns. Neolocal residence is defined by the husband and wife living separately from either spouse's parents. Bilocal residence allows the husband and wife to live within or in the vicinity of either the wife's or the husband's parents households. Duolocal residence is defined by the husband and wife living separately with their relatives. Uxorilocal and virilocal residence patterns are comprised of three secondary forms of residence: matrilocality, patrilocality and avunculocal. Matrilocality, the most commonly recognized form of uxorilocal residence, is defined by the husband and wife living within or in the vicinity of the wife's mother's household. Patrilocality, a form of virilocal residence, is defined by the husband and wife living within or in the vicinity of the husband's father's household. Avunculocal refers to residence with the grooms mother's brother and is uncommon in human societies. The distribution of residence patterns presented by Divale (1977) based on ~1,200 societies listed in the "Ethnographic Atlas" (Murdock, 1967) indicates 71% of the world's societies are patrilocality, 11% are matrilocality, 12% are either neolocal or bilocal, and 6% are avunculocal.

Cross-cultural research primarily by social-cultural anthropologists has provided a wealth of information on the social conditions and correlates of the various residence patterns. For example, historically, societies practicing matrilocality seem to be associated with recent migration, external warfare, frequent warfare, an absence of feuding within the community, significant long-distance trade relations, and stress due to contact with more dominant societies (cf. Helms, 1970; Ember et al., 1974; Divale, 1977; Peregrine, 1994). At least one researcher has noted that most of these correlates of matrilocality share a common thread of competitive interaction with other societies (Peregrine, 2001). Matrilocality may also be associated with a sexual division of labor in agricultural societies, with women doing the agricultural labor (Aberle, 1961), especially in North American societies (Ember and Ember, 1971; Divale, 1977). Patrilocality has been associated with fishing economies as well as internal, rather than external, warfare (Ember, 1975; also see Tomczak and Powell, 2003).

Postmarital residence as a social phenomenon has profound implications for the geographical distribution of biological variation, including the distribution of mtDNA, Y-chromosome, autosomal DNA, and phenotypic variation. It is clear from numerous studies of the genome that differential sex-specific migration has a profound effect on our species' diversity (Seielstad et al., 1998; Stoneking, 1998; Oota et al., 2001; Hamilton et al., 2005). Furthermore, the cultural basis of sex-specific

migration associated with postmarital residence can influence observed patterns of between- and within-population biological variability. For these reasons, the study of postmarital residence is of considerable importance to biological anthropologists studying genetic and phenotypic variation within and among populations.

Previous research by bioanthropologists

Interest in prehistoric postmarital residence practices has a long history in archaeology and is based on the intra-site spatial distribution of material culture (e.g., Tretyakov, 1934; Deetz, 1960, 1965, 1968; Binford, 1962; Longacre, 1964, 1966, 1968; Binford and Binford, 1966; Hill, 1966, 1970; Wright, 1966; McPherron, 1967; Whallon, 1968; Clemen, 1976; Brumbach, 1985; also see Longacre, 2000 for a historical perspective) or architectural features such as living floor areas (see Ember, 1973; Divale, 1977; Peregrine, 2001; Peregrine and Ember, 2002; Schillaci and Stojanowski, 2002). Despite initial popularity, however, many of these studies were criticized for unsupported assumptions, for failing to consider the depositional processes influencing artifact variability and distribution, and for adopting an overly simplistic view of social organization (cf. Allen and Richardson, 1971; Stanislawski, 1973; Lischka, 1975; Dumond, 1977; Plog, 1978). Biological approaches ameliorate some of these criticisms.

The earliest research by biological anthropologists on postmarital residence occurred in the context of general descriptive case reports. For example, Hulse (1941) found greater male craniometric variation at the late precontact Irene Mound site in Georgia which he interpreted as evidence of matrilocality, a result consistent with the ethnographic data for this area. Lewis and Lewis (1961) noted an unusually high male incidence of a particular canine crown anomaly at the Archaic period Eva site in Tennessee. The authors suggested this pattern resulted from males remaining in natal villages while females migrated from outside groups. Males at the site were less phenotypically variable for most other traits suggesting the presence of exogamous patrilocality bands.

Concerted interest in postmarital residence among bioanthropologists began in earnest with the work of Lane and Sublett (1972), Spence (1971, 1974a,b), and Corruccini (1972). Lane and Sublett (1972) investigated postmarital residence in five Seneca cemeteries in New York State. Following Whallon (1965), they assumed each cemetery represented the "relevant social units between which genetic trait variations develop (Lane and Sublett, 1972)," and that each of the five cemeteries represented an endogamous community. They proposed that, given these assumptions, the non-mobile sex would exhibit greater between-site variation. Results were consistent with a pattern of virilocal postmarital residence. Spence investigated postmarital residence at Teotihuacan, Mexico (1971, 1974a) and the Cape Kialegak Eskimo site in Alaska (1974b). Unlike Lane and Sublett (1972) who examined sex-specific between-group variation, Spence focused on within-group relationships and documented within-group male homogeneity at Teotihuacan (1971, 1974a), as well as increased female variability at Cape Kialegak (1974b). Both results suggest a virilocal residence preference. In a study examining the biological relationships among prehistoric and historic Pueblo Indian populations from the American Southwest, Corruccini (1972) documented sex differences in between-population size and shape distances. Corruccini's findings

described greater between-population distances coupled with increased within-population cohesiveness for females. These findings, in conjunction with the ethnohistoric record, implied prehistoric/historic Pueblo Indian society was likely matrilocal. In a similar study of postmarital residence at Grasshopper Pueblo, Arizona, Birkby (1982) inferred matrilocality using sex-specific cranial non-metric trait variation.

While all of these studies conducted during the 70s, and early 80s were direct investigations of postmarital residence patterns in prehistoric societies, none adopted a formal population genetics model. The theoretical framework and methodology for doing so was developed by Konigsberg (1987, 1988, discussed below) and has served as the foundation for a proliferation of recent studies on postmarital residence using prehistoric skeletal samples. Konigsberg (1987, 1988; Konigsberg and Buikstra, 1995) analyzed sex-specific variability in cranial non-metric trait frequencies at a series of Woodland and Mississippian period Illinois valley sites. Results indicated a preference for virilocal residence during the Woodland period and uxorilocal residence during the Mississippian period, consistent with the transition to agriculture where a female-based residence pattern is expected. Konigsberg's methodology, specifically determinant ratio analysis (see below), has since become standard. Stefan (1999) investigated population structure and postmarital residence among Rapa Nui late precontact and protohistoric tribal populations using craniometric data. He documented greater male postmarital mobility although the overall lack of regional diversification suggested no clear postmarital residence preference existed. These data were at odds with the ethnographic record which suggested tribal endogamy, particularly for elite lineages. In the American Southwest, postmarital residence patterns at Pueblo Bonito in Chaco Canyon, New Mexico were investigated by Schillaci and Stojanowski (2003) using a determinant ratio analysis of craniometric data, in addition to univariate methods. The results of that study indicated marginally greater female variance, suggesting the inhabitants of the regionally important pueblo were likely not matrilocal, as had been assumed (Peregrine, 2002). In a similar study, Schillaci and Stojanowski (2005) examined patterns of mate exchange and postmarital residence in a sample of prehistoric-protolithic Tewa Indian pueblos from the Rio Grande Valley of northern New Mexico. Their study of postmarital residence focused on a determinant ratio analysis of craniometric data. The results of the study indicated significantly greater within-pueblo male variation for one of two pueblos, a pattern consistent with matrilocal residence. The second pueblo exhibited greater male variation than female variation, though the comparison was not significant at the 0.05 level. Tomczak and Powell (2003) investigated postmarital residence at the early Archaic period Windover Pond cemetery using dental morphological data. They documented female variability that was twice as large as male variability suggesting a patrilocal residence preference. Although the difference was not significant, they interpreted these data in reference to data on hunting-gathering-fishing populations and sexual division of labor which, ethnographically, are associated with virilocal cultures.

Theoretical basis for postmarital residence analysis

Prior to the work of Konigsberg (1987, 1988) postmarital residence analyses were informal and not based on

explicit population genetic parameters and models. In addition, the validity of these approaches was critiqued on two accounts: skeletal samples are temporal lineages not natural populations, and genetic variability is redistributed between the sexes every generation due to autosomal inheritance (Cadien et al., 1974; Kennedy, 1981). Konigsberg's dissertation (1987) and publications that followed (1988; Konigsberg and Buikstra, 1995) are landmarks in the biodistance literature because of the analytical rigor they introduced to analyses of phenotypic variation in archaeological populations. Specifically, several models were developed to examine postmarital residence and its effects on genetic variation that incorporate, at a minimum, genetic drift (population size) and gene flow (migration). The parameter of interest is F_{ST} , a measure of standardized genetic variance that reflects the cumulative effects of migration and genetic drift on patterns of biological diversity. Konigsberg presented several migration models that partition the genetic variance into male and female components and subjected these variance components to simulations to examine the effects of differential sex-specific migration rates on F_{ST} .

The first and simplest simulation used Wright' (1951) infinite islands model in which a single population is divided into infinite subpopulations with equal migration between them. Konigsberg modified the standard recurrence relationship for F_{ST} , which predicts the degree of genetic variation in the current generation from F_{ST} in the previous generation, modified by population size and migration rate. By partitioning this model by sex, thus allowing for different sex-specific migration rates, Konigsberg demonstrated that the homogenizing effects of multi-generational gene flow do not alter the adult variability as expressed through the differential migration of the sexes. Although male and female genetic variances are equal at birth (because autosomal alleles are sorted independently of sex), Konigsberg demonstrated that, "a greater migration rate for one sex leads to that sex having greater variance within groups and less variance between groups (Konigsberg and Buikstra, 1995)." Similar results were obtained under a finite island model which is more a realistic proxy for human migration patterns.

Migration matrix methods (Bodmer and Cavalli-Sforza, 1968) provide the most general model for examining postmarital residence. Konigsberg (1987) adopted this approach to evaluate the critiques of Kennedy (1981) who proposed several forms of migration (e.g., prescribed reciprocal and non-reciprocal exchange) that are potentially problematic from a predictive standpoint. Migration matrices are based on kinship coefficients that indicate the probability of alleles being identical by descent within and between subpopulations and therefore serve as measures of genetic variance. Migration matrix methods benefit from the inclusion of "systematic pressure" such as long range migration, mutation, and natural selection (Konigsberg, 1987). The kinship matrix can be converted to a relationship matrix from which F_{ST} can be estimated, and, as with the island models, partitioned into male and female components. Konigsberg (1987, 1988) used this method to examine postmarital residence for several simulations. The first, a finite island model in which males were non-migratory and females were 50% endogamous, produced results similar to those of the previous island models. The second, the circulating conubium model in which males were non-migratory and females migrated uni-directionally to adjacent populations only, also produced results similar to the island models. Both simulations established the predicted rela-

tionship between migration and within and between population sex-specific variations. The third simulation, however, highlighted the potential complexity of post-marital residence analysis. In this simulation Konigsberg allowed for limited male migration with a finite island pattern while females were 50% endogamous and migrated in a circulating connubium pattern. This had the effect of dispersing a few males widely throughout the mating network. Despite the fact that females were more migratory than males, the sex-specific F_{ST} s indicated the opposite pattern of that expected. This result reflected the differential dispersion of the sexes throughout the mating network. In response to Konigsberg's research Aguiar and Neves (1991) investigated sex-specific within- and between-group genetic variability among 4 uxorial Amazonian Urubu-Ka'apor villages using 20 polymorphic genetic loci. They documented differences in within-sex between-group variation, as measured by F_{ST} , but no variability differences between sexes within villages and concluded that between-group analysis is more sensitive to differential sex-specific migration.

There are two categories of analysis most commonly used in biological studies of postmarital residence: bio-distance analysis and analyses of phenotypic variance. Each category includes distinct methods for analyzing both metric and non-metric data; however, all methods are based on similar theoretical and methodological assumptions (Lane and Sublett, 1972; Spence, 1974a,b; Konigsberg, 1987, 1988; Konigsberg and Buikstra, 1995). The six primary theoretical assumptions are:

1. For within-group analyses, the sex with the greater variability is assumed to be the more mobile sex. For example, greater male variability corresponds to greater male in-migration by largely unrelated males. This pattern is consistent with matrilineal residence. The non-mobile, or resident, sex is theoretically composed of related individuals with similar phenotypic variance and covariance.
2. For between-group analyses, the sex with the greater between group variability (usually some measure of biological distance), represents the non-mobile, or resident, sex. The resident sex would not experience the homogenizing effects of gene flow and will exhibit greater between group variance and divergence (e.g., Aguiar and Neves, 1991).
3. The individual skeletons that were excavated from a given cemetery were members of the community for which that cemetery served, i.e., there were no secondary or intrusive post-occupational burials.
4. The environmental variance components do not differ by sex.
5. There is no prescribed kin- or clan-structured exogamy (see Williams-Blangero, 1989a,b; Williams-Blangero and Blangero, 1989).
6. For studies relying on male and female biological distances among population samples, the samples included for study are derived from contemporaneous populations. Assessing this assumption requires careful consideration of the archaeological and temporal context of burial clusters or cemeteries (see Konigsberg, 1987; Aguiar et al., 1989; Aguiar and Neves, 1991).

In addition to these theoretical assumptions, there are also several important methodological assumptions:

1. The sex of each individual is estimated correctly.
2. For multivariate analyses relying on a variance-covariance matrix (see below), there are not more variables than observations for any given sex-specific grouping.

Methods

Biodistance analysis. Both metric and non-metric cranial and dental data have been used in studies of post-marital residence to generate biological distances among populations and among sex-specific groupings (Corruccini, 1972; Lane and Sublett, 1972; Buikstra, 1980; Droessler, 1981; Kennedy, 1981; Birkby, 1982; Stefan, 1999; Schillaci and Stojanowski, 2003). Borrowing from (Lane and Sublett, 1972), given certain assumptions (see above), the formal propositions and test implications for biodistance analyses of postmarital residence patterns are as follows:

1. If residence units are based on male-male genetic relationships, as is the case for virilocal residence patterns, then intra-cemetery comparisons between adult male and female groupings should indicate heterogeneity because most of the adult males and females will be unrelated. In addition, inter-cemetery comparisons between male groupings should also indicate heterogeneity due to isolation and genetic divergence. Finally, inter-cemetery comparisons between female groupings should indicate relative homogeneity because female residence mobility within a network will emanate from a presumably limited number of common sources.
2. If residence units are based on female-female genetic relationships, as is the case for uxorial residence patterns, then intra-cemetery comparisons between female and male groupings should indicate heterogeneity because most of the adult females and males will be unrelated. In addition, inter-cemetery comparisons between female groupings should also indicate heterogeneity due to isolation and genetic divergence. Finally, inter-cemetery comparisons between male groupings should indicate relative homogeneity because male residence mobility within a network will emanate from a limited number of common sources.

The most common between-cemetery distance measures that have been employed in post marital residence studies have been Smith's mean measure of divergence (MMD) (see Berry and Berry, 1967; Souza and Houghton, 1977) for non-metric or discrete cranial and dental data (e.g., Lane and Sublett, 1972; Buikstra, 1980; Droessler, 1981; Kennedy, 1981; Birkby, 1982; Tomczak and Powell, 2003) and the Mahalanobis generalized distance (Mahalanobis, 1936) for metric data (e.g., Stefan, 1999). There are several notable exceptions to the apparent preference for MMD and the Mahalanobis distance. Corruccini (1972) used Penrose's size and shape distances (Penrose, 1953) in his study of biological relationships among prehistoric Pueblo Indian populations in the American Southwest. Konigsberg (1987) used Balakrishnan and Sanghvi's B^2 as an alternative to the MMD (Balakrishnan and Sanghvi, 1968). Although not a distance measure, the Jaccard Coefficient (Sokal and Sneath, 1963) has been used to estimate residence patterns using non-metric cranial and dental data (e.g. Spence 1974a; Aguiar et al., 1989). The Jaccard Coefficient measures

within-sex similarity between two individuals based on patterns of non-metric trait presence and absence. This method calculates the ratio of positive matches to the sum of the positive and negative matches (also see Manly, 1995).

More recently, researchers (e.g., Steadman, 2001; Schillaci and Stojanowski, 2003, 2005) has begun to use biological distances based on the relationship matrix (R-matrix) (see Relethford et al., 1997). R-matrix distances are generated from the off-diagonal elements of a co-divergence matrix which are essentially weighted pairwise Mahalanobis distances between groups. Easy-to-use computer software written and made available by J. Relethford (RMET - <http://konig.la.utk.edu/relethsoft.html>) generates bias-free estimates of biological distances that are adjusted for potential bias associated with small and uneven sample sizes. When relative population sizes can be included in the analyses, RMET will generate weighted estimates of biological distances and population differentiation (F_{ST}). This software can be used to generate sex-specific distances among prehistoric communities, as well as among social groupings within a community. The most recent summary of R matrix analysis for phenotypic data was presented by Relethford (2003).

Phenotypic variance. There have been a number of studies that have compared male and female variances for phenotypic traits as a means for estimating postmarital residence patterns. These studies have used both univariate (e.g., Hulse, 1941; Lewis and Lewis, 1961; Stefan, 1999; Schillaci and Stojanowski, 2005), and multivariate methods (Konigsberg, 1987, 1988; Stefan, 1999; Tomczak and Powell, 2003; Schillaci and Stojanowski, 2003, 2005). As outlined earlier, for intracemetery analyses, the sex with the greater variability is assumed to be the more mobile sex. The non-mobile, or resident, sex is theoretically composed of related individuals, thus exhibiting low phenotypic variance.

Typically, in these studies comparison of some measure of variation (i.e., variance, standard deviation, coefficient of variation) between sexes is made using standard statistical tests such as an F-test or a Levene's test. The F-test is simply a variance ratio but assumes normality and is too liberal for small sample sizes. A robust alternative is Levene's test for sample medians. Levene's test is an ANOVA for k samples where the response variable is the difference between measurement observations and the sample median. Although it is not routinely done, variance comparisons should be accompanied by assessments of normality to determine if test assumptions have been satisfied. Most statistical computer packages include standard tests for assessing variable normality, such as the Wilk-Shapiro and Kolmogorov-Smirnov tests. Also, because sample sizes are often low, post hoc power analysis enables the researcher to assess the probability of finding a significant difference when one truly exists. This probability is useful for determining the potential social significance of statistically non-significant results. In other words, non-significant results may be a product of small sample sizes rather than reflecting social flexibility in residence rules. The issue of power was also discussed by Byers (2000) who presented SAS code for calculations. Applets for univariate variance analyses, normality testing, and power analysis are available at <http://statpages.org/>.

Multivariate assessment of variance differences is preferred because it considers the total pattern of variability and is not affected by family-wise error, although addi-

tional, more stringent assumptions (such as multivariate normality and complete data matrices) can be problematic. One example is Van Valen's test (1978). This analysis is based on the distance of each observation from the within-sex mean. Because the test is independent of the variance covariance matrix no missing data estimation is necessary. However, the additive nature of the test statistic highlights minor variance differences that might not be significant in a series of univariate tests. Other methods have specifically been proposed for anthropological problems. The canonical variates model presented by Key and Jantz (1990a,b) could be modified for use between males and females (discussed further below). However, most recent literature uses covariance matrix determinants. The determinant $|C|$ is a matrix scalar that serves as a measure of variability in a sample variance-covariance matrix (Green, 1976b). The mechanics of determinant calculation are complicated, particularly for matrices larger than 2×2 . An operational definition is provided in (Green, 1976b). The ratio of the female to male covariance matrix determinants $|C_{\text{♀}}|/|C_{\text{♂}}|$ measures relative sex-specific variance differences (see Konigsberg, 1987, 1988; Raemsch, 1995). If the determinant ratio is greater than 1, then greater female variance, assumed to be the result of greater female mobility associated with a patrilocal postmarital residence system, is indicated. When the determinant is less than 1, greater male variance is indicated, suggesting greater male mobility in association with matrilineal residence. Statistical significance is determined using randomization methods such as those discussed by Petersen (2000)—see below and also Manly (1998).

Ancient DNA and bone chemistry. Ancient DNA (aDNA) has the potential to be a powerful tool for investigating postmarital residence patterns. In a recent review Kaestle and Horsburgh (2002) point out that although it has been suggested that archaeological groups are likely to exhibit low levels of genetic diversity due to inbreeding and genetic drift stemming from small population sizes (Cavalli-Sforza and Bodmer, 1999), recent studies of mtDNA hypervariable region sequence diversity in ancient groups with relatively large sample sizes do not show reduced diversity (Kaestle, 1998; Stone and Stoneking, 1999). Kaestle and Horsburgh (2002) suggest that given this diversity it may be possible to investigate general and specific patterns of postmarital residence, such as endogamy/exogamy and patrilocal/matrilocal practices in archaeological groups. The assumption guiding aDNA analyses of residence patterns is similar to that guiding analyses based on morphometric data, greater diversity in the non-natal sex. This is typically measured in terms of sex-specific variation in maternal mtDNA signatures where the sex with the greater diversity is the migrant sex (see Oota et al., 2001; Williamson et al., 2002; Hamilton et al., 2005; Mooder et al., 2005).

To date, however, comparatively little aDNA research has focused on the specific investigation of postmarital residence. Shinoda and Kanai (1999) examined the mtDNA diversity of a prehistoric Jomon burial population in Japan. Their findings indicate increased haplotype diversity for a segment of the burial sample and contrasting low haplotype diversity for the remaining segment. Usher et al. (2002) developed simulation models to predict spatial distributions of male and female genetic markers for common patterns of inheritance and residence such as matrilineal/matrilocal and patrilineal/

patrilocal. Usher (2005) used genealogical data from 3,886 burials at six Anabaptist cemeteries in central Pennsylvania to investigate social organization in this largely agricultural population. The result of her analysis indicated the distribution of Y-chromosome (paternal) and mitochondrial (maternal) lineages reflected a primarily patrilocal household structure associated with endogamous corporate groups affiliated with certain churches. The majority of men within cemeteries were found in clusters of related males, indicative of a patrilocal mode of social organization. A measurable level of inbreeding, however, resulted in some husbands and wives being buried in adjacent graves who shared the same female ancestor.

Case study: Chaco culture in the American Southwest

Perhaps no other archaeological culture in the American Southwest has received as much attention in the anthropological literature as has Chaco culture (ca. AD 860–1150). Chaco culture was both extraordinarily elaborate and geographically extensive. Its scale of architecture and sphere of sociopolitical and cultural influence was unparalleled among prehistoric cultures in the Southwest. Chacoan great houses were monuments of public architecture comprising multiple multi-leveled stone-masonry room blocks and ceremonial structures. Smaller pueblos were typically associated with great houses, forming communities which were often tied to the regional core in Chaco Canyon by an elaborate road system. These communities formed a large regional sociopolitical system that covered much of the San Juan Basin and surrounding areas during the eleventh and much of the twelfth centuries (Fig. 10).

Among the great houses of Chaco Culture, Pueblo Bonito is one of the largest and most elaborate (Fig. 11). Pueblo Bonito stood four stories high, with over 600 rooms (Lekson, 1986). Construction of the pueblo began around AD 890 and lasted until sometime around AD 1130 (Windes and Ford, 1996). The size and centralized location within the Canyon suggests Pueblo Bonito was an important center within Chaco Culture's regional system, however, its function is less clear. The low frequency of domestic floor features such as hearths suggests Pueblo Bonito may not have been used solely for domestic or residential purposes, but may have served communal or perhaps religious functions for communities both within and outside Chaco Canyon (see Windes, 1984; Bernardini, 1999; Bustard, 1999).

The presence of two distinct populations at Pueblo Bonito is indicated by the results of two independent paleogenetic analyses using skeletal samples excavated from two burial clusters within the pueblo (Akins 1986; Schillaci et al. 2001). Judd (1925, 1954) suggested that there were two different populations ("Old Bonitans" and "Late Bonitans") at Pueblo Bonito based on the distribution of material culture and architecture. The burials at Pueblo Bonito are concentrated into two relatively discrete clusters of contiguous burial rooms located in the north of the pueblo and one in the west. The northern burial cluster was excavated by Pepper (1909, 1920) and Morehead in the late 1800s, while the western cluster was excavated by Judd (1954) in the 1920s. Based on the distribution of temporally diagnostic ceramic artifacts it seems that these two populations were contemporaneous for some portion of their occupations of the pueblo.

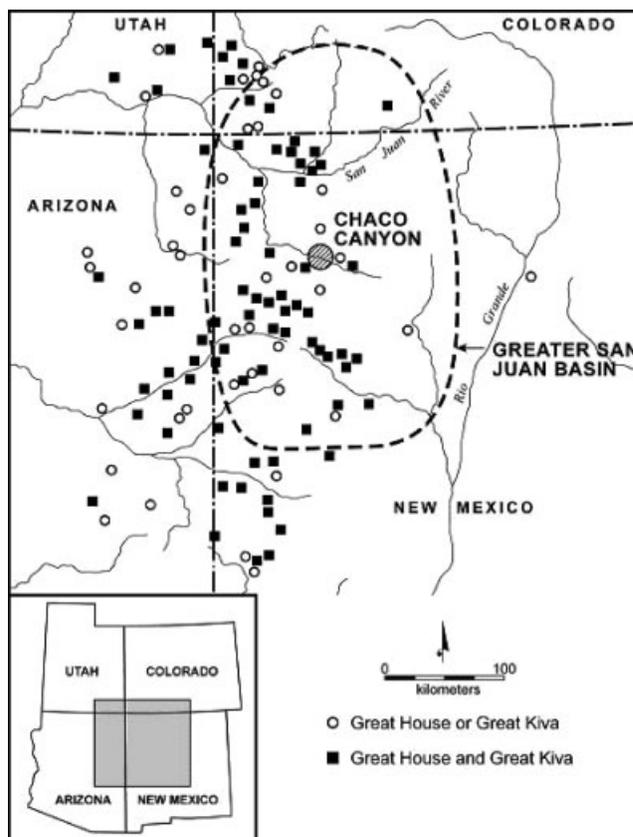


Fig. 10. Map of the greater San Juan Basin of the American Southwest showing the geographic distribution of Chaco Culture communities. (Adapted from Neitzel, 2003 and Lekson, 1991.)

The presence of both small and large scale pueblos (i.e., site size hierarchy) and the labor required to build the monumental public architecture of the great houses suggests there was a high level of social complexity with the potential for a polity-based political structure. The social and political organization of Chaco culture has therefore been the subject of intense study by southwestern archaeologists and bioarchaeologists.

Recently, one such study (i.e., Peregrine, 2001) proposed a model for explaining the organization of production at Chaco Canyon based on the development of matrilocality. This model stated that Chaco society was a corporate-oriented polity which was fostered by the evolution of matrilineal residence in a marginal environment, where a female-based social organization allowed women to maintain stable agricultural societies while men engaged in long-distance trade and raw material procurement (Peregrine, 2001). This condition fostered the development of large scale communities where leaders stressed co-operative effort aimed at group survival. In this model, subsistence production was achieved through female work groups comprising matrilineal, while in-marrying males were responsible for craft-production.

Clearly, postmarital residence plays an integral role in this model which has broad implications for the development of social complexity in the American Southwest. Historically, matrilocality has been assumed to be the ancestral pueblo pattern of postmarital residence based largely on ethnographic analogy with present-day Pueblo Indian cultures such as the Hopi and the Zuni, or based

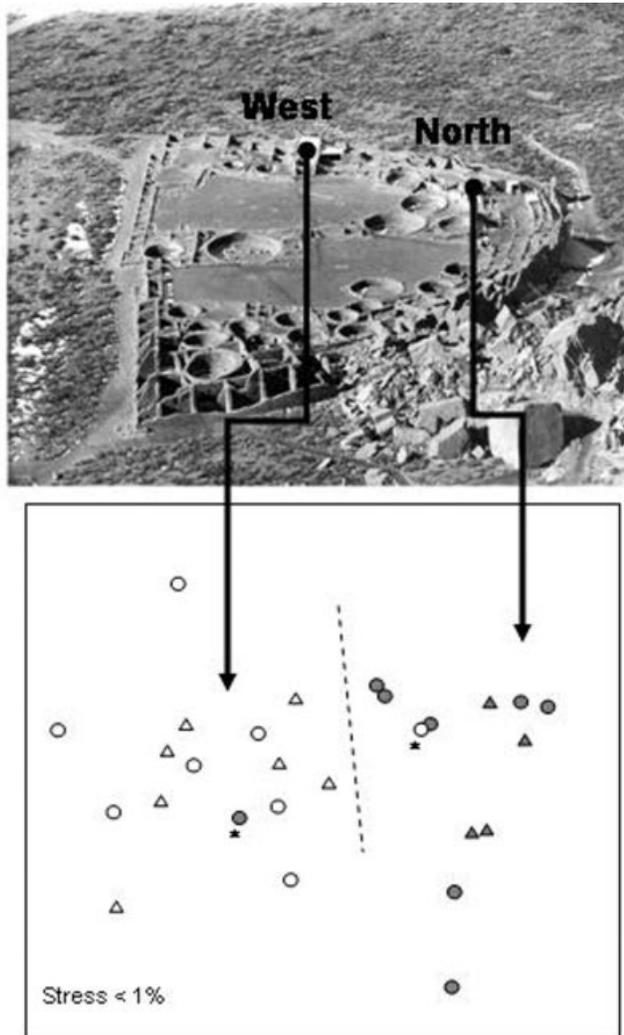


Fig. 11. (top) Aerial photo of Pueblo Bonito taken from the east. The approximate location of the north and west cemeteries are marked by arrows. (bottom) Two-dimensional multidimensional scaling plot of inter-individual genetic distances generated from the linear discriminant function extracted from the standardized values of 9 craniometric traits (orbital height, orbital breadth, bifrontal breadth, interorbital breadth, interior palate length and breadth, nasal height and breadth, and upper facial height). Filled circles, north cemetery females; filled triangles, north cemetery males; circles, west cemetery females; triangles west cemetery males. Misclassified females marked with a star. Courtesy of NPS, Chaco Culture National Historical Park, Neg. No. 30626. Photographer: Jerry Livingston.

on non-random distributions of artifact types within prehistoric pueblos. For Peregrine's (2001) model, the evolution of female-based residence pattern at Chaco Canyon was determined based on a presumed trend toward larger domestic floor areas at Chaco [see previous description of work by Ember (1973)], and the observed postmarital residence patterns in the presumed present-day descendants of Chacoans. Although these presumptions were later challenged (Schillaci and Stojanowski, 2002), Peregrine's model illustrates just how important postmarital residence can be in the development of archaeological theory, and hence the explanations of culture history and development of sociopolitical complexity which emanate from that theory.

TABLE 3. Mean genetic distances within and between cemeteries at Pueblo Bonito

| Grouping | North | West | Pooled | Between cemeteries |
|----------|-------|-------|--------|--------------------|
| Males | 0.298 | 1.067 | 0.896 | 3.010 |
| Females | 1.219 | 1.488 | 1.354 | 2.344 |

Using analyses of sex-specific univariate and multivariate variance we subsequently showed that the dominant pattern of postmarital residence for the largest burial sample at Chaco Canyon, Pueblo Bonito, was likely not female-based but rather bilocal or non-ascribed (Schillaci and Stojanowski, 2003). Although females exhibited a greater variance than males for more variables, none of the univariate comparisons between sexes was significant at the 0.05 level. Furthermore, females exhibited greater, though statistically not significantly greater, multivariate variance than males. The observed pattern of sex-specific variance was not consistent with what would be expected for a matrilineal society, but instead is more consistent with a bilocal pattern of residence, or alternatively, non-prescribed residence. In addition to greater female variance at Pueblo Bonito, a comparison of genetic distances estimated from the linear discriminant function extracted from the standardized values of 9 craniometric traits reveals the average distance among females is greater than that among males (Table 3). This condition indicates male homogeneity with greater female heterogeneity, a pattern consistent with patrilocal residence. Patrilocal residence is also indicated for each of the two cemeteries when examined separately. From the north cemetery, females exhibit a mean genetic distance that is more than four times greater than the mean genetic distance among males. Similarly, from the west cemetery, females exhibit a mean within-sex genetic distance which is greater than the mean within-sex distance among males. The mean between-sex distances were not substantially different between the two cemeteries (north $d_{\text{♂♀}} = 0.965$; west $d_{\text{♂♀}} = 1.185$). Note that because distances are not independent no tests of significance were presented.

A comparison of mean within-sex, between cemetery genetic distances indicates greater male distance than female distance indicating mate exchange between the two patrilocal or bilocal populations at Pueblo Bonito was for the most part limited, with female in-migration from common outside sources. Limited mate exchange between the two populations at Pueblo Bonito is also indicated by the results of the discriminant analysis. After testing for variable normality and equality of covariance matrices, the results of formal classification analysis indicate a relatively low misclassification error (i.e., 14.8%), with only two females misclassified. A multidimensional scaling plot reveals that these two females have closer relationships with females in the other cemetery than with females or males in their own cemetery (Fig. 11), suggesting female mate exchange between the two populations had in fact occurred, or alternatively, the two populations were drawing mates from the same populations, at least occasionally. The multidimensional plot of average distances among sex-specific cemetery samples reveals some level of endogamy may have occurred within the population represented by the north cemetery, relative to the west cemetery population (Fig. 12). Endogamy is suggested for the north cemetery population because the sexes exhibit a close genetic relation-

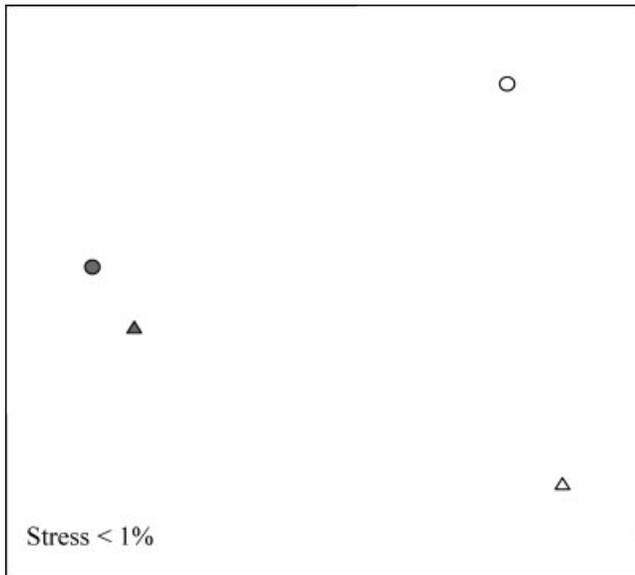


Fig. 12. Two-dimensional multidimensional scaling plot of genetic distances sex-specific cemetery. Filled circle, north cemetery females; filled triangle, north cemetery males; circle, west cemetery females; triangle west cemetery males.

ship with each other relative to the relationship between the sexes of the west cemetery. This particular finding is consistent with those presented elsewhere based on R matrix analysis of craniometric data (i.e., Schillaci and Stojanowski, 2003), and suggests there may have been some variability in mate exchange practices within Chaco society.

The case study presented above highlights the potential importance of paleogenetic studies of postmarital residence and social organization for our understanding of the development of social complexity. Although indirect estimates of residence patterns based on architecture suggest matrilineal residence at Chaco (Peregrine, 2001; but see Peregrine and Ember, 2002; Schillaci and Stojanowski, 2003), direct estimates based on sex-specific biological variation, and sex-specific genetic distances indicate bilocal or patrilineal residence-or, alternatively non-prescribed residence. The Chaco Culture example illustrates that social complexity can develop from bilocal or patrilineal agricultural societies, rather than solely from a matrilineal residence pattern. Furthermore, there may be variability in mate exchange practices in complex societies, with some level of endogamy practiced within some groups and not in others.

VARIANCE COMPARISON METHODS

The amount of phenotypic variability in a cemetery reflects, in some way, the genetic heterogeneity of the population that used it and the duration of its use. Changes in the amount of phenotypic variability may therefore reflect changes in these parameters that are recoverable using simple analytical approaches. Simple variance measures are limited, however, because it is difficult to differentiate the myriad properties of a population that affect sample variability. For example, social structure, endogamy, effective population size, short and long-term migration rates, as well as ontogenetic, and environmental variation all affect variation within the

living population (Cadien et al., 1974; Raemsch and Wilkinson, 1994; Raemsch, 1995). Sample variability itself is affected by the number of lineages buried, the length of cemetery use, and the burial catchment area. Relating “populations” to “samples” is a chronic source of concern for bioarchaeology (see Cadien et al., 1974) where temporal aggregates of skeletons are often used to infer properties of temporally static archaeological populations. Raemsch (1995) tested these relationships by comparing phenotypic variability among controlled data sets that differed in the degree of relatedness of those that comprised the sample. Although multivariate analysis suggested sample phenotypic variability can be used to infer genetic variability or subdivision within the living population, there was considerable overlap between sample variances that contained completely unrelated and closely related individuals. In addition, some samples of similar genetic homogeneity were not equally as variable.

Previous research by bioanthropologists

Because of the difficulty differentiating the causes of sample variability few have used this approach for anthropological investigation. Key and Jantz (1990a) used overall phenotypic variability to gauge cemetery use history at the Leavenworth and Bad River Phase 2 sites, both associated with the Arikara. Sample variability was compared with that for the Larson site which represents a single village, single occupation cemetery that predates the period of post-colonial demographic collapse. Significantly elevated variability at Leavenworth suggested the presence of aggregated, formerly distinct social units at this location, most likely bands that attempted to maintain their distinct social identities in the wake of epidemic disease and population aggregation. The lack of excess variability at the Bad River Phase 2 sites suggested village endogamy was not practiced among the postcontact Arikara. Key and Jantz (1990b) used the same method to investigate variability among Woodland period sites in the mid-continent. Stefan (2004) considered the effects of combining multiple museum samples to form a single geographically-restricted aggregate sample, in this case for Rapa Nui populations. Stefan found no differences in the variance-covariance matrices of different museum samples of Rapa Nui skeletons which suggests each sample was individually representative of Rapa Nui phenotypic variability.

Methods

Because this research approach is not complex, standard univariate statistical analyses can be used, for example univariate F and Levene’s tests (Stojanowski, 2001 and see above). Multivariate analyses have become the norm, however. Key and Jantz (1990a,b) proposed a comparative model based on the test statistic lambda derived from discriminant function analysis. Their method compares a baseline covariance matrix with that from the sample of interest to determine if the latter is more variable. The approach is useful because it allows the variables driving the increased variation to be identified and provides eigenvectors that allow subsidiary hypotheses about internal biological structure and relationships to be addressed using inferential statistics or graphical methods. That the method is comparative, i.e., requiring knowledge of “baseline” variability and a baseline covariance matrix, is problematic and the use of chi-square

test statistics limits the application of this model to larger samples (Petersen, 2000). Raemisch (1995) used sample covariance matrix determinants, a scalar that reflects the overall level of variability represented within the matrix (Green, 1976b), which can be compared by bootstrapping the log of the ratio of two determinants (see Konigsberg, 1987). Determinant ratio analysis was discussed above in the context of postmarital residence where it has been most heavily used. Petersen (2000) presented three variants of analysis of phenotypic variability. The first uses an F test statistic based on the ratio of standardized variances, assumes multivariate normality and is preferable only when sample sizes are large and aggregate summary statistics are available. The second assesses significance using a parametric bootstrap method, assumes multivariate normality and is preferable when sample sizes are smaller and only aggregate summary statistics are available. The third is a non-parametric bootstrap method that is the most powerful test of significance and does not assume multivariate normality but must be calculated using raw data. Petersen (2000) provides a very accessible discussion of the mechanics of these approaches and R code for the parametric and non-parametric bootstrap tests is provided by Lyle Konigsberg (<http://konig.la.utk.edu/Rstuff.htm>).

While the methods discussed above deal with appropriate statistical tests for multivariate variance comparisons, others have focused on differentiating the population parameters that may affect sample variability. Stojanowski (2001, 2003b) proposed a matrix decomposition model that estimates the number of distinct lineages buried within a cemetery and has been used as a form of non-structured cemetery kinship analysis (see above). The method assumes that each subgroup used a spatially defined, but not discrete, section of the cemetery. Subtraction of the scaled inter-individual spatial distance matrix from the scaled genetic distance matrix produces negative values for within subgroup comparisons and positive values for between subgroup comparisons. The ratio of within subgroup negative residuals to the total number of residuals simplifies to an estimate of the number of subgroups buried within the cemetery. This method is sensitive to missing data and assumes an underlying spatial proximity pattern of burial, which cannot be tested using a Mantel test and must be assumed from subsidiary data. It is also most useful in contexts in which population turnover was high such as during the colonial period. The method is, therefore, limited in application.

Another promising method to estimate the number of discrete lineages buried in a cemetery is finite mixture analysis (Pearson et al. 1992; Dong, 1997; Kramer and Konigsberg, 1999). Mixture analysis is a more general form of discriminant function analysis that does not require a priori specification of group membership (Kramer and Konigsberg, 1999). The analysis generates clusters of individuals based on phenotypic observations, provides estimates of the optimal number of clusters represented, and goodness-of-fit tests of statistical significance (Mendell et al., 1993). Mixture models are not tied to any underlying distributional assumptions and missing data are computationally non-problematic, both features which allow considerable analytical flexibility. Mixture analysis is perhaps most useful for species recognition in the fossil record (Kramer and Konigsberg, 1999). This literature is extensive and similar in scope to that presented here because of its focus on phenotypic variability.

Case study: Colonial period population aggregation in Spanish Florida

The contact period of North America witnessed dramatic changes in indigenous society with commensurate declines in population health in the wake of epidemic disease and the social disruption which ignited conflict throughout the Americas. One area where these processes were studied most extensively is La Florida, where three decades of bioarchaeological research on diet, disease, and behavior documented population decline among the Guale and Apalachee Indians of the Georgia coast and Florida interior (Larsen, 2001). Epidemics increased mortality which decreased population size and initiated a period of population aggregation and long range migration, processes with significant evolutionary effects within mission communities. Stojanowski (2001, 2003b, 2005c) studied the effects of microevolution within and among mission communities by comparing intracemetery phenotypic variation across space and through time. Of primary interest was determining which evolutionary mechanism (genetic drift or gene flow) had greatest impact on indigenous population structure and cemetery composition.

Tooth size data were collected for four mission samples from Florida and Georgia: San Luis de Apalachee, San Pedro y San Pablo de Patate, Santa Catalina de Guale, and Santa Catalina de Guale de Santa Maria (Fig. 6). Phenotypic variability was compared within chiefdoms (Guale and Apalachee) through time. Results of univariate F and Levene's tests as well as multivariate determinant ratio analyses indicated a differential effect of missionization in Guale and Apalachee. For the Guale living along the Georgia coast, the transition to the mission period witnessed an increase in phenotypic variability followed by a decline in variability during the late mission period. Stojanowski (2001) interpreted this as early initial population aggregation at mission Santa Catalina de Guale followed by a genetic bottleneck due to epidemics and genetic drift during the late mission period. For the Apalachee living in the Florida panhandle there was no immediate postcontact change in phenotypic variability followed by an increase in variability during the late mission period. This suggested the period of population aggregation began later for the Apalachee.

Additional analysis of the Guale data using the matrix decomposition model described above further refined understanding of evolution during the contact period (Stojanowski, 2001, 2003b). Stojanowski compared the largest precontact Guale sample (Irene Mound) to the early mission period Santa Catalina de Guale and late mission period Santa Catalina de Guale de Santa Maria samples. Despite the fact that variability was highest at Santa Catalina de Guale and lowest at Santa Catalina de Guale de Santa Maria, the matrix decomposition model indicated that the number of distinct lineages buried within each cemetery increased steadily through time. The precontact Irene Mound sample represented the fewest lineages and the Santa Maria sample represented the most lineages. This indicates that, despite minimal phenotypic variation, the Santa Maria sample was composed of numerous aggregated and distinct lineages and that the effects of genetic drift could be differentiated from the effects of population aggregation. The evolutionary history of the Guale entailed continuous aggregation of increasingly smaller and less variable subpopulations.

Use of simple variance measures to study evolutionary process in La Florida contributed to the general theory of post-colonial transformation of indigenous communities. Stojanowski (2005c) re-evaluated the variance data in reference to the continuing debate about New World pandemics and regional variation in demographic collapse due to European diseases. He proposed a unilineal process of demographic transition with an initial stage of population aggregation represented by increased intracemetery variability and a final stage of decreased variability associated with post-collapse communities. In this sense the Apalachee and Guale signatures did not indicate a different process of demographic change, but different timing to demographic collapse. Epidemics affected the Guale earlier because of 16th century slave raids along the Atlantic coast of La Florida; therefore, when the colony was destroyed in 1706 the Guale were reduced to a few hundred, genetically homogenous individuals. In other words, they were in the final stages of extinction. In contrast, the Apalachee were actively transitioning when the missions were destroyed in the early 18th century. This interpretation is consistent with population size data, epidemic data, paleopathology, and mortuary analyses which suggest the Apalachee were spared the worst of the epidemics until later in the 17th century. Interestingly, they are the only precontact Florida indigenous group still in existence and this research establishes direct linkage between modern populations and demographic processes, which began over 400 years ago.

TEMPORAL MICROCHRONOLOGY

The discussion of kinship analysis presented above detailed analytical protocols for sites in which internal spatial structure suggested a priori subgroup membership. These methods assumed the different burial areas within a site represented contemporaneous social divisions, families or lineages. However, discrete burial areas within a cemetery may also reflect the use of that site at different time periods allowing for analysis of temporal microevolutionary trends. Determining whether a contemporaneous social or temporal evolutionary pattern is represented by a cemetery is difficult because archaeological information must be used to divide the sample into temporal units, which often consist of discrete burial areas such as single mounds at multi-mound complexes (Konigsberg, 1987) or discrete burial areas within a larger cemetery (Owsley and Jantz, 1978), but can also be based on artifact seriations that divide the burials into temporal units (see Cannon, 1989). However, interpretations of phenotypic distances and variances are highly sensitive to these temporal scale issues (see Buikstra, 1972, 1980; Konigsberg, 1987). Patterns of biological affinity among burial subgroups are interpreted in a completely different manner if they represent social divisions within a society rather than samples of that society at different points in time. From an analytical perspective, intracemetery temporal microchronology is similar to general analyses of microevolutionary processes in which phenotypic evolution may reflect natural selection, changes in population size or changes in breeding network composition. Most visible are studies of secular trends that often invoke dietary or environmental explanations of observed changes. More contextually-grounded research targets changes in mating network composition that can be related to more general social processes within paleopopulations attributable to shifts

in human adaptive strategies or historical demographic transitions. The intracemetery approach generally obviates the assumption that the same population is sampled repeatedly, as is the case when multiple distinct sites are sequentially ordered within a region (see Konigsberg, 1987, 1990a; Konigsberg and Buikstra, 1995; Stojanowski, 2001, 2003a). In addition, intracemetery analyses do not require consideration of regional spatial structure.

Previous research by bioanthropologists

Early osteological studies specifically addressed temporal biological changes within sites but did so largely from a migrationist (replacement) perspective (see Konigsberg, 1987). Hooton's *The Indians of Pecos Pueblo* (1930) is a good example of this approach. Hooton reconstructed changes in cranial form through time at Pecos Pueblo, New Mexico and related these changes to the typological history of population contacts at the site. Current approaches use more nuanced microevolutionary modeling that considers admixture, genetic drift, and natural selection in addition to migration replacement models (see for example Weisensee, 2004). Konigsberg (1987) identified two research themes: the evaluation of provisional archaeological ordering of burial units and the study of microevolutionary processes with greater temporal precision. Neither is very common, reflecting the rare circumstances in which archaeological sites can be divided into distinct temporal units. Examples include Owsley and Jantz's (1978) analysis of discrete burial areas at the Sully site, South Dakota, Owsley et al.'s (1982) analysis of the Mobridge site, South Dakota, and Konigsberg's (1987, 1990a,b) analysis of the Klunk, Gibson and Schild mound groups in Illinois. The South Dakota research will be treated in further detail below as these studies are contextualized within colonial demographic processes. The work of Konigsberg grounds this literature within population genetic theory and forms the theoretical basis for all subsequent work.

Theoretical basis for studying temporal microchronology

Konigsberg, (1987, 1990b) formalized temporal microevolutionary studies within a population genetic framework. Two different approaches were developed. The first considered the pattern of genetic similarity through time within a lineage (Konigsberg, 1987, 1990b). This approach is germane to the current discussion because temporal sequences are analyzed within sites where it is assumed distinct subdivisions represent snapshots of a single lineage at different points in time. As such, there is no geographic component to this analysis. The second approach considers spatial and temporal relationships among multiple sites within a regional mating network (Konigsberg, 1990a; Konigsberg and Buikstra, 1995). Because the focus is between-site variation, this model will not be discussed here. However, those interested in regional biodistance analyses should consider the important implications of Konigsberg's model (1990a).

The basis of within-lineage microchronological research is the first-order autoregressive process or Markov chain process in which sequentially ordered sets of observations are correlated such that those further apart from each other in the linear sequence are most dissimilar. Konigsberg (1987, 1990b) demonstrated that genetic correlations between relatives in a multi-generational

lineage follow such a pattern. This makes intuitive sense because kinship coefficients decrease both horizontally and vertically within a pedigree in relationship to ego. Konigsberg then established that genetic drift and migration produce a similar pattern of genetic correlations. This model was tested using two simulations that considered the effects of genetic drift and migration on genetic correlations within a temporal lineage. The first was a simple model that included no demographic structure while the second considered the more realistic situation of lineage fissioning with more prescribed patterns of migration. Both confirmed that genetic correlations between contiguous time periods are positive and that these correlations approach 0 as the time between generations, the lag, increases. Konigsberg (1987) then provided, "a method for testing whether a [genetic] distance matrix *could have been* (emphasis added) generated from data which was in a first-order autoregressive form." The method uses matrix correlations to compare the fit between observed genetic distance matrices and hypothesis matrices that model an autoregressive structure.

Methods

Methods to study temporal microchronology differ little from cemetery structure analyses that target synchronic social groupings (see above). Differences derive from the post-hoc interpretive framework where microchronology examines phenotypic differences from a temporal and microevolutionary perspective. The simplest approaches use standard descriptive and inferential statistics to: 1) determine if significant differences exist among burial subgroups, 2) if statistically significant, describe the nature of the differences in terms of means and variances, and then 3) infer, using a model-free approach, the evolutionary mechanisms associated with changes of this nature. For example, decreasing variability with stochastic changes in means might reflect genetic drift and changes in population size. Directional changes in means might reflect natural selection or admixture when variability increases in concert. Admixture sourcing may be possible if comparative data from hypothesized donor populations are available (see Owsley and Jantz, 1978; Owsley et al., 1982). This approach is informal and descriptive.

Owsley and colleagues (Owsley and Jantz, 1978; Owsley et al., 1982) used a multivariate canonical variates analysis to determine whether significant differences existed among burial subpopulations and then sequentially ordered them based on comparison with reference samples of known age. Konigsberg (1987, 1990b) used the quadratic assignment procedure of Mantel (1967) to test the correlation between intracemetery subgroup genetic distances and hypothesized temporal distance matrices. By permuting the hypothesized temporal ordering of burial units, the sequence with the best fit to the temporal lag distance matrix can be determined. Both of the above approaches are primarily concerned with gene flow and genetic drift and explicitly assume natural selection is not a major effect. In fact, Konigsberg (1990a) provides a method for removing the effects of selective trends in a dataset, which assumes that selection is not the object of investigation. However, the process of morphological adaptation can also be studied formally.

The quantitative genetic phenotypic rate tests of Lande provide a formal method of evaluating whether phenotypic trends can be explained by genetic drift, and

as such test the null model of evolution by natural selection (Lande, 1976, 1979; Lande and Arnold, 1983; Turelli et al., 1988). Although there are no intracemetery papers that specifically adopt this approach, perhaps reflecting bioarchaeology's lack of involvement in studies of selective adaptation, Sciulli and Mahaney (1991) have used these methods in their analysis of microevolutionary tooth size trends among prehistoric skeletal samples in Ohio. Lande's models are promising for intracemetery research, particularly for biodistance analyses where it is often assumed the traits behave in a sufficiently neutral manner over the time periods sampled. We are surprised these methods have never been used because an intracemetery application is not affected by the sampling concerns with using different sites from a larger geographic region and assuming they represent a single biological population.

Lande's models (Lande, 1976; Turelli et al., 1988) consider both the "minimum intensity of truncation selection necessary to produce a specific change," and the "maximum effective population size . . . that would allow genetic drift to produce the same phenotypic change by random sampling (Turelli et al., 1988)." Although several variations of these phenotypic rate tests were summarized by Turelli et al., two are most useful for intracemetery analysis.

The first is a truncation selection model that estimates the minimum proportion of individuals that must die each generation from the trait in question to produce an evolutionary response of the magnitude observed. The equation is straightforward:

$$b = \pm \sqrt{-2 \ln \sqrt{2\pi} \frac{|z|/\sigma}{h^2 t}}$$

where the data are \log_e transformed, $|z|$ is the absolute value of the mean difference between sample 1 and 2, σ is the pooled standard deviation, h^2 is the narrow sense heritability for the trait, and t is the number of generations that separate the two samples. The statistic b is used to estimate the proportion of the population that must have been removed due to selection each generation; b is used as a cutoff value for the standard normal distribution (Lande, 1976). An accessible applet is provided by http://davidmlane.com/hyperstat/z_table.html. Using this approach Sciulli and Mahaney (1991) estimated that 1–2% of the population of Late Archaic Ohio Amerindians suffered dental size related mortality each generation to produce the observed rate of tooth size change during the 1000 year development of the Ohio Hopewell.

Lande, (1976, 1977, 1979) further developed a statistical test that estimates the effective population size below which drift could cause the same amount of phenotypic change. This is called the constant heritability model. Drift can be rejected as a plausible evolutionary mechanism at the 5% significance level if,

$$N_e = \frac{1.96^2 h^2 t}{(z/\sigma)^2}$$

where N_e is the observed effective population size, with other variables as defined above. If the observed effective population size is greater than this quantity then population size was too large for drift to have caused a similar rate of phenotypic evolution. This model assumes

minimal environmental effect, constant population structure, and near constant additive genetic variance and heritability. The sampling distribution must be normal and the mean and variance uncorrelated. Transforming the data to \log_e scale is usually sufficient to satisfy both assumptions (Spicer, 1993). The model does not assume the population is at mutation-drift equilibrium, which is often the case when t , the number of generations separating the two samples, is less than $N_e/5$ (Turelli et al., 1988). This model was also used by Sciulli and Mahaney (1991) in their analysis.

Although Lande's models implied a time sequence approach, that is, sampling the same population at two points in time, they have been modified to consider the codivergence among multiple populations or species (e.g., Spicer, 1993; Monteiro and Gomes, 2005). This synchronic application requires estimating the divergence time of the populations sampled. Spicer (1993) gives formal F tests for directional and balancing selection based on the constant heritability model (see Eqs. 2 and 4 in that paper). Unfortunately, the degrees of freedom are undefined if only comparing two samples and it is unclear what is meant by "single lineage" in this paper (Spicer, 1993). An alternative mutation-drift equilibrium model differentiates between balancing selection (the amount of change is too small to be due to genetic drift), genetic drift (moderate rates of change) and directional selection (significant rates of change) (Turelli et al., 1988). Lynch (1990) presents a related model. Emphasis on mutational variance means the model is only useful when t is greater than $4N_e$, an unlikely situation in most archaeological cemeteries (two samples separated by 100 generations could have a maximum effective population size of 25 individuals). Turelli et al. (1988) provide an accessible discussion of this method while Lynch (1990) and Lande (2000) provide additional details about sampling bias, multivariate extensions, and more complex selection models.

Phenotypic selection rate tests are attractive for a number of reasons. They provide formal tests of evolutionary process and rely empirically only on means and variances. Therefore, both raw and summary data can be used. They do, however, require estimation of trait heritability, effective population sizes and generation lengths. While heritability and human generation lengths are often handled in a sufficiently simplistic manner, determining effective population sizes in prehistoric societies is challenging (Steadman, 2001; Stojanowski, 2005c) and making a decision about the significance of a test statistic may be difficult if the cutoff values are close to a reasonable estimate of population size. If population size is not constant or there are demographic changes such as sex ratio imbalances and age structure differences then more complicated estimates of effective population size are needed (Hartl and Clark, 1997).

Case study: Postcontact microevolution in the Northern Plains

For this case study we chose research that focuses on migration and gene flow rather than natural selection. In the previous case study the effects of postcontact epidemics on Native American demography and microevolution were evaluated using variance comparison methods. Similar processes of admixture and migration can be evaluated using studies of temporal microchronology. Owsley and Jantz (1978) presented an analysis of intra-

cemetery variation at the Sully site, an Arikara village dating to between 1600 and 1750 located along the Missouri River near Pierre, South Dakota (Fig. 6). Approximately 500 burials were recovered that were organized into four discrete burial areas (A, B, D, E). Grave goods associated with each area suggested a provisional archaeological chronology; the earliest cemetery (D) contained the greatest frequency of lithics while the latest (B) contained the greatest frequency of metal and glass. Analysis of the archaeological materials suggested a provisional sequence of areas D, E, A, and B, from earliest to most recent.

Owsley and Jantz (1978) collected 15 craniometric measurements and subjected males and females to discriminant function analysis. Eigenvalues of the canonical variates indicated significant differences existed between the four burial areas. The authors reasoned that because Arikara villages were endogamous and clans were exogamous that the discrete burial areas were not social units but likely represented different occupation phases because the site was abandoned and re-occupied during the course of the 17th and early 18th centuries.

To validate the internal chronology, four comparative samples of known date were incorporated into the discriminant model. Each sample reflected a distinct period of Plains history: Murphy (ca. AD 1450), Rygh (AD 1600–1650), Buffalo Pasture (AD 1740–1795), and Leavenworth (AD 1893–1930). Owsley and Jantz (1978) plotted the four comparative samples on the first canonical variates for males and females and found patterning in accordance with the age of each sample (Fig. 13). Leavenworth, the youngest sample, had the most negative position on the first canonical variate while Murphy and Rygh, the earliest samples, had the most positive positions along this axis. By comparing the Sully burial areas along the same axis the authors were able to estimate the approximate age of each and in so doing validated the chronology proposed based on archaeological data.

A similar method was used by Owsley et al. (1982) to analyze the temporal ordering of three discrete burial areas at the Mobridge site, South Dakota (Fig. 6). As at Sully, the three burials areas at Mobridge were placed in temporal order based on artifact types. Area 2 produced the highest frequency of trade items suggesting a more recent date while Areas 1 and 3 were thought to represent precontact components. Canonical variates analysis of 15 craniometric variables indicated significant differences between burial areas, with Area 2 demonstrating the most negative score and Area 3 the most positive score. Comparison of canonical scores with three reference samples (Leavenworth, Buffalo Pasture, and Rygh—see above) of known age reproduced the chronological position of these samples along the first canonical axis and supported the temporal position of the Mobridge burial areas based on artifact diversity (Fig. 13).

Both studies are important for understanding the process of Arikara ethnogenesis during the 17th and 18th centuries. Because the Sully and Mobridge sites afford the opportunity to observe cranial variation of the Arikara over distinct phases of the contact period, these data can be related to broader social changes within postcontact Plains communities. In fact, the pattern of cranial variation at Sully and Mobridge was consistent with previous research documenting increased Arikara admixture with Mandan populations in the wake of smallpox epidemics that swept across the Plains during the 18th century (Jantz, 1972, 1973).

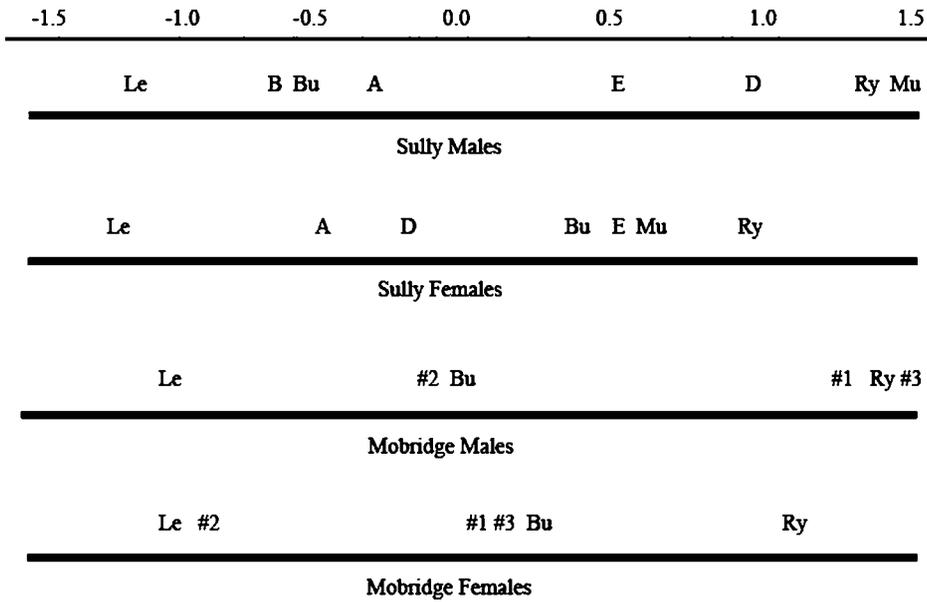


Fig. 13. Canonical variate 1 (-1.5 to 1.5) for analysis of Sully and Mobridge cranial variation. Le = Leavenworth, Bu = Buffalo Pasture, Ry = Rygh, and Mu = Murphy. Letters for Sully males and females represent the four discrete burial areas at this site. Numbers for Mobridge males and females represent the three discrete burial areas at this site.

AGE-STRUCTURED PHENOTYPIC VARIATION

Most cemeteries contain relatively intact demographic profiles that include both subadults and adults. Because the adult dentition forms and partially erupts during the juvenile years, phenotypic variation in tooth size between adults and subadults has been used to infer two different aspects of morphological variation. First, treating subadults as non-survivors or those who had no opportunity to reproduce and adults as survivors allows estimation of selection intensity. This approach is called cohort or cross-sectional analysis and compares phenotypic variation among age classes within a population at a single point in time to infer truncation or viability selection for larger or smaller teeth (Lande and Arnold, 1983; Endler, 1986). Second, reduced subadult tooth sizes have been interpreted in terms of a stress model (Guagliardo, 1982; Simpson et al., 1990). In this case, adults have larger teeth not because of phenotypic selection for this trait but because of ontogenetic disturbance and resulting diminished growth for that segment of the population suffering the greatest morbidity and ultimately a reduced lifespan (see Sweeney et al., 1971; Cook and Buikstra, 1979; Saunders and Hoppa, 1993). The stress model can only be adopted when subadults have significantly smaller teeth than adults, whereas the selection model applies in either case. The selection model assumes removal of the smallest or largest phenotypes and alleles associated with those phenotypes over long periods of time. However, for an intracemetery analysis one cannot study the evolutionary response to selection (which incorporates inheritance), but rather only the interaction of selective mechanisms with the phenotype (see Haldane, 1954; Lande and Arnold, 1983). This implies that extreme tooth sizes may be selected against directly, regardless of the genetic or environmental variation associated with their determination. To differentiate environmental and evolutionary effects, greater time depth and genotypic breeding values are needed to observe evolutionary response directly. Neither is possible with archaeological materials, and there is currently no way to distinguish the effects of ontogenetic variation from natural selection. Although research on intraceme-

tery age structure has been limited, most favor the stress model and note the tenuous relationship between fitness and tooth size over the short periods of time represented by archaeological samples (Guagliardo, 1982; Simpson et al., 1990). For cemetery samples it is also assumed that biological lineages reflect the average of evolutionary processes over the time period the sample was accumulating such that, unless selection intensity reversed course in the interim, the sample can be treated as a synchronic cohort. This assumption centers continuing debates within bioarchaeology (e.g., Cadien et al., 1974; Wood et al., 1992; Saunders and Hoppa, 1993; Hoppa and Vaupel, 2002) and is not unique to this research model. Inference of selection for tooth size (subadults have larger teeth than adults) is also subject to interpretive difficulties. Most problematic is dental attrition, particularly for mesiodistal crown size which reduces soon after eruption in prehistoric populations (see Kieser, 1990). Focus on cervical dimensions (Hillson et al., 2005) or buccolingual crown diameters mitigate this concern to some extent. Sexual dimorphism in tooth size (Kieser, 1990) is also problematic. The inability to estimate the sex of subadults (Rösing, 1983) requires pooling of adults which allows the possibility that unequal sex ratios in the adult or subadult cohort are driving observed size differences.

Previous research by bioanthropologists

Few studies have adopted an intracemetery analysis of age-related differences in dental phenotypes (not related to dental attrition). Two studies have specifically considered selection models. Perzigian (1975) analyzed age-specific differences in tooth size at the Larson site, South Dakota and interpreted the results as selection for larger teeth due to attrition-related mortality. The pattern of mean and variance differences by cohort suggested both directional and balancing selection were affecting the entire dental complex. Perzigian used the selection intensity method of Van Valen (1965, 1967). Sciulli et al. (1988) examined tooth size differences among age cohorts from four aggregated Archaic sites in Ohio using the cross-sectional methodology of Endler (1986). Results

indicated directional selection for both increasing and decreasing tooth size for specific teeth which created a more integrated dental complex among adult survivors.

Others have used age structure as a measure of ontogenetic disturbance and stress. Guagliardo (1982) questioned Perzigian's attrition hypothesis in his analysis of individuals from the Averbuch site, Tennessee. In his view, smaller subadult tooth size more likely reflects, "stressors powerful enough to influence development of the relatively stable enamel tissue [that] could also render the individual more susceptible to selective agents occurring later in life, such as childhood disease (Guagliardo, 1982)." Similar inferences were offered by Corruccini et al. (1982) at Newton Plantation, Barbados and by Larsen and colleagues at a series of Spanish missions in Florida and Georgia (Larsen, 1982, 1983; Simpson et al. 1990; Stojanowski, 2005d; Stojanowski et al., in press). Interestingly, research at Averbuch and the Spanish missions consistently found the mandible was more prone to stress-related dental reduction than the maxillary dentition.

Theoretical basis for analysis of age structure

The vastly different approaches offered by the selection and stress models require independent discussion of their theoretical bases. The theoretical basis of the selection model was provided by Endler (1986) and Lande and Arnold (1983). Endler (1986) noted that one condition of natural selection is, "a consistent relationship between [a] trait and mating ability, fertilizing ability, fertility, fecundity, and, or, survivorship." He then identified 10 different methods for detecting natural selection. His eighth method, comparison among age classes or life history stages, is the theoretical basis for intracemetery analysis of selection where the correlation is drawn between phenotype (tooth size) and survivorship (died as an adult or as a subadult). According to Lande and Arnold (1983), "[n]atural selection acts on phenotypes, regardless of their genetic basis, and produces immediate effects within a generation that can be measured without recourse to principles of heredity or evolution." That is, by comparing phenotypes among survivors and non-survivors the initial process of natural selection, phenotypic selection, can be ascertained. Measurement is accomplished by comparing phenotypes of breeding and non-breeding individuals, between age classes, between living and dead individuals, between juveniles and adults, or by using fitness component analysis (Endler, 1986). However, fitness, fertility, and fecundity cannot be measured in a skeletal sample and therefore survivorship is the only available proxy for determining breeding and non-breeding individuals. Much of the methodological development has occurred using living and dead individuals from a single population where mortality was due to short term environmental change (see examples in Lande and Arnold, 1983, also O'Donald, 1973). Because the focus is on phenotypic effect and not on evolutionary response there is no need to assume all adults in a sample reproduced. The cross-sectional approach has obvious disadvantages. The population should be sampled at a single point in time, fitness differences are crudely parsed into two categories (survivors and non-survivors), and the traits must not be age dependent (Arnold and Wade, 1984). We discussed the first point above, the second is unavoidable, and the third does not pertain to tooth sizes, assuming attrition effects can be

identified. Cross-sectional analysis is also limited methodologically (see Lande and Arnold, 1983).

The theoretical basis of the stress model has two components: 1) during growth, stress or metabolic disturbance can lead to growth disruption which ultimately results in a reduced phenotype, and 2) differential frailty within a population means some individuals are affected by environmental stressors more than others and these same individuals are those most at risk for early death. Therefore, the frailest individuals in a population are those most susceptible to growth arrest and premature mortality. The relationship between stress and growth disruption is not controversial. For the dentition, advocates of the stress model cite four sources of data (e.g., Guagliardo, 1982; Larsen, 1983; Simpson et al., 1990; Stojanowski, 2005d; Stojanowski et al., in press). First, tooth size heritability studies in many different populations indicate approximately 35% of the variation in tooth size within a population is not attributable to additive genetic variation (studies reviewed in Kieser, 1990; Stojanowski, 2005c). Second, dietary experiments using rodent models have documented relationships between carbohydrate, protein, fat, calcium, and caffeine intake and increases or reductions in tooth size (e.g., Lozupone and Fabia, 1989; Nakano et al., 1992). Third, numerous studies have documented secular trends in tooth size and related these changes to the consumption of a Westernized diet or improved dietary stability (Hanna et al., 1963; Goose, 1967; Garn et al., 1968; Lavelle, 1972, 1973; Ebeling et al., 1973; Kieser et al., 1987; Suzuki, 1993; Harris et al., 2001). Fourth, other environmental variables that are not dietary have been shown to affect tooth size, for example micro-elemental concentrations (Møller, 1967; Keene, 1971; Wang et al., 2002) and various factors of the maternal environment such as smoking (Heikinnen et al., 1992, 1994, 1997), alcohol use (Kieser, 1992; Kieser et al., 1997), low birth weight/maternal diet (Gyulavári, 1966; Fearn and Brook, 1993), and maternal hypothyroidism and diabetes (Garn et al., 1979, 1980).

Despite the abundance of work documenting relationships between dental reduction and various forms of stress, there has never been an experimental study that demonstrates causality. In addition, it may be assumed that tooth growth is similar to long bone growth for which stress models are clearly linked with shorter stature and decreased long bone dimensions (reviewed in Saunders and Hoppa, 1993). However, the determinants of tooth size are extremely complex, as evidenced by the three-dimensional geometry of enamel formation in comparison to a basically one-dimensional geometry of long bone growth. Therefore, while studies of age differences in tooth size are promising, further work is needed to clarify what mechanisms (reduced mitotic activity, reduced enamel secretion) might actually be responsible for dental reduction.

Methods

There are no formal methods for evaluating the stress model. Previous studies used simple univariate and multivariate analyses to test for size differences among adults and subadults (Guagliardo, 1982; Simpson et al., 1990; Stojanowski, 2005d, in press). Two factors that require consideration are the cutoff values for the adult cohort, generally 16–18 years of age, and the potential problem of sex ratio imbalances. The latter has been

addressed by comparing the pooled subadult sample to different ratios of the known sex adult sample, typically mixtures of 2 : 1 (Perzigian, 1975).

In contrast, methods for detecting natural selection are well developed, have a long history of practice and are generally complex. Space does not permit detailed discussion of these techniques here, and the dearth of interest in selective adaptation in bioarchaeology does not warrant an extensive review. Those interested in cohort analysis should consult Endler (1986) and references therein. It is important to remember the limitations of archaeological samples when considering the models presented. Those which assume known fitness parameters or known genealogical structures, for example the phenotypes of selected parents and their corresponding offspring, are generally not applicable in past populations. Previous work by Perzigian (1975) and Sciulli et al. (1988) has attempted to demonstrate the existence of selection, estimate its rate of change, and determine its predominant mode. Two approaches are most amenable to archaeological interpretation: mean fitness methods (Haldane, 1954, Van Valen, 1965, 1967), and estimation of selection differentials (Endler, 1986). Both are simpler methods of inference and as expected have some untenable assumptions.

Mean fitness methods relate fitness values to specific phenotypic values and estimate the proportion of deaths in a population required to cause a change in phenotypic mean and variance equal to that observed between selected and unselected individuals. A formula for this was first presented by Haldane (see Endler, 1986: Eq. 6.13), which was modified by Van Valen and simplified into a series of charts (see Van Valen, 1965: Figs. 2, 4, and 5; 1967: Figs. 1 and 2). These charts were used by Perzigian (1975). While they do overcome some of the distributional assumptions of Haldane's method, use of the charts assumes truncation selection, that is, individuals below some phenotypic threshold have 0 fitness. This is unlikely in natural populations (Endler, 1986) and the estimates of selection intensity are therefore considered to be minimum values. Endler (1986) discussed four models that do not assume truncation selection but require informed estimates of fitness associated with specific trait values. Figures in Van Valen (1965) can be used to estimate selection intensities for directional (mean changes), balancing (variance decreases), and disruptive (variance increases) selection but assume the unselected distribution is normal. Figures in Van Valen (1967) are easier to use and only require knowledge of the changes in mean and variance before and after selection. From these charts, the minimum selection intensity can be estimated directly. As a test of the presence of selection the model is rather weak.

Endler (1986) presented equations for calculating selection differentials between selected and unselected portions of a population. A measure of directional selection is given by $i = (X_a - X_b) / (v_b)^{1/2}$ where X_a is the after selection mean, X_b is the before selection mean and v_b is the before selection variance. A measure of variance selection is $j = (v_a - v_b) / v_b$, where v_a is the after selection variance and v_b is the before selection variance. Endler (1986) and Van Valen (1978) provide significance tests, which vary in their sensitivity to the distributional properties of the samples. One problem is determining whether to use selected and unselected portions of the population (adults vs. subadults) or before and after selection portions of the population (subadults+ adults, vs. just adults). The former

is appropriate with short-term fatality studies such as the Bumpus sparrow and *Geospiza fortis* datasets. The latter is more appropriate for archaeological cemeteries but the lack of independence between the sub-samples precludes use of inferential statistical tests such as those summarized by Endler (1986). The variance statistic j can also be modified to account for the reduction in variance due to concurrent directional selection (measured by i). The formula is straightforward: $j^* = j + i^2$. More complex multivariate methods were discussed by Lande and Arnold (1983) and Endler (1986). These are preferable to univariate approaches, which are affected by correlated response to selection.

Case Study: Stress and mortality in postcontact La Florida

Two decades of research on health and morbidity in colonial La Florida (see above) has demonstrated that indigenous communities at the Spanish missions suffered greater morbidity and health declined as a result (Larsen, 2001). Much of this work has focused on the dentition, in particular macroscopic linear enamel hypoplasias (Hutchinson and Larsen, 2001) and microscopic accentuated striae of Retizus (Simpson, 2001). Increased frequencies of cribra orbitalia, porotic hyperostosis, and periosteal infections may also indicate a decline in quality of life after contact (Larsen and Harn, 1994; Larsen and Sering, 2000; Schultz et al., 2001).

Phenotypic tooth size differences by age cohort have been investigated at three Spanish missions in Georgia and Florida and added a novel component to studies of morbidity in archaeological contexts (see site locations in Fig. 6). Simpson et al. (1990) examined tooth size differences at Santa Catalina de Guale located along the coast of Georgia and found significant reduction in subadult mandibular canines and premolars. The average deficit was 3%. Stojanowski (2005d) investigated subadult size bias at the Apalachee mission named San Pedro y San Pablo de Patate. Although based on a limited sample for only five variables, Stojanowski found two were significantly different at the 5% level and a third was significantly different at the 10% level. For all significant variables, subadults demonstrated smaller dentitions. Multivariate analysis using principal components also indicated subadult mortality bias. Finally, Stojanowski et al., (in press) compared age-specific tooth sizes at San Luis de Talimali. Although none of the maxillary teeth were significantly different between age classes, almost all of the mandibular teeth were larger for adults. Of 20 comparisons, five were significant at the 5% level and four were significant at the 10% level. Multivariate principal components analysis indicated a similar pattern. The individual tooth size biases ranged from 1.8 to 13.6%. Overall, adult teeth were on average 4% larger than subadult teeth. That the mandibular dentition seemed more sensitive to stress is consistent with the results of Guagliardo (1982), although we are unaware of what developmental mechanism might explain this.

One interesting result of this research is the potential use of tooth size differences as a marker of metabolic stress. This was the original intent of the Guagliardo paper. However, what is interesting among the three studies presented here is that one site, San Pedro y San Pablo de Patate, demonstrated size bias but not elevated frequencies of linear enamel hypoplasia (Storey, 1986;

Jones et al., 1991). This suggests that tooth size may be more sensitive to environmental stressors than macroscopic hypoplastic defects. However, accentuated striae of Retzius frequencies were elevated at Patale so that it cannot be claimed the population was completely unaffected by some kind of stress (Simpson, 2001). Accentuated striae formation was linked to ages of insult younger than those for hypoplastic defects, and this result, along with the tooth size differences, may indicate tooth size is also affected by stress that occurs in the earliest years of life. In summary, using age-specific tooth size differences as a marker of stress seems well supported by various types of correlation studies (see above); however, the complex process of enamel formation makes inferences about stress more tenuous. It is important to note, however, regardless of the mechanism, that age differences in the dentition may negatively impact studies that use dental size as a measure of population affinity. Future research should test for such biases or exclude subadults from the study sample.

CONCLUSION

Intracemetery biodistance approaches provide significant and unique information about site formation processes, environmental conditions, mortality, site structure, migration, and patterns of biological affinity that, when considered in concert with archaeological data, provides a complete picture of past populations. Intracemetery research also serves as a vehicle for evaluating epistemological issues, most specifically the complex relationship that exists between living human populations in which generations overlap and the resulting death assemblages created by those populations. The specific case studies presented in this review demonstrate the diverse interpretive milieu offered by intracemetery biodistance research. Analysis of the Windover population sample highlighted the contribution of kinship and cemetery structure analysis for understanding mortuary ritual, reconstructing site formation processes, and inferring aspects of hunter-gatherer population dynamics that are not possible using other methods. Postmarital residence research at Pueblo Bonito questioned archaeological use of the direct historical approach while also demonstrating how important postmarital residence is to broader aspects of human social organization. For the Southwest, entire systems theories have been built upon the matrilocality assumption. Both the study of Arikara cranial microevolution and phenotypic variance changes in postcontact La Florida are related to broader issues of colonial scholarship. Although the methods and analytical approaches differed, the processes of Native American social adaptation were outlined in the wake of demographic collapse following the introduction of European diseases to the New World. In both the Plains and southeastern US, patterns of morphological microevolution contribute to understanding of tribal ethnogenesis which has profound contemporary repercussions in this era of increasing inter-ethnic and tribal violence. Finally, the study of age-related differences in tooth size demonstrated the potential of a little used measure of morbidity, subadult tooth size deficiencies. That case study also highlighted the importance of considering carefully the demographic composition of skeletal samples that are used in broader comparative research.

The present and future state of intracemetery biodistance research

In summarizing previous research it is also useful to identify future directions. Considering the overview presented above, it is apparent that some methods are “mature” and grounded theoretically and methodologically, whereas others are still in a nascent phase in which additional baseline work is needed. In this last section we summarize the “state of the art” for each of the methods summarized and try to highlight weak areas that need further development.

Postmarital residence analysis provides a direct link between biological variation and social processes in past populations. Because the analytical protocol is well developed and relatively straight forward, postmarital residence analysis provides maximum interpretive value for minimal methodological requirements. The theoretical foundation of postmarital residence analysis is also well established, largely from the work of Konigsberg (1987, 1988). This approach is mature and well developed and should continue to contribute to studies of past human social organization.

Temporal microchronology is a very powerful approach that allows analysis of microevolutionary process at fine time scales but is subject to the whims of the specific cemetery. If distinct temporal units are not identified then nothing more can be said. However, the theoretical justification and methodological approaches for studying within-site temporal microchronologies are well developed, also primarily through the efforts of Konigsberg (1987, 1990a,b). We, therefore, consider this a fairly “mature” approach whose potential significance is hindered only by the vagaries of archaeological site formation processes.

Analysis of overall phenotypic variability is methodologically simple but fraught with interpretive problems. There are many causes of phenotypic variability, and it is difficult to distinguish among them in archaeological samples. We, therefore, consider this approach to be in an early stage of development. The theoretical justification for the analysis is poorly developed and until the relationship between genotypic and phenotypic variation, and between living populations and the aggregate death assemblages they create, is better understood the study of intracemetery variability will remain vague and underdeveloped. Given the relatively weak level of inference available from such an approach we suspect limited improvement in the future.

The study of age structured phenotypic variability is also a potentially very powerful tool but one that is theoretically underdeveloped. The most problematic concern is the inability to differentiate ontogenetic from selective processes, requiring the researcher to decide between the stress or selection models (if subadult size bias is documented) a priori. This is undesirable. The selection model is theoretically and methodologically well developed, however model building has occurred outside of anthropology using data sets that differ considerably from those represented in archaeological cemeteries. Much of the biological literature uses either fossil taxa or mortality samples related to catastrophic environmental events. The applicability of the same models to archaeological samples requires further consideration. In addition, inter-generational selection models must be wary of correlated response and must provide a realistic link between mortality and tooth size differences within a population. Thus far this has not occurred.

The stress model may be more appropriate, although it too requires further theoretical work. Tooth growth is not similar to long bone growth in which mitotic activity occurs in an essentially single, linear dimension. Tooth sizes reflects both mitotic activity, enamel secretion rates, and the internal epithelium morphology (Hillson, 1996). Experimental models are needed to firmly document a relationship between stress and perturbations in tooth growth that lead to diminished crown size. It is important to stress that the issue is not whether metabolic insult leads to dental growth disruption, decades of hypoplastic defect and accentuated striae of Retzius research document this association, but the specific model in which this growth disturbance leads to crown size reduction in the planes typically measured by odontometrists. Therefore, analysis of phenotypic variation in relationship to age structure is still under-developed but has significant future potential.

More than any other approach, kinship analysis has the greatest unrealized potential given the long history of interest in these studies spanning at least four decades. In considering this corpus of literature two themes became apparent. The first is a distinct methodological focus: which traits are best suited to kinship analysis and what methods can be used to detect the presence of closely related individuals. The second is a descriptive undertone that serves primarily archaeological purposes, that is, reconstructing site formation processes or merely noting that close kin were buried in a particular cemetery. To this end, we have two comments.

First, it is now abundantly clear that morphology sometimes can and sometimes cannot be used for kinship analysis. This fact reflects the vagaries of trait segregation within lineages and is unavoidable (Rösing, 1986a). Nevertheless, morphology will not be completely replaced by genetic data anytime soon. Multiple studies have demonstrated the ability of morphological data to perform at this scale of resolution (Rösing, 1986a; Shinoda and Kunisada, 1994; Oota et al., 1995; Spence, 1996; Corruccini and Shimada, 2002; Corruccini et al., 2002; Adachi et al., 2003, 2005; Velemínský and Dobisková, 2005) without simple appeals to trait heritabilities. We, therefore, feel that kinship analysis is mature from a theoretical and methodological perspective, although further understanding of the mechanisms of inheritance of phenotypic traits are needed.

Second, most cemeteries contain closely related individuals, a fact promoted by Cadien et al. (1974) three decades ago. It is probably more noteworthy to report on a cemetery that does not appear to contain genetic relatives. Therefore, simply documenting the presence of kin-structured burial does not advance anthropological knowledge. We would like to stress that kinship analysis should be one component of a broader research program rather than the research objective itself. In reality, very few studies of kinship move beyond the descriptive phase. Notable exceptions are Gamble et al. (2001), Duncan (2005), and the research of Corruccini and Shimada (Corruccini and Shimada, 2002; Corruccini et al., 2002; Shimada et al., 2004). The potential of kinship analysis is, however, more significant. The most obvious benefit is the ability to identify family groups within the context of the greater population in which they lived. This is why the large cemetery approaches discussed above are so important. Identification of families adds a new level to the standard hierarchy of population biology (individual, subpopulation, population, species). The placement of individuals within families

within a subpopulation allows much finer-grained consideration of dietary differences, disease experience, demographic factors of mortality and fertility and overall levels of adaptation within paleopopulations. The last three decades of bioarchaeological research could be reconsidered in this light. In addition, this scale of resolution can assess differential frailty and provide one of the best ways to evaluate the "osteological paradox (Wood et al., 1992)." Therefore, kinship analysis, as well as the other methodological approaches summarized in this review, has the potential to significantly advance our understanding of past populations. We hope this review stimulates additional research in new and unique directions.

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