

Assessing Multiple Lines of Evidence for Gene Flow in Archaeological Contexts

A Dissertation Presented for the

Doctor of Philosophy

Degree

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Dedicated lovingly to Alfred, my constant companion.

In memory of Harriett Woods and Jon Mallard.

Acknowledgments

Thank you to my committee: Ben, Graciela, Dave, and Jim. We're finally here, and you have been of tremendous help in getting me to the finish line (even if sometimes I lagged behind).

I am always happy to tell people what they mean to me in person, but public acknowledgments make me uncomfortable. In the meantime, to my family and friends...well, you already know.

Abstract

This multi-study dissertation assesses the ability of two skeletal analysis methods—a model-bound quantitative genetic method (Relethford-Blangero) and a model-free biological distance method (Mahalanobis' D^2)—to evaluate gene flow in the U.S. Southwest and Northwest Mexico based on archaeological models. The first study uses dental metric data from the Sonoran Desert and Mogollon Rim (c. 1600 B.C. to A.D. 1450) to pilot the Relethford-Blangero method in this context. Notably, the method shows that populations from two large sites have less than expected dental variance, failing to support a gene flow event despite material culture pointing to at least two coexisting communities. This suggests even supported conclusions from a material culture perspective will not necessarily match the biological relationships experienced by past communities. The second study compares both method groups using a sample of five sites that overlap temporally (c. A.D. 1100-1450) from the Mogollon Rim region, and also compares different groups of skeletal traits (cranial, dental, and postcranial) to each other to determine the efficacy of using each to understand gene flow. While there are some consistencies between skeletal trait groups, their congruence lacks a clear pattern. Biodistance results lack consistency regarding which groups may be most closely related, while the Relethford-Blangero method compliments archaeological data in some instances. The third study uses data from the limbs and their girdles to evaluate a larger geographic and temporal region. Sites from across the Puebloan world (c. A.D. 840-1590) are compared to address how well postcranial data mirror the archaeological models. Though not all results are consistent with archaeological models, there is a pattern showing that the ways of interacting for the Western Pueblo (Arizona) are different than those of the Eastern Pueblo (New Mexico), supporting separate cultural classifications devised by archaeologists. In addition, the lower limb appears to drive the overall postcranial signal more than the upper limb alone. Overall, while the quantitative genetic method adds additional details to the archaeological models, biodistance is sometimes difficult to interpret. The quantitative genetic method should be added to the analytical toolkit in all cases, not just those of potential ambiguity.

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Chapter 1
BACKGROUND

I. Preface

The design of this dissertation has changed form since its proposal to the National Science Foundation in July 2018, the award of the Doctoral Dissertation Improvement Grant (#1945986) in March 2020, and the completion of the dissertation in 2021. As the reader is likely aware, in February 2020, the novel coronavirus (COVID-19) arrived to the United States, prompting significant pandemic shutdowns beginning in March. While the NSF grant was awarded to fund travel for data collection at the National Museum of Natural History (NMNH; Washington, D.C.) and Maxwell Museum of Anthropology (MMA; Albuquerque, New Mexico), both museums instituted moratoriums on visiting researchers beginning March 2020. Travel out of state from my own institution (University of Tennessee, Knoxville) was restricted until October 2020, but upon the lifting of those restrictions, it was still not possible to travel to these museums. As of August 2021, visiting research still has not been entirely rescheduled at NMNH, and all research involving human remains of Native American origin has been suspended indefinitely at MMA. This impacted the structure of the third paper (Chapter 4) in that archival data from only the postcrania (Auerbach, 2007) had to be used rather than cranial, dental, and postcranial data collected by me.

More importantly, the structure of the NSF grant proposal also included active dialogue with descendant communities in Arizona and New Mexico, particularly to get their perspectives while still asking questions about quantitative genetic and biological distance methods of studying gene flow. However, both Hopi and the Nineteen Pueblos, as well as their Diné neighbors, were affected by the pandemic in ways that dramatically affected tribal members and their public health infrastructure, causing closures of tribal offices as well as pueblos and reservations themselves. Consequently, this dialogue did not occur. With questions regarding the ethics of data collection on human remains (particularly those identified as Native American) and the use of archival data from those remains becoming more and more critical, this is a loose thread that I hope to tie together as we are able to turn our attention back to a cooperative model of research. As a discipline, and particularly within the American Association of Biological Anthropologists, we have not yet resolved how to move forward with non-destructive analysis on human remains, and the question of archival data is an even more distant resolution.

II. Migration, Gene Flow, & the Question of Past Population Interaction

This dissertation considers evidence for the interactions of populations, or single groups of people (Futuyma & Kirkpatrick, 2017), in the past as reflected by biological variation preserved in skeletal anatomy. As I explore in more detail below, these interactions may take multiple forms. Trade, warfare, cultural assimilation, kinship organization, post-marital residency, and diplomacy are but a few of the ways in which human populations interact. These all impact the biology of groups, sometimes in ways that are genetically or biologically indistinguishable. For example, the migration and assimilation of one group into another local group could result in a mating relationship between them, though gene flow may not necessitate the movement of peoples. Trade, warfare, or less organized encounters between groups could also result in mating relationships. Likewise, the sharing of material culture does not imply trade, nor does it necessitate mate exchange between groups. Thus, associating biological evidence with

archaeological evidence to build models of human interactions in the past is contextual, nuanced, and often open to debate (El-Najjar, 1978; Auerbach, 2010; Sassaman, 2010).

There are examples throughout history relating various types of human interaction. Migration, for example, may bring groups of people into contact that otherwise may not have interacted (Janzen, 2012; Clark et al., 2019), some of which result in detectable gene flow (e.g., Hunley & Healy, 2011; Beaty, 2012). The definition of migration often varies by researcher (Anthony, 1990). However, a minimal definition proposed by Cabana & Clark clarifies the process as “a one-way residential relocation to a different ‘environment’ by at least one individual” (2011:5). The ramifications of such a definition are two-fold: a physical movement takes place, and it has some sort of transformational quality (whether in the physical environment or on a cultural basis) (Little & Leslie, 1993). As will be discussed, this research project adopts Cabana & Clark’s minimal definition with slight modifications.

Economic pressures may result in migrations (Janzen, 2012), including indentured servitude (Madrigal et al., 2012), as may atrocities of forced relocation such as the Atlantic slave trade (Chakraborty, 1986). Migrations, whether resulting in gene flow or not, can be multi-causal population interactions. Today’s migrants to the U.S.-Mexico border, for instance, are commonly driven by collapsing economic infrastructures, environmental pressures, warfare and crime, or a combination of any of these factors (Massey & Parrado, 1994; Chavez, 1998; De León, Gokee, & Forringer-Beal, 2015; Meierotto, 2015). Not all interactions, of course, should be considered a migration, nor do they necessarily coincide with gene flow. In the past just as today, trade or the exchange of ideas could result in changes to material culture, architecture, or cultural practices (Clark, 2011), and frontier zones often serve as places of cultural exchange as well as cultural innovation (Lightfoot & Martinez, 1995). Warfare, too, could result in an aggressor population supplanting another and taking over the original occupants’ homeland, assimilating with the original occupants, or pillaging the land of its valuable resources and leaving. Any of these scenarios could result in gene flow, but do not inherently do so.

Human interactions are therefore complex and often enigmatic, a fact that becomes truer as we attempt to understand them further and further into the past. The scholarly landscape is rife with interpretations of human social and biological interactions throughout human history, arising from different disciplines with different central interests. Whether because or in spite of the many different questions we ask about the past, even if we may arrive at broad consistencies in our understanding of how groups of people relate to each other across time and space, it can still be difficult to pinpoint specifics such as the timing of group interaction, the nature of those interactions (e.g., trade, migration, etc.), or the complexities surrounding group identity as seen by the bearers of those identities. Critically, though, our ability to see the *inconsistencies* and interpret them is a key element of these reconstructions. There are major components of population history whose understanding can be enriched by more thoroughly exploring mismatches between different aspects of the same population processes. Migration is one of those recurring historical events that can benefit from such a perspective, noting both the consistencies and the inconsistencies in reconstructions using different data types.

Migration extends beyond physical movement. Factors such as population size, demographic composition, environmental change, and between-group social relationships both affect and are

affected by the migration of a group (of any species) from one place to another. The movement of larger-scale populations, for example, could either be precipitated by an organized effort (such as the movement of multiple groups to Cahokia at approximately A.D. 1000; Pauketat, 2009) or driven by a natural calamity (e.g., the depopulation of the Four Corners during the 12th-13th centuries potentially due to drought; Varien, 1999, 2010), both circumstances motivated by and affecting natural conditions. For humans, this complexity is heightened as a consequence of cultural diversity. As populations encounter each other and interact, cultural elements such as material goods and social belief systems may be exchanged and may change form.

However, *how* cultural change occurs, and subsequently how that relates to the biological processes that may also result from human migration, is not very well understood. A frequently encountered assumption in academic literature is that migration and gene flow are equivalent processes. This assumption is problematic. While migration is a complex intertwining of cultural and biological elements, gene flow is a strictly biological process. To assume equivalence in these processes either oversimplifies the complexity of migration or overcomplicates the idea of gene flow beyond what gene flow research can actually show. Researchers have come to know gene flow, at its simplest, as the introduction of alleles from one population to another (Futuyma & Kirkpatrick, 2017). Sometimes these alleles are novel, but not always; that is, alleles identical by state but not identical by descent could be exchanged through gene flow and thus serve as invisible signatures of gene flow (Falconer and Mackay, 1996). In association with this, population differentiation (as measured by F_{st}) is often used as a measure of population distance and thus genetic exchange (Cavalli-Sforza, Menozzi, & Piazza, 1994; Futuyma & Kirkpatrick, 2017). Among most species, a physical movement accompanies the process of gene flow. Evolutionary biologists, therefore, generally consider gene flow in combination with migration or dispersal. Depending on the context, this may be a reasonable assumption, as it often is for non-human organisms.

Humans complicate this narrative. While gene flow in humans *often* accompanies migration — for example, the Neolithic expansion (Currat & Excoffier, 2005), the Bantu migration (Scheinfeldt, Soi, & Tishkoff, 2010), and European colonization of the Americas (Hunley & Healy, 2011) — they are not synonymous processes. There are examples of human migration in history that have *not* accompanied a gene flow event because of cultural influence. For example, studies of immigrating populations to the United States during the first two decades of the twentieth century show that immigrants generally stayed genetically isolated and did not intermarry, even with members of their own culture who were already present from previous immigration waves (Pagnini and Morgan, 1990). While conceptually linking gene flow and migration has significant precedent in non-humans, the cultural diversity of human interactions precludes this assumption in our own species.

This complicates our understanding of *both* human migration and gene flow. Gene flow becomes, instead, one of several considerations in the study of migration - a consequence of the process rather than the entire story (Fix, 2011). We continue to fill in narratives of past migration with material archaeological findings such as parts of room blocks or domestic items, genetic evidence indicating the movement of disease vectors, faunal bones from the movement of domesticated animals, changes in linguistic structure over broad time periods, and a host of other factors. As a result, migration hypotheses are often based on multiple lines of evidence (Rouse,

1986), of which evidence of human gene flow is one of many considerations. Some researchers advocate this approach as a way to validate different methods (Chakraborty, 1986), but that presumes that each method should arrive at the same results. Realistically, hypotheses derived from different data sources do not necessarily result in similar conclusions – nor *should* they, in most cases. Rather, different data sources address different aspects of the same hypothesized interactions. Understanding the bridge between different data sources becomes critical to compiling these migration narratives, yet we as scholars remain far from being able to do this consistently and effectively.

In the case of biological and archaeological data, bridging the differences in interpretation between data types is an area of research that would benefit from significant growth (Sassaman, 2010). Yet relating the process of human gene flow to material elements of the archaeological record within the same temporal context presents numerous challenges for researchers. These two types of evidence inherently measure different aspects of population interaction – one biological, one material. While methods that measure gene flow address the biological aspect of inter-mating between groups, they do not provide complete insight into the social nature of those relationships. Likewise, the movement of archaeological materials or evidence of outside influence does not necessarily imply a mating relationship, nor does it always co-occur with a movement of groups of people. This critique of conflating material culture with biology when it comes to interpreting archaeological culture change has been levied before. Godfrey & Cole (1979), for instance, critiqued Schneider (1977) and his suggestion that the diffusion of culture may be interpreted using a model of evolutionary (genetic) inheritance. Instead, they argued that the predictability we see in human behavior, which is ultimately borne out through material culture, is a result of shared genes rather than genetic predisposition. Likewise, more recent scholarship has emphasized the importance of not interpreting the spread of material culture as a proxy for the movement of people or genes without appropriate context (Bellwood, 2001; Sassaman, 2010; Clark, 2011), and Hakenbeck (2008) cautions that interdisciplinary research must avoid the pitfall of diluting complex concepts from other disciplines in a way that does not accurately portray the complexity of the problem. Researchers are generally aware of the discrepancies between different data types, but the question remains: how do we bridge that gap?

Anthropologists have made important contributions toward resolving differences in interpretation between different types of evidence to understand past population interactions (Knudson & Stojanowski, 2008). Some have addressed the lack of concordance head-on (e.g., Cordell, 1977; El-Najjar, 1978; Cameron, 1995; Blom, Hallgrímsson, Keng, Lozada, & Buikstra, 1998; Bellwood, 2001; Beekman & Christensen, 2003; Hunley & Long, 2005). Beekman & Christensen (2003), for instance, argued that divergences in data set correlation should be used to refine migration hypotheses rather than be used solely as a demonstration of inaccuracy in one of the methods (contra Chakraborty, 1986). Further, they emphasized the importance of studying social and environmental factors in understanding the impetus for migration, a departure from the general tendency of archaeologists (e.g., Burmeister, 2000) to use migration to explain patterns of material culture (2003, 2011). Yet, despite these studies, explanatory mechanisms for this lack of concordance between data types remain unresolved. Cabana & Clark (2011) argue that we lack a sufficient theoretical framework to act as a foundation on which to set expectations for what these mechanisms should look like.

As a result of lacking this framework in anthropological studies of migration, several crucial questions remain unanswered: How *should* we expect migration to be preserved in biological and material culture contexts, and how closely would evidence of each agree? If researchers find either matches or mismatches in different lines of evidence, how should these be interpreted as showing support or lack of support for past migration hypotheses? Furthermore, what if one or more of those lines of evidence suffers from insufficient sample sizes, patchy temporal and geographic spread of samples, and/or inadequate analytical tools?

It is the lattermost question, particularly in relation to analytical tools, that is of central concern to this study. Without a firm understanding of the efficacy of any given line of evidence, it is difficult to ascertain whether the comparisons of disparate types of evidence may be interpreted as biologically or culturally significant. Though the use of different types of data to assess the validity of each other in studying the same migration phenomena may not be prudent, the use of the same types of data to assess the validity of different methods for studying *part* of these migration phenomena has more potential to yield revealing mismatches that can be explained. In order to refine expectations for the relationship between biological evidence and material culture in studies of ancient migration, this study explores two methods for inferring gene flow from skeletal data (Mahalanobis' D^2 and Relethford-Blangero), while controlling as much as possible for the noted concerns about sampling. By addressing the inference of gene flow as a major, albeit incomplete, element of the migration narrative, we may bring ourselves one step closer to understanding the process of past migration.

III. Gene Flow: The Creator and the Constrainer

Evolutionary statistician Sewall Wright (1931) described gene flow as a creative force, free to spread genes and gene combinations from one population to another with the movement of individuals and groups (Slatkin, 1987). The relationship of gene flow to within-species variation, and more specifically within-population variation, informs our understanding of human migration. Situating the process of gene flow within evolutionary theory, as both Darwin (1859) and Wallace (1863, 1889) did, allows researchers to understand its relationship to other evolutionary processes and to recognize its role in our species' population history (Lynch, 2007). Wright (1931) referred to gene flow as migration and demonstrated its effects in terms of changes in gene frequency. The baseline statistic for the gene frequency departure of any one subgroup toward the population average he described as

$$\Delta q = -m(q - q_m)$$

where m is the proportion of the population exchanged, q is the population average gene frequency, and q_m is the gene frequency of the subgroup. The parameter m is also referred to in later literature as the migration rate (Harrison & Boyce, 1972; Falconer & Mackay, 2009; Futuyma, 2013). It was Wright who popularized focusing on small populations of limited variance affected by non-adaptive modes of evolution, as changes would be more easily detectable within these populations than larger, more varied ones (Larson, 2006).

While scientists and statisticians have focused considerably on other mechanisms of evolution – natural selection (Fisher, 1930; Haldane, 1932), mutation (Morgan, 1903), and genetic drift

(Wright, 1931, 1932) – gene flow remains a less thoroughly researched topic, particularly in the context of human evolution. The study of gene flow in any species is complicated by interactions with other mechanisms (Bohonak, 1999), with considerable focus being levied upon drift. Gene flow and genetic drift, both non-adaptive mechanisms, tend to counteract each other. While drift propels genes or combinations of genes towards fixation or loss, tending toward population isolation (Wright, 1931), gene flow between populations prevents differentiation.

From a population genetic perspective, over time gene flow is a homogenizing force between populations (Harrison & Boyce, 1972), though it initially increases heterozygosity within populations as a result of the introduction of additional variation (Falconer & Mackay, 2009, but see Chakraborty, 1986). The addition of new variation increases a population's effective size (N_e) and slows the rate of allele fixation (Slatkin, 1987; Bohonak, 1999), thereby reducing the likelihood of genetic drift driving that population to an isolated peak on the adaptive landscape (Wright, 1932).

Wright's island model (1943, 1951) is often used to represent population structure and dispersal, though Slatkin & Barton described it as an "extreme in long-distance gene flow" (1989:1352). Regardless of distance, every population is equally accessible from every other, simulating immigration from a common and constant gene pool (Bodmer & Cavalli-Sforza, 1968). Wright's fixation index, or F_{st} , is a parameter that measures population heterozygosity under the conditions of this island model, with increasing homozygosity assumed to be progress towards fixation (1965, 1969). The island model assumes equilibrium among populations, an assumption often violated by attempts to consider regional F_{st} in terms of gene flow (Hutchison & Templeton, 1999).

As gene flow persists over time, however, it gradually decreases genotypic and phenotypic differentiation as well as within-population variance between mating populations (Hutchison & Templeton, 1999), prompting the consideration of persistent gene flow as a "constraining force" (Slatkin, 1987). Slatkin (1987) concluded that gene flow's influence as a constraining or creative force is dependent on the demographic stability of a species' substructure over time, with greater influence more likely when that structure is unstable as a consequence of frequent demographic changes. These changes may be due to regional colonization, extinction, and/or changes in geographic range. Though Hiorns & Harrison (1977) suggested when migration and selection are both large, it would take over one hundred generations for population gene frequencies to be homogenized among humans, Frankenberg & Konigsberg (2011) demonstrated that within fifty generations of a gene flow event, random genetic drift will hinder the ability to differentiate the post-migration population from one that has experienced regional population continuity. The effect is even more apparent in small populations. Hutchison & Templeton (1999) demonstrated that increasing geographic distance between populations also allowed for increased influence of genetic drift relative to gene flow, which could increase F_{st} variability as geographic distance increases.

Isolation by distance (IBD) is another, perhaps more commonly used, gene flow model that assumes the correlation of gene frequencies in finite groups of equal size decreases exponentially with increasing distance r (Kimura & Weiss, 1964; Malécot, 1969). Like the island model, this model represents more of a null hypothesis than an actual expectation; geographic distribution of

populations is rarely orderly, and population size and mobility are rarely constant across space and time (Bodmer & Cavalli-Sforza, 1968). Modeling continuously distributed populations, Slatkin & Excoffier (2012) surmised that heterozygosity will decrease linearly as a function of distance, resulting in clines from constant range expansion in the absence of selection. This model employs the concept of neighborhoods; within them, mating is effectively random, but individuals will travel only a limited distance after birth. Because of this limitation on mobility, immigrant populations within this model are more genetically similar in terms of gene frequency than immigrants in the island model. Importantly, this means their migration less effectively counteracts drift (Falconer & Mackay, 2009).

IBD thus forms the theoretical underpinning for commonly used forms of examining population structure, namely biological distances (biodistances), commonly estimated through a minimum Euclidean distance, such as Mahalanobis' D^2 , calculated on osteometrics, anthropometrics, or genomic sequences (Relethford, 2016). The logic of these methods is that populations that have more recently derived from a common ancestor, or have more recent gene flow, will have more similar morphology than populations with more ancient common ancestry or no gene flow. While this set of assumptions may be reasonable within a circumscribed geographic area and time period, these methods are more prone to error over longer distances and time, and so are poor models for human relationships (Hunley, Healy, & Long, 2009; Roseman, 2016; contra Betti, 2014). Thus, other methods for estimating gene flow are more generally appropriate for assessing human gene flow, namely the relationship matrix approach developed by Relethford and Blangero (1990) based on a more general model of deviations from expected variation.

The Relethford-Blangero (1990) approach to modeling genetic structure among human populations is based on a multivariate quantitative extension of the population genetic approach (Harpending & Ward, 1982) for comparing estimated expected heterozygosity versus observed heterozygosity among a set of populations. The method uses a relationship matrix (R-matrix), which provides a scaled set of variances and covariances of traits among populations from a regional centroid to ascertain their genetic distances. With these as a basis for analysis, the method provides an estimate of expected within-population variance. When compared against the observed variance, then, a positive residual would reflect greater-than-expected variance, and thus support evidence for gene flow from outside the region of study (i.e., the populations included in the model). Negative residuals do not inherently discount the existence of gene flow within a population, but the model does not provide evidence. This approach, furthermore, is robust to uncertainty about the heritability of traits under study (Relethford and Blangero, 1990). As I discuss in more detail in Chapter Two, while this method is a more precise assessment of gene flow than what is offered by biodistance methods like D^2 , it is not without its uncertainty with respect to interpretations about the timing and sources of genetic exchange.

IV. Human & Non-Human Gene Flow Research

Research on gene flow in non-human organisms is abundant in categories of direct observation, experimentation, and the tracing of genetic signatures. Direct methods estimate dispersal distances and breeding success to infer gene flow, while indirect methods employ allele frequencies and genomic sequence differences to estimate the amount of gene flow that must be present to produce those patterns (Slatkin, 1987). Because the ability to disperse one's genes is

dependent on multiple factors, including life history, morphology, behavior, and habitat, all can be used to inform estimates of long-term migration (Bohonak, 1999). A significant fraction of the current biological literature, particularly those studying kingdom Animalia, focuses on interspecific gene flow and hybridization rather than intraspecific group differentiation (Eckert & Carstens, 2008; Olave, Martinez, Avila, Sites, & Morando, 2011; Martin et al., 2013). In part, this is because intraspecific data sets often have fewer phenotypic characters for phylogenetic analysis (Posada & Crandall, 2011). Consequently, genomic research is often implemented as a confirmation or correction for phylogenetic research performed using morphological data (e.g., Martin et al., 2013), though phenotypic research is still a crucial point of understanding for the differentiation between species (Ackermann et al., 2006, Damasceno & Astúa, 2016). Reptilian gene flow and population structure research in particular has been popularized thanks to the sensitivity of class Reptilia to paleoclimatic change (Kornilios et al., 2012).

Gene flow, if one adheres to the Biological Species Concept (Shanker et al., 2017), can prevent local differentiation and ultimately speciation (Slatkin, 1987) because it acts as a barrier to differentiation between populations (Holliday, 2003; Falconer & Mackay, 2009). A cessation of gene flow, in contrast, may result in biospeciation (Kramer, 2005). Yet even in instances of phylogenetic branching as a consequence of local adaptations, a complete cessation of gene flow may not have occurred (Ehrlich & Raven, 1969), resulting in morphospeciation (Kramer, 2005), or simply a change in morphology that is not linked to the origin of a new species. Other species concepts may more adequately address the realities of hybridization (Holliday, 2003).

Investigations into hybridization have been especially popular within non-human focused literature, and are generally related to the idea of heterosis, or hybrid vigor (Falconer & Mackay, 2009). As described by Holliday (2003), hybridization in animals can result in either introgression, in which novel genotypes develop in a hybrid zone but cycle back into parental populations, or hybrid speciation, in which the parental species produce a hybrid population that subsequently becomes a new third species. Given the difficulty of identifying hybridization in the fossil record, however, Lieberman (2003) countered that hybridization should act as the null hypothesis in investigations of speciation.

In human ancestry, the criteria for identifying hybridization from hominin fossils was once poorly described (Ackermann et al., 2006). Recently, however, that has changed, and we now have strong evidence that mating between hominins did occur. Ackermann and colleagues (2019) compiled what is known about hybridization in human evolution from multiple perspectives, resulting in a comprehensive array of expectations to identify hybridization events. These range from evidence of genomic introgression, non-human primate (and non-primate) pedigreed experiments, and mosaic or rare trait presence, particularly in the craniofacial region. The “hybrid” concept in anatomically modern humans (*Homo sapiens*) today, however, is inappropriate because it conceptually fits within a now widely rejected racial typology that mirrors the biological concept of subspecies (but see Long & Kittles, 2003). The hybridization and race concepts are difficult to fit within the scope of actual human diversity because of distinct nesting patterns (Long, Li, & Healy, 2009; Hunley, 2011) and a more complex relationship of allele frequencies between populations around the world (Lewontin, 1972), particularly in populations near regional borders (Hunley & Cabana, 2016).

Compared to many other organisms, the feat of assessing variation in human populations is substantial, with humans being “at the molecular level...one of the most uniform species on Earth” (Lynch, 2007:63). Yet the variation that does exist is very informative to gene flow research. As several studies note, the level of human genetic variation and the presence of ancestral alleles decline, F_{st} values increase, and linkage disequilibrium increases as a function of geographic distance from Africa (Ramachandran et al., 2005; Crawford, Akey, & Nickerson, 2006; DeGiorgio, Jakobsson, & Rosenberg, 2009) in the manner of a more complicated isolation by distance, though no single model perfectly explains the patterns observed (Hunley et al., 2009; Hunley & Cabana, 2016). In the Americas, which contain some of the lowest diversity regions in the world, within-population gene identity — the probability that two random alleles from the same locus are identical by state — tends to increase from north to south, indicating a decrease in diversity related to geography. Populations that are historically believed to have experienced little European gene flow have less diversity than expected based on this trend, suggesting that these gene flow events have increased within-population diversity compared to what they would be without gene flow (Hunley & Healy, 2011).

Gene flow research in modern human populations is largely performed on a regional basis, excepting major hypothesized large-scale migrations. Fix (2011) distinguishes the former as short range migrations, and the latter as long range migrations. Chakraborty (1986) likens gene flow to tidal waves ebbing and flowing with major known historical events such as political invasions and the slave trade in the Americas. Migrants, then, alter the receiving population’s genetic makeup (Bolnick, 2011). For this reason, Harrison & Boyce (1972) advocated for the incorporation of population movement in inferences of human population structure.

Several studies have found ancient demographic signals pervasive enough to be detected separately from the influence of climate and other selective pressures on a global scale (Betti, Balloux, Amos, Hanihara, & Manica, 2009; Hunley et al., 2009). Even so, gene flow questions remain difficult to address in human populations without the assistance of reliably written records, strong interpretations of material culture, or language similarities. The success of matching genetic or phenotypic conclusions with other lines of evidence, though, is mixed. Crucially, the transmission of genetic material and cultural or linguistic artifacts may differ. While genetic material is only transmitted vertically from parent to offspring, material goods and elements of language may be transmitted both vertically and horizontally (between related or unrelated individuals) (Hunley & Long, 2005). Further, estimates of gene flow events from both genetic and morphological data can be a result of either recent gene flow or shared common ancestry prior to a population divergence without subsequent gene flow (Li et al., 2008). Both of these realities suggest that the addition of more than one type of data set may add clarity to the interpretation of possible gene flow events and migration, but they must be considered carefully before declaring that the results of different methods support each other.

V. Precedence of Quantitative Genetic Methods in Archaeological Contexts

Even within constrained temporal and geographic ranges, any biodistance model that assumes genetic population structures are reflected in similar phenotypic expression cannot unequivocally ascertain the sources of those similarities (e.g., shared ancestry, gene flow, or convergence). For this reason, it is useful in establishing the precedent for this dissertation to briefly review those

studies that have used other approaches to determining evidence in support of gene flow from osteological study, namely those that have used the Relethford-Blangero model.

Steadman (2001) employed Relethford & Blangero's (1990) methodology to evaluate gene flow potentially resulting from interregional migration patterns within Mississippian and Late Woodland period groups in the Illinois River Valley (United States), as well as potential impact from the decline of Cahokia, a major political center located in what is today southwestern Illinois. Specifically, Steadman tested two archaeological models: one that suggested Mississippian culture developed because of migration from Cahokia and the American Bottom (c. A.D. 1000), and the other that development in the Illinois River Valley was largely due to in situ development. Using craniometric data, she determined that the central Illinois River Valley sites had greater than expected variance (supporting gene flow), while the lower Illinois River Valley sites had less than expected variance (failing to support gene flow). Biological distance results showed that the Late Woodland populations were very phenotypically similar, likely experiencing strong interregional gene flow. However, evidence of gene flow is not found among the Mississippian groups, suggesting a lack of interregional mobility and a smaller interaction sphere than that found among Late Woodland groups, resulting in population continuity rather than significant impact from the decline of Cahokia.

Schillaci (2003) used the Relethford-Blangero model in an analysis of population diversity at Chaco Canyon during the Pueblo II-III periods (A.D. 890-1140), one of the major site complexes I analyze in Chapter Four. Schillaci was one of the early researchers to demonstrate support for the assumption that Chaco was not a site of biological homogeneity. He tested three archaeological models for population development at Chaco: the migration of at least two cultural groups from nearby regions (La Plata-area groups during the Basketmaker III period as well as Cibola-area groups during the following Pueblo I period), migration into Chaco by Mesoamericans, or population aggregation of San Juan Basin, La Plata, and/or Cibolan region groups followed by limited gene flow after aggregation. Were none of these to be accurate, his alternative model was in-situ development of one Basketmaker III population, resulting in morphological homogeneity. Using craniometric data, he concluded that some parts of the Chaco sphere (e.g., Pueblo Bonito) had high levels of gene flow and were subsequently very diverse, while others had very low differentiation (possibly the result of biased sampling). While Mesoamerican origins were difficult to exclude using these data, the results demonstrate it is an unlikely scenario. The levels of diversity were most consistent with the first and third hypotheses, to the exclusion of the fourth model.

Byrd (2014) recently employed the Relethford-Blangero model to estimate possible gene flow and mobility from Early Agricultural Period (2100 B.C.—A.D. 50) indigenous groups from the Sonoran Desert. Using craniometric data from three site-complexes (Santa Cruz River, Cienega Creek, and La Playa), Byrd tested the hypothesis, based on a lack of differentiation in material cultural, that forager-farmers of this region were phenotypically homogenous because of an exchange of mates between communities. Results did not support this hypothesis, demonstrating high differentiation and possibly differential levels of gene flow between males and females. Specifically, greater than expected variation in males may suggest greater mobility among males in this context. Because of geographic and temporal overlap in Byrd's (2014) research as well as later works (Byrd, 2019a, 2019b), I use several of the same parameters in my study for ease of

comparison. This includes heritability and population size parameters, which will be described further in Chapter Two.

VI. Research Questions

This dissertation explores how biodistance and quantitative genetic toolkits relate to each other in terms of results and their potential to be interpreted within the broader context of ancient gene flow and migration. Biodistance methodology is useful for exploring the possibility of common ancestry and the similarity of populations through trait means (Relethford & Lees, 1992), but if an influx of genes from a neighboring group does not change the mean state of the trait, these methods may not accurately reflect gene flow between groups, and consequently may not accurately reflect population interactions. In regions such as the Southwestern United States, where variation is already reduced (from a global perspective) because most groups share recent common ancestry, we would expect phenotypic means to be similar, and so the application of traditional biodistance measures alone are likely inappropriate for detecting gene flow events.

Quantitative genetic methods, in contrast, are less dependent on population mean differences. Under the quantitative genetic framework, heritable continuous (non-discrete) differences between populations are used to create and evaluate models of evolutionary change (Falconer & Mackay, 2009). This is a theoretical paradigm that is not often used to pursue questions about the relationships between and changes in human groups within their respective archaeological contexts, though there are exceptions (Steadman, 2001; Schillaci, 2003; Ortman, 2010; Byrd, 2014). Under this paradigm, researchers can use the expected consequence of evolutionary dynamics on group variance—in this case, increased variance that occurs as a consequence of gene flow—as a method for capturing the gene flow effects of migration on biology.

This dissertation addresses four research questions regarding the skeletal assessment of gene flow:

1. Does the inference of gene flow differ between a quantitative genetic study and a biodistance study of the same skeletal material? Are differences informative? For example, quantitative genetic estimations may support gene flow for one site in a region, so should it be expected for that site to have greater biodistance from other sites included in the model?
2. Are important nuances about group interactions captured using one biological method that are not inferable from the other, or do both methods need to be used in conjunction to achieve better resolution about gene flow?
3. Do different regions of the skeleton (e.g., cranium versus dentition) provide consistent evidence for gene flow and for biodistances?
4. How does each method compare to hypotheses of migration developed from the context of material culture?

These questions will be addressed by comparing the results of biodistance and quantitative genetic analyses within three related archaeological contexts from the Southwestern U.S. and Northwestern Mexico.

VII. The Southwest As Context

In this dissertation, I apply the model-bound and model-free methods to Indigenous remains from the U.S. Southwest and Northwestern Mexico (Figures 0.1, 0.2) from prior to European contact to understand how, if at all, the quantitative genetic toolkit may provide better resolution of gene flow than biodistance analyses do on their own. The U.S. Southwest (henceforth, “Southwest”) offers a temporally fine-grained and abundant archaeological, historical, and ethnographic record, with several large collections of well-documented and well-preserved human remains. The ethical considerations surrounding research into these remains will be discussed in Chapter Five. Though the regional focus of this dissertation is geographically constrained to modern-day Arizona, New Mexico, and Northwestern Mexico, and the groups living in the region are closely related, there is sufficient variation between groups to make this analysis feasible: while previous biodistance studies have shown that Southwestern groups were more similar to each other than to adjacent or distant regions, the peoples of this region are morphologically distinct enough to be differentiated in cluster analyses (Turner, 1998; McClelland, 2003; Byrd, 2014, 2019b; O’Donnell & Ragsdale, 2017).

Specific movements in this region have been the subjects of great interest among researchers (Figures 0.1, 0.2). Early migrations northward from Mexico (originating from both the Sonoran Desert and further south), for example, were hypothesized to be the origins of Basketmaker II peoples (c. AD 400) of the Colorado Plateau and Four Corners regions (Morris & Burgh, 1954; Matson, 2016; Whiteley, 2016). Other researchers have noted potential Mexican influence in ceramics of southeastern Arizona and southwestern New Mexico (e.g., Di Peso, 1976, Nelson & LeBlanc, 1986, Lekson, 1992) as well as from the remains of non-local macaws (*Ara militaris*, *Ara macao*) at sites in the Mogollon Rim region (Olsen & Olsen, 1974). Byrd (2014) has also demonstrated the likelihood of localized movements within the Sonoran Desert based on phenotypic variance of human remains. Together, these researchers and others have described a scenario in which constant movement, particularly northward, is present from roughly the beginning of the Early Agricultural Period (c. 1600 B.C.) to the end of Pueblo IV (c. A.D. 1450).

There is also significant evidence for movement in the opposite direction – the southward migration of Ancestral Puebloan peoples from the Four Corners and Colorado Plateau as the result of environmental and social pressures has been hypothesized and supported for nearly a century (e.g., Gladwin & Gladwin, 1935; Haury, 1945, 1958; Hill, Clark, Doelle, & Lyons, 2004; Glowacki, 2011; Borck, Mills, Peeples, & Clark, 2015; Clark et al., 2019), particularly based on ceramics (e.g., Reid & Montgomery, 1998) and architectural differences (e.g., Riggs, 2001). A wide-spread drought in the Four Corners/Colorado Plateau region is currently thought to be the major factor pushing the Ancestral Pueblo southward (Dean & Funkhouser, 1995; Lipe, 2010; Matson, 2016). This movement is supported by stable isotope analysis (Ezzo, Johnson, & Price, 1997), though strontium analysis can only identify non-local individuals rather than from where in the study region they might have originated. Ortman (2010) also used the Relethford-Blangero method on craniometric data to support an origin of northern Rio Grande peoples from Mesa

Verde near the Four Corners. Importantly, this population movement occurred in two waves: the residents of the Colorado Plateau moved into the Mogollon Rim and Phoenix Basin regions, while those closer to the Four Corners in southern Colorado and Utah moved primarily along the northern Rio Grande (Clark et al., 2019). Not only were these waves geographically independent, they were also archaeologically different. While Clark and colleagues (2019) demonstrate that individual from the Colorado Plateau likely coexisted with locals while still retaining material aspects of their ethnic identity (e.g., kiva and roomblock layouts), while those from the Four Corners more thoroughly assimilated with locals (the “Tewa ethnogenesis”) and adapted to local ways of life that can be seen through kiva layouts and pottery styles.

From an archaeological standpoint, migration has been a topic of considerable interest in the Southwest even when the subject was out of vogue during the processual paradigm (Adams, Van Gerven, & Levy, 1978; Anthony, 1990; Härke, 1998). In part, this is due to the emergence of Southwestern archaeology as a subject of institutional interest under the umbrella of the culture historical paradigm. Because there exists what some researchers would consider clear evidence of site intrusion (e.g., Grasshopper Pueblo in Arizona) throughout the region, culture historical thinking was, at least initially, a natural fit to the questions being asked about migration. Early in Southwestern archaeology, this led to the perception of cultural groups as bounded groups of biologically-related peoples, largely static and easy enough to detect through artifact discontinuity (Adams et al., 1978; Anthony, 1990; Härke, 1998). While elements of this theoretical tradition still exist in Southwestern archaeology (e.g., the tracking of artifacts as evidence of migration), and short or continuous migrations continue to be difficult to identify in the archaeological record (but see Thomas, 1973, and Kent, 1992), the ways of identifying population interaction have evolved to include interactions such as mimicry (Zedeño, 1994) and complex displays of ethnicity and identity (Clark, 2001; Neuzil, 2008). Additionally, increasingly sophisticated methods of modeling population movement have contributed to our understanding of migration in this region and others (e.g., Anderson & Gillam, 2000; Surovell, 2000). Examining *how* to identify a migration archaeologically was something Anthony (1990) cautioned against (contra Burmeister, 2000), but it is a question that has and continues to dominate migration research in the Southwest. Because of the increasingly nuanced questions being asked of regional patterns of migration and gene flow, the theoretical and methodological literature surrounding archaeology of the Southwest continues to increase in abundance. This makes the archaeological record of the region particularly useful for studying gene flow.

VIII. Forthcoming Manuscripts

Chapters Two, Three, and Four each consist of independent manuscripts (“articles”) addressing a portion of the research questions described above. Chapter Two is the pilot study upon which the methods for the two following chapters were based, including the preparation of data within the R programming environment (R Core Team, 2020) and the use of the Relethford-Blangero method. This study uses archival odontometric data from northwestern Sonora, Mexico, and east-central Arizona dating to the Early Agricultural Period (1600 B.C. to A.D. 50) and the Pueblo III-IV periods (A.D. 1240-1450), respectively, to evaluate external gene flow across a broader geographic and temporal scale against a model of cultural exchange from the Sonoran Desert into Mogollon settlements in Arizona.

Chapter Three compares the Relethford-Blangero method to Mahalanobis' D^2 . Using a restricted context (east-central Arizona, Pueblo III-IV periods) that approximates Wright's (1943) island model to the best of our ability in this region, I interpret the presence of gene flow in five pueblos likely occupied by local Mogollon and/or non-local Ancestral Puebloan peoples. Because of the significant research in this region for more than a century, archaeologists have developed hypotheses about which cultural groups occupied these sites based on archaeological findings (e.g., Gladwin & Gladwin, 1935; Haury, 1958; Reid & Montgomery, 1998; Riggs, 2001) and the input of local Indigenous groups (e.g., Kuwanwisiwma, 2018). Additionally, I compare results of the two methods using cranial, dental, and postcranial data to address whether they are capable of producing the same results. If one or more do not, this may have implications for how we interpret results from skeletal analyses.

Chapter Four uses archival postcranial data from Auerbach (2007) to establish regional gene flow patterns across a wider geographic region, including sites from Chapter Three and additional sites from northern Arizona and New Mexico. This study examines the utility of the Eastern and Western Pueblo division commonly found in archaeological and ethnographic research (e.g., Kidder, 1917) and the potential role of the Continental Divide in those divisions, as well as whether the results of analyses using the postcrania are congruent with archaeological hypotheses and/or biodistance precedents.

Chapter Five will discuss the broader implications of Chapters Two, Three, and Four in terms of the archaeological hypotheses, comparisons of different methodologies and data types, as well as ethical considerations in doing non-destructive research with Native American remains.

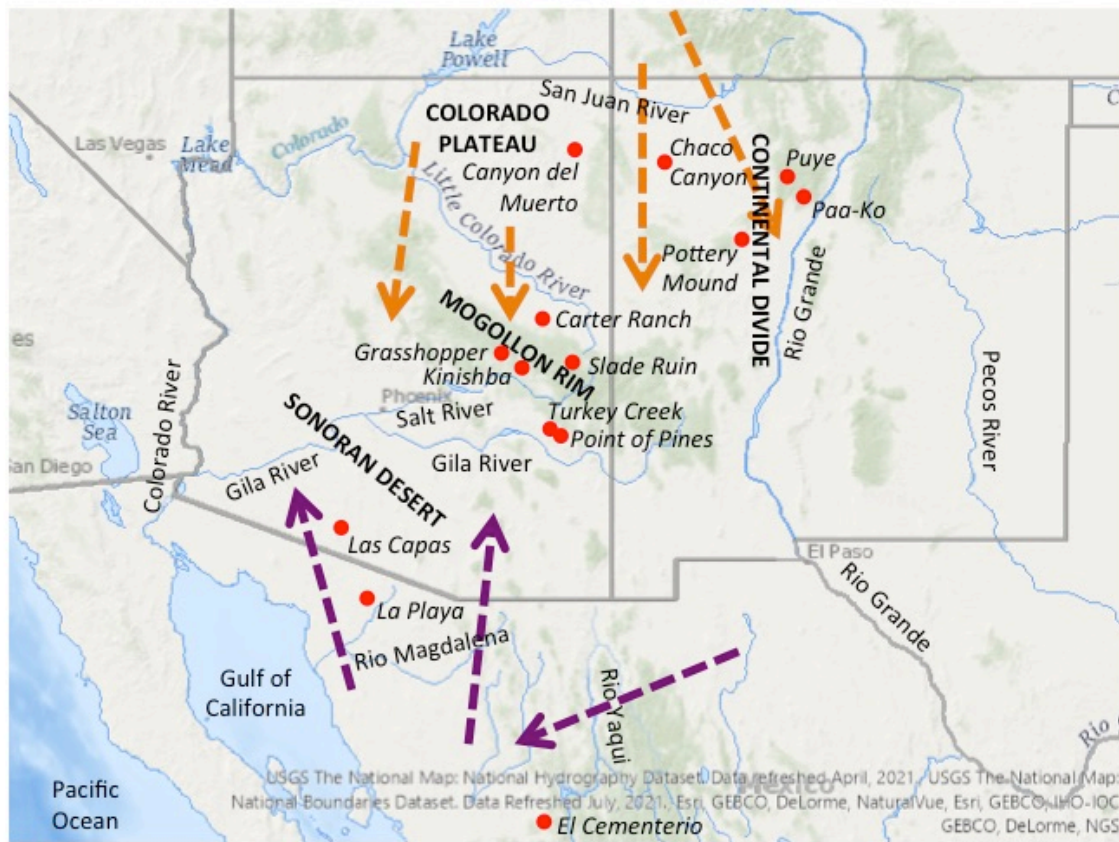


Figure 0.1. Map of geographic context. Purple arrows indicate human population movement in the Sonoran Desert and northern Mexico (c. 1600 B.C. – A.D. 1450), orange arrows indicate movement from the Colorado Plateau and southwestern Colorado (c. A.D. 1200-1450). (Map adapted from the United States Geological Survey, <https://apps.nationalmap.gov/viewer/>)

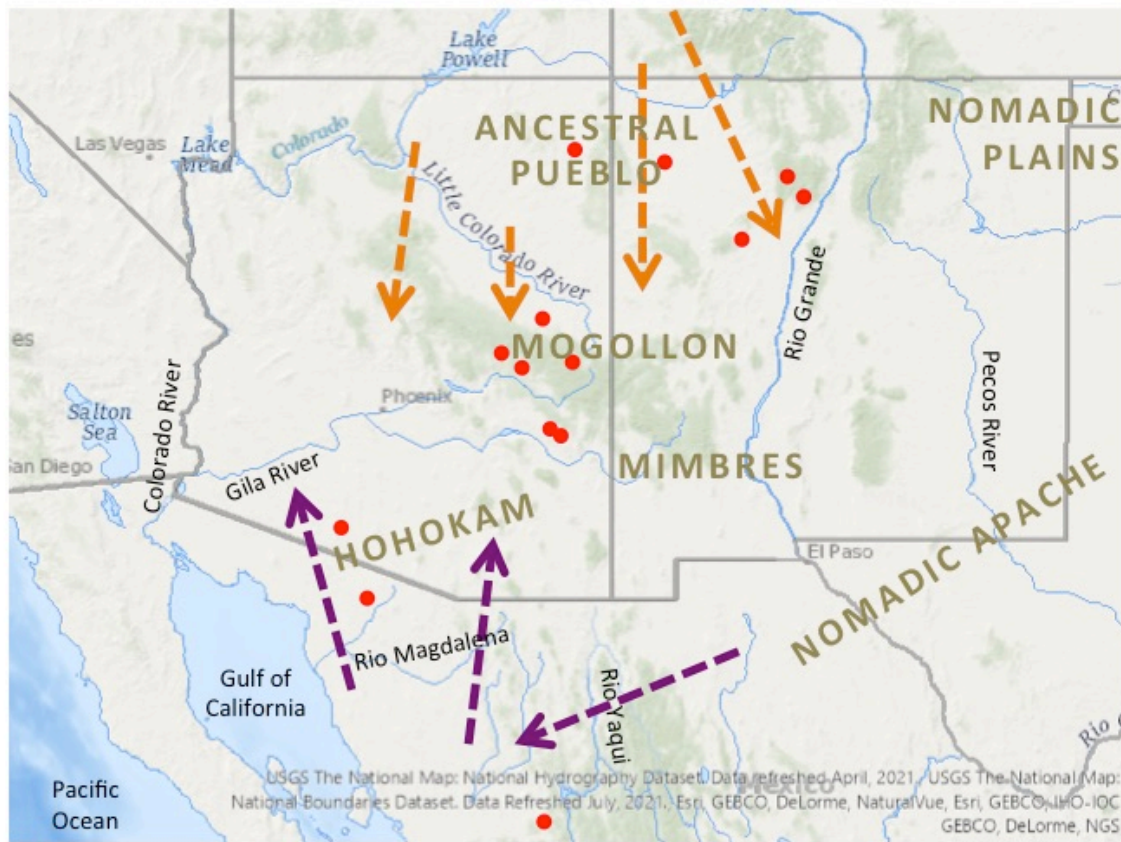


Figure 0.2. Map of major archaeological culture areas in study region. Purple arrows indicate human population movement in the Sonoran Desert and northern Mexico (c. 1600 B.C. – A.D. 1450), orange arrows indicate movement from the Colorado Plateau and southwestern Colorado (c. A.D. 1200-1450). (Map adapted from the United States Geological Survey, <https://apps.nationalmap.gov/viewer/>)

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Chapter 2

IDENTIFYING AND INTERPRETING THE MOVEMENTS OF GENES AND MATERIAL CULTURE AMONG PRECOLONIAL SITES IN THE SOUTHWEST US/NORTHWEST MEXICO USING QUANTITATIVE GENE FLOW ANALYSIS

Disclosure Statement & Introduction to Article 1

As a pilot study, Article 1 in this dissertation establishes the potential usefulness of the quantitative genetic gene flow model in studying groups from the Southwestern United States and Northwestern Mexico. The analytical methods described in this paper are mostly consistent across all three articles. Article 1 pilots the methodology using data from human molars and a subset of the site groups used in Articles 2 and 3.

The focus of Article 1 is on the comparative value of “biological” categories of data versus “archaeological” categories. Specifically, we compare human dental measurements to interpretations of material culture from the same archaeological sites. These sites have been heavily researched from an archaeological perspective, research that has borne out significant consensus regarding migration and gene flow. The hypothesis we focus on is a southward migration of individuals from the north into the mountains of the Mogollon Rim. In addition to comparing the skeletal data to the archaeological interpretations, we explore the possible interpretations that may result when analyzing two data types does not result in the same overall interpretation.

This study produced some findings that were opposite our expectations. The Mogollon populations in particular had less than expected variance, which failed to support archaeological hypotheses of gene flow. Those results were the impetus to the rest of the analyses in this dissertation.

This manuscript will be submitted for publication shortly. I performed the analysis (including coding and interpretation) as well as the initial writing. This manuscript uses archival data recorded by others, including co-author JTW. My co-authors (JTW and BMA) acted as mentors and editors. It is prepared for submission to the *Journal of Archaeological Science*, to be submitted under the following citation:

Mallard, A.M., Watson, J.T., & Auerbach, B.M. (In prep). Identifying and Interpreting the Movements of Genes and Material Culture Among Precolonial Sites in the Southwest US/Northwest Mexico Using Quantitative Gene Flow Analysis.

Abstract

Particularly in conjunction with other lines of evidence, anthropologists frequently use skeletal trait metrics to identify relationships between archaeological populations. One of the major categories of questions that may be addressed using skeletal metrics is between-site group relatedness, specifically relatedness through gene flow. While gene flow may be difficult to ascertain using traditional biological distance studies, a quantitative genetic framework of methods provides the ability to evaluate gene flow using skeletal trait variance rather than trait means. In this study, we calculate relationship matrices (after Relethford & Blangero) to evaluate variance of odontometric traits of the molar occlusal surface, specifically comparing the expected versus actual amount of variance in the context of archaeological hypotheses. We examine six archaeological groups from the southwestern U.S. and northwestern Mexico,

including the Early Agricultural period sites of Las Capas (1600-800 B.C.) and La Playa (1600 B.C.-A.D. 50) and the Postclassic period site of El Cementerio (A.D. 1000-1521) in Sonora, Mexico, as well as the Pueblo III-IV period sites of Grasshopper, Turkey Creek, and Point of Pines (A.D. 1200-1450) in Arizona, United States. Using the Relethford-Blangero method, results suggest populations from the Pueblo III-IV sites have less than expected dental variance, while the other sites (with the exception of the later phase at La Playa) have greater than expected variance, indicating possible gene flow. The results for the Pueblo III-IV sites are particularly surprising, given material culture-based hypotheses suggesting the presence of at least two coexisting communities. Though the archaeological hypotheses are generally consistent, this analysis fails to support a gene flow event for these sites. The sites with greater-than-expected variance, however, may have received external gene flow from elsewhere in the region. We conclude that, even though archaeological hypotheses may be well-supported, it is not a given that the biological relationships of past communities from the same sites will be simple to interpret.

Introduction

Archaeologists confront an ongoing challenge in ascertaining the physical movement of artifacts and people, and subsequently interpreting the circumstances of that movement with the best possible accuracy. While identification and interpretation are distinct steps in research method, the challenges they present are generally encountered simultaneously. Evidence of possible artifact or population movement in the past leads to inquiries of *what* process is being detected, and *how* that fits into what is already known about the archaeology of a region. It is well established that material culture similarities between localities may arise from convergence, copying, or trade, or a complex history of all three (Carr, 1995), so material similarities are only one aspect of an in-depth inquiry. Likewise, biological similarities between groups of people may represent shared ancestry, gene flow, phenotypic convergence, or any combination of these factors (Roseman, 2016), and so the observation of similarities in human skeletal morphology alone is inconclusive.

The multi-causal nature of both cultural and biological change inherently results in some degree of ambiguity. Though researchers strive to accurately identify a particular process as the cause of patterns in diversity (e.g., Beekman & Christensen, 2003), one must take great care to allow and account for uncertainty. This challenge is often amplified when making sense of multiple categories of evidence at once, such as comparisons of material culture and skeletal biology. Yet these contrasts also provide opportunities for understanding the dynamics of past population interactions that would otherwise be unavailable when examining one category of evidence alone, even when the exchange of genes is not predicated on the exchange of cultural ideas or vice versa.

Nevertheless, especially in studies using both sources of evidence, it is difficult to evaluate which one provides greater clarity about the types of interactions that occurred among groups across a landscape. In most studies, the research question determines the source of evidence that is given primacy over others, but this choice itself also makes implicit arguments about population interactions. A focus on skeletal data, for instance, could inherently take the position that genetic exchange is not rigidly bound to the trade of cultural ideas. Moreover, employing either cultural or biological contexts to support arguments about change in the other assumes that these contextual relationships may deliver clear interpretations about the movement of peoples in the past. This assumption is not always appropriate. Though correlates of biology and culture are often interpreted in conjunction with each other, congruency in the evidence derived from each should not be an expectation (Bellwood, 2001; Beekman & Christensen, 2003; Cabana, 2011).

We are therefore left to understand whether biological evidence and material culture can be usefully studied in the context of each other to arrive at a robust analysis of population interactions within an archaeological model. In this study, we explore these interpretive distinctions by testing different models of population interaction in the Southwest United States and Northwest Mexico (Figure 1), each derived from archaeological evidence of cultural change. Because of a wealth of material evidence for ancient migration in this region, it is well suited for exploring the congruence of gene flow analyses and patterns of change or stasis in material culture. Patterns of ceramic technology (Reid & Montgomery, 1998) and architecture (Clark, 2001; Riggs, 2001) have indicated distinct cultural patterns in the region, resulting in numerous

interpretations of migrant presence at individual sites. We will be evaluating specific models of gene flow, which, as we discuss below, should be detectable under circumstances where a sufficient number of individuals from two groups of quantifiable morphological dissimilarity have historically exchanged genes and overcome the effects of random genetic drift (we assume little or no natural selection given the short temporal periods we include in this study).

Using dental metric data, we evaluate the congruence of material culture and skeletal data using quantitative genetic theory. Based on the material culture evidence from the sites used, we hypothesize that the sites that have been interpreted as having a migrant presence will likewise also suggest gene flow in the biological analyses. However, differences between material culture findings and quantitative genetic data may lead to differing conclusions about the nature of these population relationships.

Background

Measures of Biological Relatedness

While genomic data are generally considered most effective in terms of interpreting genetic relationships and the evolutionary forces that shaped them, they are not infallible in their ability to detect group relatedness (Meyer, Ganslmeier, Dresely, & Alt, 2012; Horsburgh, 2015; Johnson & Paul, 2016). As these authors show, lineal or familial relatedness, let alone kinship (as either a cultural or a biological construct) are difficult to determine from molecular evidence, especially in the context of archaeological research. Furthermore, molecular data are often unavailable or lack the resolution necessary to ascertain individual relationships. Despite increasing success in analyzing ancient human DNA (aDNA) (Raghavan et al., 2014; Rasmussen et al., 2015), sometimes the degradation of organic material has proceeded too far to retrieve data beyond broad group relatedness. Such information may reveal common regional ancestry, but only in exceptional cases provides the detail necessary to trace microevolutionary events such as those associated with regional movements over short temporal periods (for example, Prendergast et al., 2019). In addition, permission-granting institutions or descendant populations may also prohibit destructive analysis, including that necessary to retrieve aDNA. In these situations, a phenotypic proxy for genetic data must be employed for practical, legal, and/or ethical reasons.

Skeletal metrics are frequently used in an alternate umbrella of methods as a proxy for genomic research to infer population relatedness and gene flow, especially in the Southwest. Among the most commonly used category of methods is biological distance (“biodistance”). Biodistance methodology, measured through analytical approaches such as Mahalanobis D^2 or, less commonly, the Mean Measure of Divergence (Irish 2010), uses morphological similarity as a proxy for genetic relatedness (Stojanowski & Schillaci, 2006). As a consequence of using a common proxy, they also share a critical weakness when used outside the intra-site context. When comparative populations are phenotypically similar, it is more difficult to isolate them, particularly when they share recent common ancestry. Minor deviances in the mean morphology of groups may be overly emphasized at the inter-site level, giving the impression that very closely related groups are less similar than they actually are (Stojanowski & Schillaci, 2006).

Significant to the context of our study, biodistance methodology is not strictly a test for gene flow. While gene flow may be inferred, researchers ultimately do so under the assumption that more morphologically similar skeletal populations are similar as a consequence of gene flow as opposed to common ancestry. Two populations with a larger biological distance, meanwhile, might be inferred to lack gene flow or have a weaker signal. However, under population genetic models, we cannot assume that gene flow always results in decreased morphological distinctions. Over time gene flow will homogenize the mean morphology between groups. But if two populations have been separated for sufficient enough time for genetic drift to have an effect, as we explain in more detail below, it may always be assumed that gene flow will increase variance in traits (Relethford & Blangero, 1990).

Researchers generally consider gene flow to be at odds with genetic drift. While gene flow may be responsible for increasing similarities between populations, genetic drift causes them to differentiate from each other. Given that the homogenizing influence of gene flow between populations tends to lessen with increased geographic distance (Slatkin, 1987; Bohonak, 1999; Hutchison & Templeton, 1999), genetic drift would be allowed to differentiate them more. Interpreting this process as separate from relationships due to common ancestry, however, is rarely straightforward. While biodistance methods have been used to arrive at conclusions about evolutionary forces on a short timescale, they are not tests for the presence of those forces.

We therefore argue that a reliance on biodistance methods makes assumptions that rely on group phenotypic means as an indication of evolutionary forces, but these are better indicated by changes in trait variance. Especially in regions with low diversity and/or recent shared ancestry, differences in phenotypic means are often statistically nonsignificant even in the presence of gene flow, which partially explains previous interest in rare traits (Stojanowski & Schillaci, 2006). These circumstances are common in the Americas, where human genomic diversity is at its global lowest (Reich, 2012; Skoglund & Reich, 2016) and shared ancestry is, from an evolutionary standpoint, recent, particularly within geographic regions (von Cramon-Taubadel, Strauss, & Hubbe, 2017).

In contrast, quantitative genetic tests use the same metric data as biological distance tests but focus on trait variance rather than mean similarities. This theoretical paradigm is not often used to pursue questions about relationships between archaeological human groups, though there are exceptions (Steadman, 2001; Schillaci, 2003; Schillaci & Stojanowski, 2003; Vidoli, 2012; Byrd, 2014). Because gene flow is one of the more prominent mechanisms responsible for patterns of diversity on a microevolutionary time scale in the same region, analytical methods that measure gene flow through variation within groups are more useful. Gene flow between populations will result in an increase in trait variance, even if the trait mean does not change (Slatkin, 1987; Relethford & Blangero, 1990; Relethford, Crawford, & Blangero, 1997; Bohonak, 1999). This is because gene flow introduces new gene variants (alleles) into a population, which in turn may increase the variation in the expression of traits within a population, especially with a sufficient amount of new genetic variance to overcome the effects of genetic drift. Increases in variation do not automatically result in a change in trait means, however. In a region with phenotypic means as homogenous as the Southwest, therefore, the examination of phenotypic variance is a critical advantage over mean phenotype comparisons.

The assessment of gene flow in a quantitative genetic framework rests on the theoretical basis that gene flow between populations initially brings more variation into a given population than would be expected under circumstances with no gene flow occurring. Over time, the genetic (and subsequently phenotypic) differences between those populations decreases (Slatkin, 1987; Bohonak, 1999; Hutchison & Templeton, 1999), especially if gene flow persists. As outlined by Relethford & Blangero (1990), based on a theoretical model for genomic data by Harpending & Ward (1982), we can use the expected variance within a population compared to its actual variance as an indicator of gene flow, focusing on comparison of within-population variance of trait measurements. While both quantitative genetic and biodistance methods address different products of gene flow as an evolutionary process, the results of the quantitative genetic model are less easily conflated with other causative factors (e.g., common ancestry).

Establishing Models of Past Regional Interactions in the Southwest U.S. & Northwest Mexico

Movement in the ancient U.S. Southwest and Mexican Northwest, as interpreted by anthropologists, occurred frequently and served as a critical aspect of establishing and reinforcing group identity. Ethnographic accounts from modern descendant groups suggest that Ancestral Puebloan peoples found the process of movement culturally meaningful, especially when practiced on a cyclical or recurrent basis (Naranjo, 1995; Varien, 1999; Bernardini, 2005; Fowles, 2011). Similar emphases on movement have been documented historically by descendants of other groups in the region, such as the O'odham in south-central Arizona (Darling, 2011). These descendant accounts provide illuminating context to broad archaeological conclusions regarding population movement, such as the possibility of frequent migration between regional environments such as the Mogollon Plateau, surrounding mountains, and the Sonoran Desert during the 13th-14th centuries (Reid & Montgomery, 1998) (see Figure 1).

Though migration was a major part of this region's history, to describe all migration scenarios as uniform would be an oversimplification, even within similar timeframes. While significant trends are visible, e.g., the southward movement of Ancestral Puebloan peoples from the Colorado Plateau during the Pueblo IV period (A.D. 1275-1400) (Gladwin & Gladwin, 1935; Haury, 1945; Bernardini, 1998; Reid & Montgomery, 1998; Turner, 1998; Clark, 2001; Riggs, 2001; Neuzil, 2008) and subsequent movement of other groups such as the Hohokam in response (Hill, Clark, Doelle, & Lyons, 2004), even these migrations seem to have differed based on origin, destination, and group composition, which had a profound influence on their relationship to the receiving populations. For example, Clark and colleagues (2019) outlined the differences between the Kayenta migration into the Mogollon Rim and Tonto Basin regions compared to the movement of those from Mesa Verde into the Northern Rio Grande region, noting that archaeologically the former seem to have remained a visible minority, while the latter assimilated with the locals, resulting in ethnogenesis of a new group (Tewa). Furthermore, though archaeological and environmental research has indicated that these particular Pueblo IV movements were a response to natural and social environmental pressures (Dean & Funkhouser, 1995; Reid & Montgomery, 1998; Glowacki, 2011; Borck, Mills, Peeples, & Clark, 2015), the scale and timing of these movements were not identical. Though the detection of movement is largely supported in the Southwest US and Northwest Mexico, the nature of catalyzing forces, processes, and outcomes of these movements is complex.

The struggle to expand the detection of movement (whether of material goods or cultural ideas) into a viable interpretation of that movement is clear in research focusing on interaction between the Southwest/Northwest Mexico and the remainder of Mesoamerica. Significant influence from central Mexico has been inferred in Salado ceramics throughout southeastern Arizona and New Mexico (Di Peso, 1976; Nelson & LeBlanc, 1986; Lekson, 1992) during the thirteenth century. Additionally, the faunal remains of macaws whose natural ranges occur from southern Sonora to northern Oaxaca (*Ara militaris*) and eastern Mexico through Central and South America (*Ara macao*) are found across the Southwest/Northwest Mexico (Olsen & Olsen, 1974), suggesting the presence of trade networks. McGuire (1980) has also argued that while the overall argument for such interaction between the Southwest/Northwest Mexico and Mesoamerica has merit, certain elements of that interaction have been exaggerated. Whether gene flow was a part of these interactions between the Southwest/Northwest Mexico region and Mesoamerican communities is a question that has largely remained open to interpretation.

Carr (1995) cautions that many trade objects are not ideal for tracking the actual movement of people because of their likelihood to be copied, which is problematic for some of the hypothesized connections between the Southwest/Northwest Mexico and Mesoamerica. Rather, utilitarian objects and crafting techniques, as items of lower visibility and message content, should be the focus instead of decorative objects. To that end, undecorated plainware ceramics (Clark, 2011), perforated plates (Lyons, 2003), the presence of ball courts (Johnson, 1961), the layout of room blocks (Clark, 2001) and kivas (Stone, 2002), and masonry techniques (Riggs, 2011) have all been used in the Southwest/Northwest Mexico to track the movement of ancient migrants. Zedeño (1994) found that technological indicators could accurately identify ceramic origin even when the superficial decoration suggested a different provenience. A major question that remains, though, is even if it can be demonstrated that the movement of artifacts or technological styles may be equated to the movement of people, what does that say about *how* migrating and receiving populations interacted with each other on a social level? While great strides have been made in addressing that question, the biological consequences of these social interactions often remain only superficially interpreted.

A quantitative genetic study by Byrd (2014) indicated likely movement and subsequent gene flow for Early Agricultural period (2100 B.C.-A.D. 50) males across the Sonoran Desert (including southern Arizona and northern Sonora), particularly when compared with females from the same sites. Her subsequent study of broader Southwestern regional gene flow suggested greater than expected trait variance in this early period and locale, supporting population movement northward from the Sonoran Desert to northeastern Arizona (Byrd, 2019a). Other small-scale regional studies of human skeletal variation at Grasshopper Pueblo (dental: McClelland, 2003), sites around the Mogollon Rim (cranial: Byrd, 2019b) and Chaco Canyon (cranial: Schillaci, 2003; Schillaci & Stojanowski, 2005) have been performed, but to date the largest regional examination of phenotypic variance and its relationship to archaeological migration models has been Byrd's (2019a) multiscalar craniometric study, which supported a large-scale southward migration from the Four Corners region but had mixed support for smaller-scale regional migration hypotheses.

The sites used in our analysis (Figure 1, Table 1) are dated to two major time precolonial periods in Southwest/Northwest Mexico region: the Early Agricultural period and the Pueblo IV period

(Table 1). These are two temporal contexts that represent significant cultural transitions in the region. The Early Agricultural period marks the introduction of maize cultivation in the Sonoran Desert, supporting a regional network of trade and interaction (Mabry, 2008). Individual Early Agricultural period sites lack archaeological evidence for migration (Carpenter, Sánchez, Watson, & Villalpando, 2015), though Byrd's (2019a) study suggests the gene flow results do not match this conclusion. We will test the archaeological model by hypothesizing less than or equal to the expected population variance, with the understanding that the biological relationships between groups may not be fully inferred by this model.

The later Pueblo III-IV periods bear evidence for a depopulating event of the Colorado Plateau, with consequential migration southward in Arizona and New Mexico (Reid & Montgomery, 1998; Riggs, 2001; Lyons, 2008; Neuzil, 2008; etc.). Given the significant number of studies suggesting a model of regional movement into the mountainous areas south of the Mogollon Rim from the north, we would expect to see evidence of gene flow in the form of greater than expected phenotypic trait variance.

We also analyze one additional Mexican Postclassic (A.D. 1000-1521) site (El Cementerio) further south in Sonora. Based on material culture and cranial deformation patterns, Watson & García (2016) suggest they were a population likely engaged in trade with, and possible mimicry of, cultures based along the West Mexican Coast but find no evidence of migration or gene flow. Because of the proposed timing and direction of migrations further north in the region, hypotheses do not currently suggest that the population at El Cementerio would be experiencing gene flow from Southwest/Northwest Mexican groups. We therefore expect to see phenotypic variance less than or equal to what would be expected under normal conditions.

Materials

Archaeological Sites and Context

A list of the Southwest U.S. and Northwest Mexican sites and the dating of their occupation is presented in Table 1. Early Agricultural period (2100 B.C. – A.D. 50) sites include Las Capas, located in south-central Arizona, and La Playa, located in northwest Sonora, Mexico. La Playa may be divided into two phases – San Pedro (1600 – 800 B.C.) and Cienega (800 B.C. – A.D. 50) – which are considered separately in the analysis. Pueblo IV sites (representing roughly A.D. 1200 – 1450) in central Arizona around the Mogollon Rim include Point of Pines Pueblo, Turkey Creek Pueblo, and Grasshopper Pueblo. Because of close geographic proximity, Point of Pines and Turkey Creek are aggregated in all analyses. The Postclassic (A.D. 1000 – 1521) site of El Cementerio in central Sonora, Mexico, is an additional later group.

Dental Metric Data

Numerous studies have used metrics of permanent dentition to assess individual or population relatedness (Harris & Bailit, 1988; Christensen, 1997; Stojanowski, 2004; Hanihara & Ishida, 2005; Thompson, Hedman, & Slater, 2015). Because of the mineral content found in dental enamel, teeth generally preserve their morphological integrity better than bones over time (Ten

Cate, 1994; Scott & Turner, 1997). Consequently, the use of dental dimensions for quantitative genetic research is a useful alternative to craniometrics in archaeological contexts where preservation has been inconsistent or cranial deformation has occurred, such as among some of the sites used in this study. As in other studies of dental metrics, we used two standard measurements of the widest crown dimensions of each tooth: the mesiodistal dimension (tooth length) and the buccolingual dimension (tooth breadth, which is perpendicular to the former) (Moorrees & Reed, 1964; Kieser, 1990; Hillson, 1996; Scott & Turner, 1997). These measurements are known to vary between human groups enough to serve as reliable measures of biological distance and variation (Hanihara & Ishida, 2005).

We relied on archival data to perform the study's analyses. Most measurements for La Playa were recorded by one of the authors (JTW) (Watson, 2005), while measurements for Grasshopper were recorded by Dr. John McClelland (McClelland, 2003). Remaining measurements from La Playa as well as those from El Cementerio, Point of Pines, and Turkey Creek were recorded by graduate students at the University of Arizona with negligible interobserver error. Any teeth whose crowns were too worn to be accurately measured were excluded from the samples following Watson (2008). Final analysis was performed using a total of 143 individuals (see Table 1). Because sexual dimorphism is negligible with most dental metrics (Garn, Cole, Wainwright, & Guire, 1977; Mayhall, 1992; Scott & Turner, 1997; Hillson, 1998; but see Schwartz & Dean, 2005), the sexes were pooled in this study with no additional correction for body size.

Methods

All metric data were entered into the R statistical environment (R Core Team, 2016). For Grasshopper Pueblo, only metric data from the molars were available; therefore, only molars are used in this study, despite the indication by Harris (2003) that multiple tooth classes are preferable because tooth type accounts for most of the variation in dentition. To ensure that no individual from any sample would influence the statistical results more than another, we used only unilateral measurements; if both teeth in a position were present, the left tooth was chosen to be representative. Generally, there is very little, if any, difference between the same tooth on different sides (Potter & Nance, 1976; Scott & Turner, 1997).

Relethford & Blangero's (1990) method to infer gene flow and relationship matrices is available as a statistical program, RMET 5.0, from John Relethford's software website (<http://employees.oneonta.edu/relethjh/programs/>). Because RMET requires complete datasets, missing data was imputed into R (R Core Team, 2016) by regression, as outlined by Little & Rubin (2002). Imputation was performed only for individuals with eight of twelve measurements already present (after von Cramon-Taubadel & Pinhasi, 2011). Any individuals with more than four measurements missing were excluded from the sample. Regressions were created within major groups – the early and late phase sites – to minimize possible confounding of sources of variation in the analysis (regressions are described in Appendix A). Final sample sizes are reported in Table 1. The older sites have notably smaller samples than the later sites. However, RMET is robust to the effects of swamping from large and unequal samples (Relethford, 2003).

Once imputations were performed, complete datasets were input into RMET. RMET includes two primary types of analysis. One is the calculation of a relationship matrix, or R-matrix, based on the genetic model by Harpending & Ward (1982) and adapted to quantitative traits by Relethford & Blangero (1990). This is essentially biological distance model that allows for visualization via principal coordinates plot. The second is the calculation of statistics for the Relethford-Blangero model of gene flow, as outlined in Relethford & Blangero (1990). This model utilizes a quantitative genetic approach comparing expected and observed variance among sites. The model requires a narrow-sense heritability (h^2) value to set expectations for how much of the variance in phenotypic traits may be inherited. Many analyses of craniometrics have used the value $h^2 = 0.55$ (Powell & Neves, 1999; Ross, Ubelaker, & Falsetti, 2002; Schillaci, 2003; Schillaci & Stojanowski, 2005; Byrd, 2014) or $h^2 = 1$ (Steadman, 2001; Tatarek & Sciulli, 2000; Gonzalez-Jose, 2001). A heritability value of 1 is often used as a default; this value implies that the genotype matrix (**G**) is equal to the phenotype matrix (**P**), or an assumption of complete heritability (Cheverud 1988). It is worth noting that von Cramon-Taubadel (2014) cautions that population distances based on this assumption are subsequently minimum estimates of genetic distance; they are thought to be proportional on a global scale (Roseman & Weaver, 2007). While dental heritability may vary, it is estimated to be moderate to high with a value ranging from 0.5 to 0.9 (Stojanowski & Schillaci, 2006). For comparability to the Sonoran craniometric study by Byrd (2014), which included individuals from both Las Capas and La Playa, a heritability of 0.55 was chosen. However, it should be noted that this does not imply that cranial and dental heritability is the same, nor is it appropriate to use a heritability value specifically calculated for one population in studies of another (Stojanowski & Schillaci, 2006). Despite questions regarding the exact value of this statistic, the Relethford-Blangero method is insensitive to heritability values (Relethford & Blangero, 1990) provided they are not extremely low (von Cramon-Taubadel, 2014 defines extremely low as 0.2 or less).

Census population size is also used in the calculation of expected variance, which should be weighted by population size (see equation 12 in Relethford & Blangero, 1990). As this is rarely known in bioarchaeological contexts, the population size is set to 1 for all populations studied to remove the effects of scaling (Relethford & Blangero, 1990). This practice forces the model to assume that genetic drift is equivalent between periods, an assumption that is reasonable when temporal periods are short. Under these conditions, all of the difference between expected and observed variance should be attributable to external gene flow.

The variance of a particular quantified trait in any given population is assumed to be proportional to that population's heterozygosity, provided the population itself is panmictic (randomly mating) (Relethford & Blangero, 1990). In order to determine the potential impact of gene flow upon populations, expected and observed variance must be quantified. The expected variance, or expected heterozygosity, of the population for a single trait $E(\bar{v}_i)$ is represented by the equation

$$E(\bar{v}_i) = \frac{[\bar{v}_w (1 - r_{ii})]}{1 - F_{st}}$$

where $\bar{v}_w$ is the phenotypic mean within-group heterozygosity among populations used in the study, r_{ii} is the distance of a population from the centroid, and F_{st} (or r_0) is the genetic distance variation about the centroid for all populations. A multivariate extension of this equation

(equation 25 in Relethford & Blangero, 1990) is used for analyses in our study. The sign of the residuals will allow us to gauge the presence of gene flow. A positive residual indicates greater than expected variance, which is likely if a gene flow event has occurred recently. A negative residual indicates less than expected variance, which suggests that a gene flow event in the recent past is unlikely. The residual is calculated by subtracting the expected variation from the actual variation

$$\bar{v}_i - E(\bar{v}_i)$$

as indicated by Relethford & Blangero (1990) and Relethford et al. (1997). Such methodology is useful for the study of gene flow in archaeological populations (e.g., Steadman, 2001; Schillaci, 2003; Byrd, 2014), provided samples are roughly contemporaneous and contain groups that may have indeed shared mates based on archaeological or historical evidence (Relethford & Blangero, 1990). While current archaeological hypotheses do not necessarily support instances of gene flow for all of the sites in our study, there is raw evidence of possible outside influence on material goods at several of them.

Though the Relethford-Blangero analysis is the primary concern in this study because of its background in quantitative genetics, the estimated *R*-matrix of population distances, also computed in RMET, may add some additional clarity to our results. The *R*-matrix is essentially a matrix of standardized genetic variances and covariances based on quantitative traits. Diagonal values of this matrix provide minimum genetic distances of each population from an overall centroid (Relethford et al., 1997). Genetic distances reported here are bias-corrected.

The creation of an *R*-matrix also allows for calculation of Wright's fixation index, or F_{ST} . Wright's F_{ST} is a demonstration of microdifferentiation among populations used in the study; a lower value (closer to 0 than 1) indicates a closer genetic relationship. Though it is a useful metric for overall population relationships, it should be noted that there are some concerns about its use with populations that are not at equilibrium in gene flow and genetic drift (Bohonak, 1999; Hutchison & Templeton, 1999; see Long & Kittles, 2003 for further concerns about F_{ST} on a global scale). It should be interpreted with caution.

A limitation worth considering in this context, particularly with those time gaps that are broader, is the ability to detect gene flow using distance methods such as *R*-matrix. Frankenberg & Konigsberg (2011) used simulations to demonstrate that, with time, genetic drift tends to bring populations back to their genetic state before gene flow occurred, making gene flow difficult to distinguish from regional continuity if observed too long after a migration event. Extending the logic of their conclusions, we contend that the effects of drift could be used to further interpret results from the Relethford-Blangero analysis across time periods. For example, assume three time periods are represented in an analysis, where A is the earliest, C the most recent, and B the middle period (see Figure 2). In cases where C has greater-than-expected variance, while B and A do not, then this could be unambiguous support of gene flow in the more recent sites (Figure 2a). However, it does not exclude gene flow from occurring in sites from period B or A, though this would be dependent on the amount of time that has elapsed between them as well as the population sizes in each. If there is reason to suspect small population sizes, or the time between A and B is greater than between B and C, then the evidence against gene flow is equivocal (Figure 2b). Similarly, should B and C be temporally closer (e.g., Postclassic phase and Pueblo

IV Mogollon versus San Pedro phase among our sites), but period B sites have the greater-than-expected variance while sites from period C do not, one cannot definitively conclude that gene flow did not happen in period C sites (Figure 2c). However, it is less likely that gene flow would have occurred in period C sites in this scenario and been missed (because of the effects of genetic drift) than it would have in the first scenario (Figure 2a). Generally, small sample sizes may also make a migratory event difficult to catch. For these reasons, Frankenberg & Konigsberg (2011) concluded that quantitative skeletal trait methods are best utilized in conjunction with other lines of evidence. Given these concerns, the context of archaeological evidence, in the form of our models, is therefore critical to our study.

Results

The results of the Relethford-Blangero analysis are presented in Table 2 along with simplified notes on archaeological evidence for migration into each site. For both San Pedro phase populations, residuals have a positive value. Based on the work by Relethford & Blangero (1990), this suggests greater than expected variance in both contexts. The San Pedro component of La Playa has a residual of 0.525, while Las Capas has a very high residual of 1.043. Based on the archaeological evidence for migration between these sites during this time, a positive residual was hypothesized.

For the later Sonoran Desert populations, results were somewhat more consistent with hypotheses. We had anticipated that variance would be less than expected in the Cienega phase of La Playa, given the lack of archaeological evidence for incoming populations. The results support this hypothesis, indicating that La Playa loses substantial variance over time with a residual of -0.639 during the Cienega phase. El Cementerio, meanwhile, is more ambiguous in terms of whether influence from West Mexican Coast further west and south was the result of trade, cultural mimicry, or actual gene flow. Watson & García's (2016) conclusion is that they were engaging in a peripheral trade network and some mimicry, but the variance is greater than expected with a residual of 0.190.

We see particularly interesting results from the Pueblo IV Mogollon sites, whose material culture has been heavily studied over the past century. Based on the archaeological and architectural evidence of migration into Grasshopper, we had expected there to be a great deal of variance that might be indicative of significant gene flow. However, the observed value was lower than the expected, with a residual difference of -0.549. Based on geographic proximity, we had also expected the aggregate of Turkey Creek and Point of Pines to have higher variance. Like with Grasshopper, we see the opposite result: the residual difference is -0.570. All three of these sites are in a region and timeframe that has had substantial archaeological support for migration, but they lack biological support for gene flow as far as odontometrics are concerned.

R-matrix distances are reported in Table 3. The unbiased F_{st} estimated from the *R*-matrix is roughly 0.093, indicating an overall low genetic distance among populations. This value confirms the small biological distances presented in prior studies (e.g., Byrd, 2014). Given that these are populations that share ancestry in the recent evolutionary past, this is an expected outcome. From the *R*-matrix we also calculated a principal coordinates plot based on the first two

eigenvalues. These eigenvalues together account for 80% of the total variation among all groups, with 47.6% loaded on the first eigenvector and 32.4% loaded on the second eigenvector. Figure 3 displays the genetic distances between sites. Both temporal divisions at La Playa plot in close proximity to each other. As a continuous occupation, this is expected. Meanwhile, Grasshopper and the Turkey Creek/Point of Pines aggregate also plot near each other, which is expected in an isolation by distance framework in which populations that are temporally close would be more similar to geographically near populations than to those that are farther away. Las Capas and El Cementerio, in contrast, are more isolated, though Las Capas is close to La Playa if only the first eigenvector is considered. The relationships of populations from these sites, and the relationships to evidence for gene flow, are considered in more detail in the Discussion.

Discussion

Our results reflect the complexity of relating group relationships through material culture to biological relationships, specifically gene flow. While some results supported our expectations for gene flow based on archaeological models, others, especially those for the Pueblo IV sites, did not. Several patterns therefore require further exploration. Most important, our results reinforce the need for caution in expecting congruence between biological and cultural evidence for migration and interaction in the past, while also highlighting the beneficial nuances that using our analytical approach offers in disentangling these patterns.

As noted in the Results, genetic distances among our sites are small. For comparison, Relethford and Harpending (1994) reported an average F_{st} of 0.112 for craniometric traits among three regions (Europe, sub-Saharan Africa, and eastern Asia) using the same heritability variable ($h^2 = 0.55$) we use here. The unbiased F_{st} among our populations is 0.093 (Table 3). We must take into account, however, that making such comparisons is potentially problematic, in part because we are comparing different traits, and also because F_{st} estimates are sensitive to a number of factors that we cannot take into account, such as population census size and genetic drift (Relethford & Harpending, 1994; Bohonak, 1999; Hutchison & Templeton, 1999). Nevertheless, it does imply that the individuals from our sites are closely related, much as we would expect based on the population history of the Americas. Furthermore, the genetic distances among sites, as demonstrated through principal coordinates analysis (Figure 3), reflect similar geographic and temporal contexts, which we would expect. The temporal phases from La Playa and the Pueblo IV period Mogollon sites cluster, respectively. Given El Cementerio's geographic distance with respect to the other sites as well as its possible relationship to Mesoamerica, it also fits reasonably well with archaeological expectations. It is surprising, however, that Las Capas does not plot closer to La Playa. This may reflect effects of the provisional evidence for gene flow into Las Capas and La Playa, though it is also possible it is an artifact of the small sample size for Las Capas. Sliva (2015) postulates that the presence of a distinctive projectile point (Empire point) found only at La Playa and the early phase at Las Capas, which differs from the local San Pedro point, indicates a direct migration and foundation event.

It is apparent that the two earliest sites, both from the San Pedro phase, exhibit greater evidence for gene flow compared to most of the ones that follow (the exception being El Cementerio, which is the most southerly in our sample). This is consistent with craniometric

research by Byrd (2019a) that included both Las Capas and La Playa individuals from this phase. There are several explanatory scenarios that may be plausible. One is that the overall pattern of the results reflects an early pulse of gene flow that started to homogenize over time. At the La Playa site, for instance, we see greater than expected variance during the earlier San Pedro phase, in contrast to a lower-than-expected variance in the later Cienega phase. At this one site, it may be indicative of an early pulse of gene flow on a smaller scale. As migration throughout the Southwest became more widespread, what was once new variance may have ceased to be new. This is a natural outcome of persistent gene flow: over time, this microevolutionary force stops introducing new variance and starts contributing to genetic homogeneity, acting as a more constraining force on population variance (Slatkin, 1987; Bohonak, 1999; Hutchison & Templeton, 1999). We may be seeing this happen at La Playa on a smaller scale, which would confirm the site's continuity as interpreted through the archaeological record (Carpenter et al., 2015). An alternative explanation is that, following the results reported by Frankenberg and Konigsberg (2011), it is possible that localization of populations would have prompted greater genetic drift and decreased gene flow over time, producing similar patterns within La Playa and across the region.

On a regional scale, we might interpret the Pueblo IV period Mogollon sites similarly, though the results require additional consideration. Grasshopper Pueblo and the aggregate of Turkey Creek and Point of Pines have negative residual variances, similar to each other in magnitude. If we consider that this may be the homogenizing stage of gene flow, we may be seeing evidence that at these temporally later and geographically more northern sites, new variance was not being introduced via external gene flow. Under this interpretation, the process of gene flow shifted to its role as a constrainer of variance. However, the lack of evidence to support gene flow among these sites, especially Grasshopper, is unexpected when compared to our archaeological model. Archaeological (Reid & Whittlesey, 1982; Reid, 1989; Zedeño, 1994; Reid & Montgomery, 1998; Riggs, 2001) and isotopic (Ezzo, Johnson, & Price, 1997) evidence strongly suggested external migration happened at these sites and during the Pueblo IV period, and so our results complicate the overall interpretations of interactions among populations in Mogollon sites. As we discussed in the Methods (Figure 2), though, evidence of lower-than-expected variance in the later time period does not exclude the possibility of gene flow. Instead, it is possible that gene flow did occur but was not sufficient to overcome the effects of genetic drift.

Though it is farther south in the Sonoran Desert, the evidence supporting gene flow into El Cementerio, which is closer in time to the Mogollon-area sites than the Sonoran Desert sites, does indicate that some gene flow could have been taking place into the region more recently. Because of El Cementerio's position between the northwestern Sonoran populations and West Mexican Coast or Mesoamerican groups, macro-regional interaction is likely. While the material culture and cranial modifications may have resulted from trade and mimicry (Watson & García, 2016), the dental variance suggests there may be some gene flow. In addition, differences in population sizes between El Cementerio and the Mogollon sites, especially if there were non-mating subpopulations living in the Mogollon sites, could have created different conditions for genetic drift to affect loss of variation. It is also possible that if sites like Grasshopper represent the fusion of groups from different origins in the region, the sample used in this study only includes one of those groups. A closer examination of the individuals who comprise our samples, and if there is hidden substructure in the way these sites were sampled, will await future study.

We must also consider the possibility that the biological and archaeological evidence genuinely do not, and will not, coincide at some of these sites. If the archaeological and architectural differences noted at the Mogollon sites are simply localized differences, we would expect to only see differences in the material culture as opposed to quantitative genetic traits. The residents of Grasshopper Pueblo, for example, may have exhibited different material cultures, representing both local and nonlocal populations in the archaeological record. This does not, though, require that they exchanged genes. It is also possible that they spent their childhoods in different places, resulting in differing strontium signals (Ezzo et al., 1997), but are biologically homogeneous in any detectable way because of shared ancestry.

Sample size may be a factor in some of these results. For example, we note that the three sites with the smallest sample sizes (Las Capas, La Playa - San Pedro phase, and El Cementerio) are the three with positive residuals. They could indeed have recently experienced gene flow events. However, it is also possible that this is an artifact of the statistical model. More individuals for Las Capas ($n=5$) in particular would potentially elucidate more of what is happening during the San Pedro phase. However, this phase has not produced as many skeletal remains as later temporal contexts because of preservation (Byrd, 2014). This is consistently an issue in many geographic and temporal contexts in bioarchaeology, which can unfortunately be problematic for quantitative genetic studies. In practice, gene flow in archaeological contexts can be a problematic area of study. Our traditional ways of evaluating archaeological sites are often difficult to correlate with this complicated microevolutionary process. Interpretations must be quite nuanced as a result, otherwise we risk missing part of the broader picture. In this study, our most unexpected conclusion is that, at sites where we have often interpreted a material culture representing the interaction of diverse peoples, we see biological variance that would indicate the opposite. In one small snapshot of time, however, we may be seeing only part of an evolutionary process that occurs over much longer time periods.

It is certainly possible that this is a unique example that would benefit from larger sample sizes. It is also possible that the use of molar dental dimensions did not provide enough variance, though we are encouraged that the principal coordinates analysis shows the two phases of La Playa and the three Mogollon sites respectively in close proximity to each other. These are expected features of the *R*-matrix, demonstrating that at least some of the important geographic and temporal relationships are being conveyed.

What is most illuminated from this study is the difficulty in comparing archaeological context with biological context. This is especially pertinent to the study of ancient peoples because we often use material culture as a proxy for biological relationships, particularly when skeletal material is unavailable or unusable. In some contexts, it is all we have for making inferences about population interactions. However, we likely cannot be sure that this proxy is sufficient. Diversity in archaeological goods may not correlate directly with biological diversity, as other researchers have shown. Because of trade, it is possible that material culture may start to look more homogenous over large stretches of land, but actually be more biologically diverse because of the early stages of gene flow. Likewise, more archaeological variance may not be an indication of biological diversity, particularly over large regions, because of a lack of interaction between groups.

It can be difficult to tease apart what is happening in the ancient past, but that does not imply a fruitless task. Nuanced conclusions are critical in cases such as these. For example, Watson & García (2016) explore several possible conclusions about El Cementerio with the archaeological and osteological evidence they have, evaluating the merits of each. No individual line of evidence would have resulted in the nuanced interpretation they present. While in this study, several sites do not show archaeological and biological congruence, this mismatch contributes to more interesting conclusions altogether (Auerbach, 2010; Sassaman, 2010).

Conclusion

Regardless of any ambiguities in the interpretation of our analyses, we can provisionally conclude that gene flow likely did occur across the precolonial Southwest US and Northwest Mexico region, but that gene flow followed both a temporal and geographic pattern. While we may be seeing some signal of gene flow among Sonoran populations prior to European contact, the cause is not entirely clear. One explanation, given the higher-than-expected variance in the Sonoran populations, is that we see an initial burst of new variation that resulted from gene flow into the region. This variation appears to subsequently lessen as time progresses, in favor of a trend of homogenization. This is visible in the later Mogollon sites, where variance is lower than expected by a fairly large margin. If this is indeed what happened, it fits well with the current understanding of how gene flow proceeds over time, either within regional homogenization or because smaller breeding populations over time increased the effects of genetic drift on reducing genetic variation.

It would be prudent to further examine our assumptions about the correlation of biological and archaeological evidence, both in the Southwest and others. However, despite ambiguities, we can still learn a great deal about the movement of past peoples by combining the data we gain from archaeological evidence and models of gene flow like that of the Relethford-Blangero method, as well as more traditional methods of measuring biological distance. Gene flow is a complicated mechanism to understand and interpret, and looking at more than one source of evidence is key to increasing our understanding of ancient peoples and their relationships.



Figure 1.1. Map of collection proveniences used in study. (Image adapted from <https://www.google.com/earth/>)

Table 1.1. Context of Samples Used in Analysis

Site	Designation	Estimated Dates	Source of Dates	N	Repository*
Las Capas, Arizona, USA	AZ AA:12:111 (ASM)	San Pedro phase, Early Agricultural period 1600-800 B.C.	Mabry (2008)	5	ASM
La Playa, Sonora, Mexico	SON F:10:3 (ASM)	San Pedro phase, Early Agricultural period 1600-800 B.C.	Carpenter et al. (2015)	12	INAH
		Cienega phase, Early Agricultural period 800 B.C.-A.D. 50	Carpenter et al. (2015)	25	INAH
El Cementerio, Sonora, Mexico	SON P:10:8 (ASM)	Postclassic period A.D. 1000-1521	Watson & Garcia (2016)	12	INAH
Grasshopper Pueblo, Arizona, USA	AZ P:14:1 (ASM)	Pueblo III-IV period A.D. 1275-1400	Longacre & Reid (1974)	52	ASM
Turkey Creek Pueblo, Arizona, USA	AZ W:10:78 (ASM)	Pueblo III period A.D. 1240-1300	Johnson (1965)	24	ASM
Point of Pines Pueblo, Arizona, USA	AZ W:10:50 (ASM)	Pueblo III-IV period A.D. 1260-1450	Haury (1989)	12	ASM

*ASM = Arizona State Museum (Tucson, USA); INAH = Centro Instituto Nacional de Antropología e Historia (Hermosillo, Sonora, Mexico)

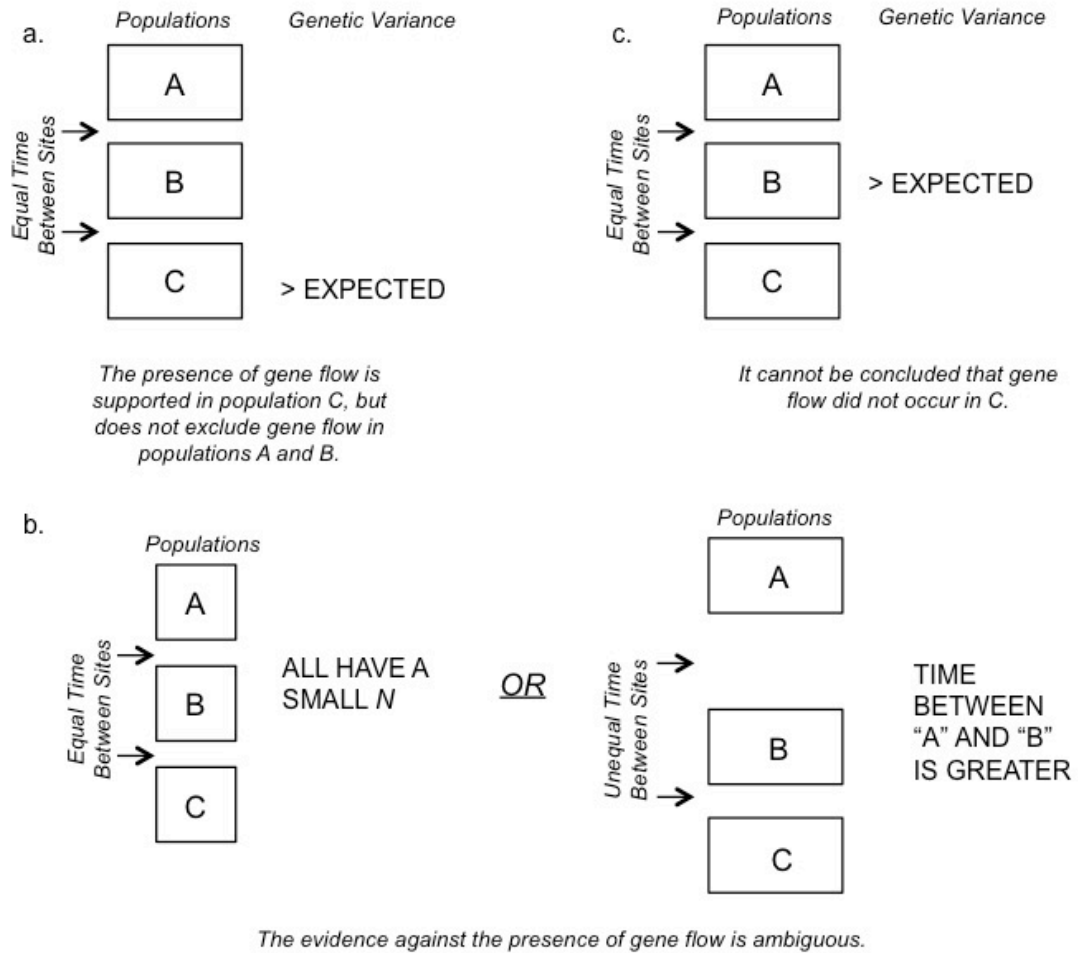


Figure 1.2. Gene flow scenarios and their ambiguity due to genetic drift

Table 1.2. Results of Relethford-Blangero Analysis

Population	Archaeological evidence of migration?	r_{ii}	Observed	Expected	Residual	Evidence for gene flow? (this study)
La Playa (San Pedro phase)	yes	0.068663	1.846	1.321	0.525	yes
Las Capas	yes	0.124669	2.284	1.242	1.043	yes
La Playa (Cienega phase)	no	0.076934	0.671	1.309	-0.639	no
Grasshopper	yes	0.087734	0.745	1.294	-0.549	no
Turkey Creek/ Point of Pines	yes	0.031002	0.805	1.375	-0.570	no
El Cementerio	no	0.174622	1.361	1.171	0.190	yes

Table 1.3. R-Matrix Results

Population	Biased r_{ii}	Unbiased r_{ii}	SE
La Playa (San Pedro phase)	0.110330	0.068663	0.036476
Las Capas	0.224669	0.124669	0.080637
La Playa (Cienega phase)	0.0969350	0.087734	0.016459
Grasshopper	0.097350	0.087734	0.016459
Turkey Creek/ Point of Pines	0.044890	0.031002	0.013433
El Cementerio	0.216289	0.174622	0.051071
<i>Total F_{st}</i>	<i>0.131743</i> <i>(biased)</i>	<i>0.093937</i> <i>(unbiased)</i>	<i>0.015487</i> <i>(SE)</i>

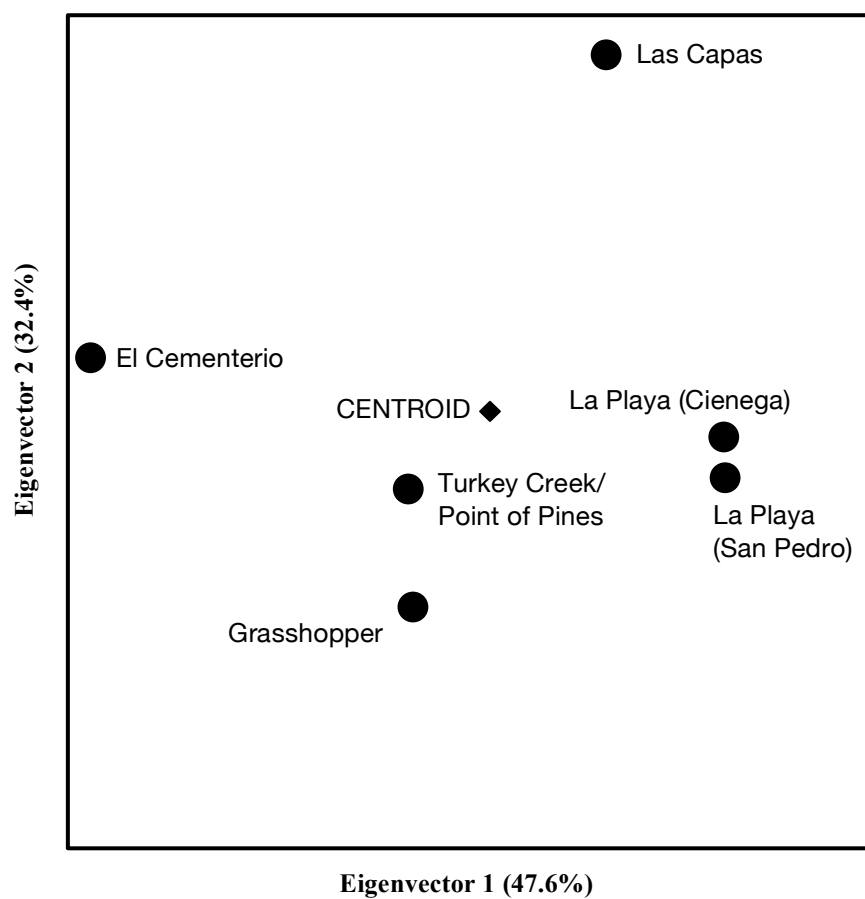


Figure 1.3. Principal coordinates analysis of samples

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Supplemental Information: Imputation Regression Formulae from Article 1

All formulae for missing teeth are based on a present tooth in the same arcade using the same crown measurement, chosen based on the smallest standard error.

Table S1.1. Dental abbreviation key

Code	Key
U	<i>upper tooth</i>
L	<i>lower tooth</i>
M	<i>molar</i>
1	<i>first molar</i>
2	<i>second molar</i>
3	<i>third molar</i>
MD	<i>mesiodistal measurement</i>
BL	<i>buccolingual measurement</i>

Table S1.2. Regression formulae for Early Agricultural sites (Las Capas, La Playa)

Tooth	Formula	SE
UM3.MD	$UM3.BL = 8.71297 + 0.05667 * UM1.MD$	0.15534
UM3.BL	$UM3.BL = -0.3729 + 0.9650 * UM2.BL$	0.1752
UM2.MD	$UM2.MD = 7.4028 + 0.2770 * UM3.MD$	0.1364
UM2.BL	$UM2.BL = 6.26732 + 0.47388 * UM3.BL$	0.08604
UM1.MD	$UM1.MD = 5.5461 + 0.4629 * UM2.MD$	0.2347
UM1.BL	$UM1.BL = 9.43858 + 0.20919 * UM3.BL$	0.09409
LM3.MD	$LM3.MD = 8.1742 + 0.2200 * LM1.MD$	0.1847
LM3.BL	$LM3.BL = 5.2533 + 0.4540 * LM1.BL$	0.1847
LM2.MD	$LM2.MD = 6.2407 + 0.4292 * LM1.MD$	0.1016
LM2.BL	$LM2.BL = 5.95158 + 0.43572 * LM1.BL$	0.07636
LM1.MD	$LM1.MD = 9.3480 + 0.1305 * LM3.MD$	0.1095
LM1.BL	$LM1.BL = 8.3274 + 0.2462 * LM3.BL$	0.1002

Table S1.3. Regression formulae for Pueblo IV/Postclassic sites (Grasshopper, Point of Pines/Turkey Creek, El Cementerio)

Tooth	Formula	SE
UM3.MD	$UM3.MD = 0.7773 + 0.8639 * UM2.MD$	0.1047
UM3.BL	$UM3.BL = 4.35925 + 0.55850 * UM1.BL$	0.09486
UM2.MD	$UM2.MD = 4.98960 + 0.50477 * UM3.MD$	0.06119
UM2.BL	$UM2.BL = 7.07048 + 0.40113 * UM3.BL$	0.07184
UM1.MD	$UM1.MD = 6.12145 + 0.44620 * UM2.MD$	0.06908
UM1.BL	$UM1.BL = 5.39698 + 0.54317 * UM2.BL$	0.04897
LM3.MD	$LM3.MD = 6.9671 + 0.3483 * LM2.MD$	0.1432
LM3.BL	$LM3.BL = 1.6759 + 0.7801 * LM1.BL$	0.1298
LM2.MD	$LM2.MD = 8.37873 + 0.22076 * LM3.MD$	0.09078
LM2.BL	$LM2.BL = 6.29099 + 0.40466 * LM3.BL$	0.07245
LM1.MD	$LM1.MD = 6.2090 + 0.487 * LM2.MD$	0.0682
LM1.BL	$LM1.BL = 5.0161 + 0.5591 * LM2.BL$	0.0663

Chapter 3

THE COMPATIBILITY OF SKELETAL REGIONS IN ASCERTAINING POPULATION INTERACTION AND GENE FLOW: A STUDY OF SITES FROM THE LATE PUEBLOAN PERIOD SOUTHWESTERN UNITED STATES

Disclosure Statement & Introduction to Article 2

Article 2 uses the methods piloted in Article 1 and applies them to a constrained geographic and temporal context: the U.S. Southwest from roughly A.D. 1100 to 1400, which spans the Pueblo III and Pueblo IV periods. Several sites from the previous analysis are investigated again: Grasshopper, Point of Pines, and Turkey Creek pueblos. While we aggregated Point of Pines and Turkey Creek in the Article 1 analysis because of geographic proximity and to increase sample size, in this analysis I chose to separate them to allow for more detailed inquiry into possible gene flow events in the Mogollon mountain region. In addition, I add the sites of Kinishba and Slade Ruin to approximate as much of Wright's island model as may be possible in Southwestern bioarchaeology, a precedent set by Schillaci (2003) and Byrd (2014).

This analysis focuses closely on the analytical contributions of the Relethford-Blangero method and Mahalanobis D^2 biological distance method to understanding regional gene flow patterns in the U.S. Southwest. Specifically, I ask whether a more nuanced picture results from combining the two methods relative to using one or the other. Though the context is specific to the region, the questions about methodology are applicable to numerous contexts.

Because the specific context of Article 2 is different from that in Article 1, results from the analyses will not be identical for each site. This is because of the nature of the model, which is discussed in this analysis as well as Chapter Five. This is a key issue that will also emerge in Article 3. When the model contains different populations and different parameters (e.g., dental versus cranial measurements), it is not a given that sites which previously had greater than expected variance in the first study will again have greater than expected variance in the second study. This is because the "expected variance" is no longer the same value. If one study contains a larger pool of variance among all populations than the other study, expected variance will be greater; a smaller pool of variance, then, will result in an expected variance that is smaller.

I performed the analysis (including coding and interpretation) as well as the writing of this manuscript, which also incorporates archival data used with permission. It is written and organized in the style of the *American Journal of Physical Anthropology*, to be submitted under the following citation:

Mallard, A.M. (In prep). The Compatibility of Skeletal Regions in Ascertaining Population Interaction and Gene Flow: A Study of Sites From the Late Puebloan Period Southwestern United States.

Abstract

While biological distance studies using osteometric data are common in anthropology, generally they rely on one class of skeletal data: cranial or dental. It is generally assumed that either is acceptable for performing between- and within-population analyses. Recently, postcranial data has also been suggested as an alternative, despite potential issues due to environmental effects. This study assesses the ability of these classes of skeletal data to produce the same results. Using a sample of five Mogollon Rim, Arizona sites that overlap temporally (c. A.D. 1100-1450), I

compare results gleaned from cranial, dental, and postcranial data using both biological distance (Mahalanobis' D^2) and quantitative genetic (Relethford-Blangero) methods. Biodistance results are inconsistent in modeling which of the five populations may be most closely related. Quantitative genetic results suggest some consistencies, particularly between cranial and dental data. However, overall there is no pattern to which classes of data produce the same results, and for which sites. The Relethford-Blangero method sometimes compliments the archaeological data, but not consistently.

Introduction

This study compares methods of ascertaining evidence for gene flow between past human populations among different regions of the skeleton within a specific archaeological context. Researchers rely on contextual evidence from archaeological sites, from artifacts to architecture to biological traits, to reconstruct the relationships and interactions of the groups inhabiting those locations. Questions about biological affinity within and between sites encompass one aspect of investigating these relationships. Its determination through biological distance (biodistance)—the multivariate difference in (often osteometric) traits between groups—has become a widely-used approach (e.g., Sutter, 2000; McKeown & Jantz, 2005; Durand et al., 2010; Ragsdale and Edgar, 2015; Waters-Rist et al., 2016; O'Donnell and Ragsdale, 2017; Movsesian & Bakholdina, 2017; Byrd, 2019a, 2019b). Researchers interpret evidence for more recent genetic affinities from groups with smaller distances, with other sources of archaeological evidence used for context. However, as reviewed by other researchers (Stojanowski & Schillaci, 2006), small biodistances between some groups could arise from multiple causes, including morphological convergences, recent shared ancestry, or genetic exchange in the form of gene flow.

Broadly, while gene flow introduces new alleles between populations, it ultimately has a homogenizing effect between them (Falconer & Mackay, 2009). Given a rate of genetic exchange between groups that is sufficient enough to overcome the effects of genetic drift, the groups will, over time, appear more morphologically similar than they initially did. Genetic drift will therefore have more impact between smaller populations, as drift is more influential in evolutionarily neutral traits among populations with fewer individuals, even though it is less likely to occur between smaller populations (Hastings & Harrison, 1994). As a result, gene flow increases variation in traits within populations as novel alleles are introduced, while decreasing variation between populations (Williams-Blangero & Blangero, 1990; Relethford & Blangero, 1990). Thus, as used in this study, the consequences of gene flow may be leveraged to determine if groups in the past interacted in ways commensurate with genetic exchange (Relethford & Blangero, 1990; Relethford, Crawford, & Blangero, 1997). This model-bound approach, the Relethford-Blangero method, provides an alternative to model-free biodistance methods, such as Mahalanobis D^2 distances (see Methods below) (Pietrusewsky, 2014; Auerbach, in press).

In the Relethford-Blangero method, a relationship matrix, or R-matrix, is used to ascertain how the observed population variance contributes to the overall relationship of populations to each other around a common centroid. It is based on the genomic model by Harpending & Ward (1982) and adapted to quantitative traits by Relethford & Blangero (1990). The accuracy of these methods has been tested using anthropometric samples compared to pedigree (Relethford & Blangero, 1990) and genetic (Relethford, Crawford, and Blangero, 1997) data in an effort to test hypotheses of local gene flow. Similar results between the quantitative genetic model-bound approach with both pedigree and genomic evidence demonstrate the efficacy of Relethford and Blangero's (1990) model to detect increases in observed variance over expected variation among traits, a hallmark of gene flow. Moreover, while gene flow at smaller scales is difficult to ascertain using biodistance methods, as differences in trait means may be minimal, the Relethford-Blangero method is more sensitive to subtle differences in variance in limited geographic contexts (Relethford, 1988; Steadman, 2001; Schillaci and Stojanowski, 2006; Byrd, 2014, 2019). It should be noted that very limited gene flow occurring in conjunction with small migrations may not be visible using either method. Because the model requires that all input

populations be potentially mating groups, it is necessary to employ the method using a limited temporal and geographic range (Relethford, 2016).

The quantitative genetic model assumes that populations are identical in source and rate of gene flow from populations *not* included in the model. This method is theoretically grounded in Sewall Wright's (1943) island model of gene flow, wherein every island exchanges genes equally with every other island. This model serves as the null hypothesis. If either of those assumptions is violated, which is likely among human populations (Bodmer & Cavalli-Sforza, 1968), the actual variance will differ from what is expected. Greater than expected variance (a positive residual value) indicates that a group has likely experienced a recent gene flow event from a group not included in the model. Less than expected variance (a negative residual value), or observed equaling expected variance, indicates a group has likely *not* experienced gene flow from external groups in greater quantity or frequency than the remaining groups. Because this theory is based on Wright's island model, it is most effective at detecting gene flow on a temporally and geographically small scale because a more constrained context better approximates the conditions of Wright's model. The context used here is as constrained as possible, given the nature of bioarchaeological collections.

Gene flow is not migration, though they are often invoked synonymously. Migration is defined through multiple modalities, which may tend toward the biological, the cultural, or varying combinations of the two (Cabana & Clark, 2011). While the processes of gene flow and migration often occur together, to assume that they do is problematic. Migration occurs for a variety of reasons including, but not limited to, patrilocal and matrilineal mating traditions (Stojanowski & Schillaci, 2006), the cultural importance of movement (Naranjo, 1995), the seasonal availability of resources (Thomas, 1973; Kelly & Todd, 1988), and various other factors that cause a population to move from one home to another (Anthony, 1990). Some of these are inextricably linked to a gene flow event (such as any variety of extralocal mating), but others (such as trade) are not. For this reason, as reviewed in another recent study by the author (Mallard et al., Chapter 2), contextual archaeological evidence of interactions between groups may not be reflected by measures of gene flow. Artifactual styles may be exchanged or copied without gene flow, for example, or gene flow may occur without evidence for an exchange of material culture (Beekman and Christensen, 2003; Auerbach, 2010).

The resulting lack of expected congruence between cultural and biological evidence, as well as the ambiguity in interpreting close biodistances as consequences of gene flow rather than convergence, make the evaluation of past gene flow from human remains, material culture, and other cultural phenomena difficult. Molecular methods, particularly through ancient DNA, can be effective but are not infallible. The interpretation of lineal relations is not always clear from molecular methods (Meyer, Ganslmeier, Dresely, & Alt, 2012; Horsburgh, 2015; Johnson & Paul, 2016), if this type of destructive analysis can be performed at all. Thus, a reliance on skeletal metrics, which are nondestructive and serve as a proxy for genomic research due to the proportional relationship between the phenotype and the genotype (Cheverud 1988), as well as general congruences between morphological and genetic affinities (Relethford, 1994; Roseman and Weaver, 2004; von Cramon-Taubadel, 2009, 2011; Betti, Balloux, Amos, Hanihara, & Manica, 2009), is a reliable (though not unproblematic) alternative.

Yet, even with the practical advantages of using skeletal metrics to ascertain population relationships, it remains unknown if different regions of the skeleton reflect similar information about biodistance. Dental metrics have been argued to have high heritability over the periods of time considered in microevolutionary studies (Dempsey, Townsend, Martin, & Neale, 1995; Hanihara & Ishida, 2005), and dimensions of the cranium are likewise reflective of neutral evolutionary processes (Roseman, 2004; von Cramon-Taubadel, 2009). Similarly, some dimensions of the postcrania, namely long bone dimensions (especially the femur), may be both highly heritable and reflective of neutral evolutionary processes over short evolutionary periods (Auerbach, 2010; Hulsey, 2016; Savell, Auerbach, & Roseman, 2016; Agostini, Holt, & Relethford, 2018). Limited study provides mixed evidence for the congruence of craniometrics and dental metrics in model-free estimates of biological affinity (Falk & Corruccini, 1982; Campbell, 2016; O'Donnell & Schillaci, 2021). No study, though, has yet examined the correspondence of different aspects of the skeleton to each other in the context of model-bound approaches, namely the Relethford-Blangero method.

In light of the above, I investigate here the capabilities of model-free versus model-bound (e.g., quantitative genetic-based) methods of estimating evidence for gene flow, and how the choice of metrics for either method affects the interpretation of gene flow. I expect, based on the precedence of other studies, that dental metrics and craniometrics will provide similar measures of biodistance, as well as similar evidence of gene flow based on the Relethford-Blangero approach. In contrast, I expect dental metrics and craniometrics to have dissimilar patterns for biodistance, and I do not expect the long bones of the limbs to reflect the same neutral evolutionary processes as the cranium (but see Agostini et al., 2018). Relethford-Blangero estimates of gene flow should be similar between dental, cranial, and postcranial metrics, though, as gene flow should contribute equally to the variances of all aspects of the skeleton. To assess these questions, I use skeletal metrics obtained from late Puebloan period individuals who lived in what is now Arizona, a group and time period chosen because of its robust archaeological record and well-developed models of population movement and interaction.

Archaeological Context

In the sample for this study, measurements were obtained from individuals buried, and who presumably lived at, five archaeological sites that consisted of pueblo-style dwellings. These sites are all located in east-central Arizona: Grasshopper (AD 1275-1400), Point of Pines (AD 1260-1450), Turkey Creek (AD 1240-1300), Kinishba (AD 1200-1400), and Slade Ruin (AD 1100-1300) (Figure 2.1). All sites represent the Mogollon culture, but some may have varying amounts of Puebloan intrusion. The sites are geographically close and overlap in temporal context, therefore their residents could reasonably have exchanged mates with each other and with groups living in the broader region, resulting in gene flow.

The late pueblo periods during which these sites were occupied are generally categorized into the Pueblo III and Pueblo IV periods. These periods are demarcated, among other events, by the large reduction in population size of the Four Corners region on the Colorado Plateau, which researchers in part argue to have occurred in response to a multi-year drought at the end of the thirteenth century potentially complicated by an over-reliance on maize and demographic pressures (Lipe et al., 2010; Matson, 2016). Grasshopper, Point of Pines, and Kinishba pueblos

were occupied through the period of this migration event (see Table 2.1 for sources of dates), and so individuals buried at these sites may reflect gene flow resulting from the movement of peoples, either directly from the Four Corners region or other areas of the broader region (Ezzo & Price, 2002). There is some evidence to support the presence of non-local groups along with local Mogollon individuals at Grasshopper Pueblo based on artifacts, architecture, and skeletal analysis (Ezzo, Johnson, & Price, 1997; Reid and Whittlesey, 2005; Riggs, 2007), as well as Point of Pines based on architecture (Stone, 2000; Lyons, Burgess, Marshall, & Smith, 2018). Ceramic analysis at Kinishba indicates influences from groups that lived in the Four Corners as well as groups located west of the Mogollon Rim (Welch, 2013). As noted above, however, a migration of peoples does not inherently result in gene flow.

Given this context, I hypothesize that gene flow patterns and biodistance analyses will not present similar results across the five sites under study. The three sites that were occupied into the Pueblo IV period would be expected to show clearer signs of gene flow in contrast with the two Pueblo III-only period sites (Turkey Creek and Slade Ruin). As all the sites were part of the same broad culture (Mogollon), biodistances should be similar among the sites, though if signs of gene flow are indicated by the use of model-bound (Relethford-Blangero) methods, I would expect biodistances to be greater among the three later period sites than between the two Pueblo III-only period sites.

Materials & Methods

Osteometric Data

As noted above, osteometric data were obtained from individuals interred at five Pueblo III and Pueblo IV period sites located in eastern central Arizona (Figure 2.1, Table 2.1). Metric data collection was primarily performed by the author, with a few exceptions. Individuals from Grasshopper have been repatriated and reburied, so archival data from Byrd (2019; cranial) and McClelland (2003; dental) were used with permission from each author. Individuals from Kinishba were also recently repatriated and reburied, so archival data from the Arizona State Museum's standardized osteological forms were used; no dental metric data were available for this site.

Traits were chosen to reflect aspects of morphology thought to reflect population relationships. All dental measurements are taken from the cervical area of dentition, which will be unaffected by dental wear and are often used in biological distance analyses (Pilloud & Kenyhercz, 2016). Cranial dimensions were restricted to the viscerocranium to avoid the effects of cranial modification (Ross & Ubelaker, 2009; Püschel, Friess, & Manríquez, 2020). Postcranial dimensions largely consist of dimensions that reflect body size and proportions, most of which have evolved in response to directional selection (Auerbach, 2007; Roseman & Auerbach, 2015; Savell et al., 2016), but are thought to be stable over short temporal periods and thus reflect population history (Auerbach, 2010).

All dimensions taken from skeletons are presented in Table 2.2. These were recorded using standard osteometric methods for cranial and postcranial measurements (Howells, 1973; Buikstra

and Ubelaker, 1994; Langley, Jantz, Ousley, Jantz, & Milner, 2016) as well as dental dimensions (Moorrees and Reed, 1964; Kieser, 1990; Hillson, 1996; Scott & Turner, 1997). For those data collected by the author, dental measurements were collected using Mitutoyo digital sliding calipers fitted with a PaleoTech attachment for dental dimensions. Cranial measurements were assessed using an Immersion Microscribe GX2 to measure three-dimensional points in space. Postcranial measurements were collected, depending on the measurement, using digital sliding calipers, spreading calipers, or an osteometric board. Because data recorded via microscribe is collected in three-dimensional coordinate form, linear inter-landmark distances were calculated from these data within the R programming environment (R Core Team, 2020) using a custom-written script by the author. While interobserver error cannot be accounted for with the archival data, tests for intraobserver error for those measurements recorded by the author were performed using repeated measures ANOVA, and errors were non-significant.

Only unilateral measurements are used here; if an element was present on both sides and neither had signs of pathology that were suspected to affect the measurement, only the measurement from the left was used. Bilateral asymmetry is generally considered insignificant in the dentition (Potter & Nance, 1976; Scott & Turner, 1997), and while significant bilateral asymmetry is observed in the long bones of the limbs (Auerbach and Ruff, 2006), there is no appreciable difference in variances between sides in limb long bones (Auerbach, pers. comm.). If the left side was missing, the right side measurement was used. Any measurements that were still not available were replaced by the trait mean within that site. While this reinforces the mean, it does not make assumptions about the variance of dimensions and so has the least impact on variance-dependent analytical methods like RMET (see below) (Little and Rubin, 2002). Cranial and postcranial data were then z-score standardized to remove the size differences introduced by sexual dimorphism. Because most differences in dental dimensions between the sexes are negligible (Garn, Brace, & Cole, 1977; Mayhall, 1992; Hillson, 1996; Scott & Turner, 1997; but see Schwartz & Dean 2005), this was not performed for dental metric data.

Analytical Methods

Following initial preparation using R, data were input into the software program RMET. RMET is a statistical program developed and made freely available by Dr. John Relethford (n.d.). RMET allows for two types of analysis: a relationship matrix (R-matrix, a variance-covariance matrix) and an analysis of trait variance. The quantitative genetic analysis performed by RMET results in a Relethford-Blangero model, assessing the presence of gene flow using trait variance represented by metric data. As noted in the Introduction, gene flow between populations, according to quantitative genetic theory, will at first bring more variation into a population than would otherwise be expected. Over time, the genetic and phenotypic difference between those populations will decrease (Slatkin, 1987; Bohonak, 1999; Hutchison & Templeton, 1999), particularly if that gene flow persists. The main focus of analysis for this model, therefore, is the comparison of within-population variance of trait measurements. As outlined by Relethford and Blangero (1990), the expected variance within a population may be compared to its actual variance as an indicator of gene flow.

All RMET analyses were conducted using the available data for each site as described above and in Table 2.2. Eight dental metrics, six craniometrics, and eleven postcranial metrics were

examined separately within each sex. In postcranial dimensions, five upper limb dimensions and six lower limb dimensions were examined together and by limb. They were separated to ascertain if the upper limb or lower limb produced more consistent results with cranial or dental dimensions; I expect them to have similar results.

Both the R-matrix and Relethford-Blangero model require the estimation of narrow sense heritability (h^2) to approximate relative genetic similarity within and between populations. Though researchers should not expect equivalence in heritability for skeletal elements or teeth (Stojanowski and Schillaci, 2006), the same heritability value ($h^2 = 0.55$) is used here for all elements because dental heritability ranges from 0.5 to 0.9 (Stojanowski & Schillaci, 2006), which falls between the two commonly used values of 0.55 or 1.0 for craniometric data (Byrd, 2014). Importantly, Relethford & Blangero (1990) have demonstrated that heritability values do not greatly affect the results of their models, provided values are not too low (defined by von Cramon-Taubadel, 2014, as 0.2 or less).

For the Relethford-Blangero model, census population size may also be used as a factor. However, because this figure is rarely known in bioarchaeological contexts, it is here input as 1 for all populations to remove the effects of scaling (Relethford and Blangero, 1990). This practice also forces the model to assume that genetic drift is equivalent between groups. Given the short evolutionary time period represented by these archaeological sites, genetic drift should have little effect on the results. Frankenberg and Konigsberg (2011) show that a gene flow event must be biological “captured” within fifty generations to be detectable; these sites and their occupations are well within that time frame. Under these conditions, any difference between expected and observed trait variance should be mostly attributable to the presence or absence of external gene flow.

From the R-matrix, Euclidian distances between centroids were calculated for use in biodistance analysis, namely Mahalanobis D^2 . The D^2 , as noted in the Introduction, is a widely used measure of biological distance in anthropological, especially bioarchaeological, research (Relethford, 2016). The Mahalanobis D^2 is a multivariate method that uses Euclidean distances between groups in a transformed multidimensional space that resolves the issue of intercorrelation found in some other methods (Relethford and Lees, 1992). Small sample sizes can bias estimates of biological distance (as small samples will have biased means); in most cases, sites have sample sizes over 10, except for Slade Ruin and Kinishba. A correction factor may be applied based on the number of traits (t) and sample sizes of the two sites (n_i and n_j) between which distances are calculated [$t(n_i + n_j)/(n_i n_j)$] (Relethford, 2016); D^2 values with this correction factor are presented in Table S2.1.

Results

Results of the Relethford-Blangero method analysis are reported in Table 2.3 (and full results in Table S2.2). Despite the differences among the anatomical regions, results of Relethford-Blangero analyses are largely consistent. Grasshopper Pueblo, which is noted to have multiple lines of evidence for both local and non-local inhabitants, has a positive residual, which supports the presence of gene flow among analyses of all skeletal trait sets in both sexes. Kinishba,

another site that ranges both Pueblo III and Pueblo IV periods and has some evidence for the appearance of migrants in later time periods, presents opposite results for the crania and postcrania in general; postcranial data generally indicate gene flow in all instances except female upper limb dimensions, while crania do not indicate gene flow. In contrast, Point of Pines, which also extends between both periods, generally has a negative residual, with the exception of the cranial analysis in males and the dental analysis in females. Of the Pueblo III-only sites, Slade Ruin has a consistently negative residual in both sexes, with the exception of the dental analysis for females. Nearby Turkey Creek is more varied in support for the presence of gene flow, particularly the postcranial analyses. To understand how the upper and lower limbs may differently reflect gene flow in ways obscured by combining both, a comparison of both is presented in the far right two columns of Table 2.3. The limbs differed only in Turkey Creek females and Kinishba females, and there is no pattern to that differentiation.

Among the Relethford-Blangero residuals, the signs of residuals agree among dental, cranial, postcranial sets of traits in the majority of instances. Correspondence between dental and cranial traits occurs in 5 of 8 comparisons (2 among females, 3 among males), and the signs of residuals between dental and postcranial traits agree 5 of 8 comparisons (3 among females, 2 among males). Cranial and postcranial traits have a similar correspondence, with 6 out of 10 comparisons in agreement (3 in each sex). In most cases, the lower limb appears to have greater effect on the overall postcranial residuals.

Table 2.4 presents the R-matrix diagonal values for each site by skeletal region and sex, as well as estimated F_{st} values. As noted in the methods, this is calculated using a population size of 1. The r_{ii} values reflect the variance of standardized allele frequencies. Paralleling the results of the Relethford-Blangero method analysis, sites with higher residuals (Table 2.3) tend to have more variance in allele frequencies for a given skeletal trait group and sex. F_{st} , which measures genetic differentiation between populations, is difficult to interpret as it is affected by rates of gene flow as well as population size. Nevertheless, results indicate that dental and postcranial dimensions reflect similar F_{st} values, and therefore population distances, compared with cranial dimensions in both sexes.

The Mahalanobis D^2 results (Table 2.5) are less consistent. Most of the analyses show the closest relationships (smallest Euclidean distance) between Grasshopper and Point of Pines pueblos. The exceptions are male dentition, where Grasshopper and Turkey Creek are closest, and female postcrania, where Kinishba and Turkey Creek are closest. Beyond the closest relationships, there does not appear to be patterning in the proximity of relationships. The principal coordinates analysis demonstrates this lack of consistency (Figure 2.2). Further, comparing the first two eigenvectors, the cranial data explain the least amount of variance for both sexes (80.5% females, 75.8% males), while the postcranial data explain the most variance for both sexes (95.4% females, 98.1% males). Geographic proximity is not a good predictor of biological similarity. It is notable that the sites with closest geographic proximity—Turkey Creek and Point of Pines—are often the most distant from each other and never the least distant. Other geographically proximate sites, such as Grasshopper and Kinishba, are likewise often not the most similar in biological distances.

Discussion

The results of this study present a varied and potentially nuanced perspective in using various sets of skeletal traits in the Relethford-Blangero model-bound method for ascertaining extralocal gene flow, as well as the interrelationships among these sites using Mahalanobis D^2 . Despite statistical noise related to body size and environmental factors (Agostini et al., 2018), the signals for gene flow using the Relethford-Blangero method are generally consistent among skeletal regions, with some notable exceptions. Comparing the cranial and postcranial analyses yields somewhat more inconsistency than the dental does to either. The sign of the residual is opposite in these categories among both sexes from Kinishba, males from Turkey Creek, and females from Point of Pines. While cranial measurements are solely representative of the face due to potential influence of artificial cranial modification, and therefore likely influenced by similar evolutionary processes, postcranial measurements represent both the upper and lower limb. In contrast to these subtle differences, biological distances are widely different between regions of the skeleton within both females and males. Discussion of the latter results will therefore focus on comparing the same trait groups between the sexes.

Evidence for Extra-Regional Gene Flow

The residual variances from the Relethford-Blangero analyses, despite differences between sets of skeletal traits in some cases, broadly indicate mixed signals for changes in gene flow into the Mogollon region between the Pueblo III-only sites (Turkey Creek and Slade Ruin) and those that extended into the Pueblo IV period. Dental traits generally support gene flow into the region during both time periods, while cranial and postcranial traits present a mixed pattern. In all cases, there is support for extra-regional gene flow at Grasshopper Pueblo, supporting the evidence obtained from other studies of skeletal data as well as artifacts and architecture (Riggs, 2007). Cranial data also point toward gene flow into Point of Pines, while gene flow was mixed or not supported for Turkey Creek, Slade Ruin, or Kinishba. Postcranial traits present a different pattern, which aligns with my hypothesis: Pueblo IV sites (at least Grasshopper and Kinishba) have signs of extra-regional gene flow, matching evidence for migration (or copying of pottery styles, implying nonlocal contact with other cultures) suggested from the archaeological record.

Overall, given the mixed results across the skeleton, it is not possible to reject the hypothesis that increased extra-regional gene flow occurred in the later time period sites compared with the earlier time period, though the results are ambiguous. Despite a small sample size, evidence is consistent that gene flow into the population at Slade Ruin is not supported. Evidence for gene flow from outside the region is strongest for Grasshopper Pueblo, given the consistency of the residuals across the skeleton. As reported by Riggs (2001, 2007), there are clear distinctive contemporaneous architectural styles, especially in kiva design, present at Grasshopper that would indicate that more than one cultural tradition was present in the structure of the pueblo. This hypothesis is supported biologically by McClelland's (2003) dental nonmetric analysis and would align with expectations of migration into the region and the coalescence of multiple cultures following the Colorado Plateau depopulation event. As noted in the Introduction, evidence for migration into Kinishba pueblo is more circumstantial, largely based on changes in ceramic design that incorporate Hohokam styles during the later period of the site's occupation.

Postcranial traits support gene flow as being a component of this change, while cranial data do not. The small sample size at Kinishba is likely driving this ambiguity.

In contrast with these three sites, Point of Pines and Turkey Creek have ambiguous results, though the preponderance of evidence suggests that gene flow is not supported at Point of Pines, while there is evidence in support of gene flow at Turkey Creek, contrary to expectations. Point of Pines and Turkey Creek are geographically the most proximate sites, though the former was occupied for over a century longer than the latter. Both pueblos were located in the Mogollon mountain region (Figure 2.1), though both were sizeable settlements. The lack of evidence in support of gene flow into Point of Pines is unexpected, as archaeological evidence supports the intrusion of people from the Kayenta area of the Colorado Plateau during the late thirteenth century (at the end of the Pueblo III period) (Stone, 2000; Lyons et al., 2018). Their presence at Point of Pines was brief, spanning approximately three decades before they abandoned the pueblo, leaving local populations behind to occupy it throughout the Pueblo IV period. The general lack of gene flow may be interpreted as a lack of intermarriage between the local Mogollon population and the Kayenta outsiders, a pattern that stands in contrast with evidence for gene flow at Grasshopper and, more ambiguously, Kinishba in the presence of non-Mogollon peoples. Turkey Creek was occupied at the terminus of the Pueblo III period, and so it is possible that it represented an aggregation of groups along the frontier of the Mogollon; additional archaeological context is necessary to further support this hypothesis, though study of the construction and architecture of Turkey Creek supports a single, hierarchically cohesive social structure (Lowell, 1988).

While the magnitude of residuals using the Relethford-Blangero analysis is of dubious analytical merit, in part because they are sensitive to sample size and population size (Relethford & Blangero, 1990), there are potentially important differences in these magnitudes between sets of skeletal traits. It is notable that most dental trait residuals, whether supporting or failing to support the presence of gene flow, are of very low magnitude in comparison with cranial and postcranial trait sets (Table 2.3). This suggests that the method is only weakly differentiating the populations when dental data are used; most groups are close to the expected amount of variation, though the residuals are non-zero. This may be a result of constraints on dental size and shape, in part by their functionality (Dempsey & Townsend, 2001), as well as limited variance in dentition compared with other aspects of the skeleton. This may explain the weak ability to differentiate patterns of gene flow through dentition, though other studies using different populations have not found this to be a problem (Mallard, Watson, & Auerbach, Chapter Two; Stojanowski, 2003, 2004). There is also an indication that the lower limb is driving the postcranial signal (see Table 2.3), and despite femoral length as likely evolving in response to neutral processes (Savell et al., 2016), it remains unclear how this would impact observed versus expected variance.

Biological Distances Among Sites

Biodistance estimates vary in pattern and magnitude across regions of the skeleton, and between the sexes within regions. As noted in the Results, in many cases sites that have the closest minimum distance between their centroids using one aspect of the skeleton are farthest apart in another. For example, among females, Turkey Creek and Point of Pines are the farthest apart in

Euclidean distances in the cranium (1.60, range of 0.34–1.60) while being among the closest for dental traits (0.19, range 0.11–0.38) (see Table 2.5) and geographic distance. Thus, comparative interpretation of biodistance analysis using different aspects of the skeleton is difficult and in many instances contradictory, a pattern observed by others (Campbell, 2016).

There is no consistent pattern of differences between the sexes in biological distance. Previous biodistance study of pueblo cultures in the broader region have yielded inconsistent evidence for matrilocality, patrilocality, or bilocality (e.g., Schillaci and Stojanowski, 2002; Byrd, 2019b), and so there is no clear expectation for either sex to appear more morphologically similar given geographic distances among sites. In the cranium, for example, both females and males exhibit relatively large D^2 values between proximately-located Turkey Creek and Point of Pines, while Grasshopper and Kinishba, which are closer to each other than either is to other sites in the sample, have relatively smaller D^2 values. This pattern is reversed in the postcranial dimensions.

In comparisons within skeletal regions (e.g., the cranium alone), there are some patterns in biological distances that provide potential nuances to the results of the Relethford-Blangero analysis. As stated above, Turkey Creek and Point of Pines had temporally overlapping occupations while also being geographically close, though the former does not present the signs of intrusions by outsiders present in the latter. Nevertheless, gene flow is supported for individuals from Turkey Creek, while it is not for the sample from Point of Pines (despite contrary archaeological evidence). The large biological distances within the cranium may reflect the effect of gene flow at Turkey Creek, while the Point of Pines population was perhaps more restricted. In both the cranium and dentition, there is likewise moderate to large distances (relative to the total range of each) between Slade Ruin and Turkey Creek, as well as between Slade Ruin and Point of Pines. If sample size and other sources of bias in the calculation of Mahalanobis distances are not creating spurious results, it is possible that this indicates populations at the Pueblo III Slade Ruin and Pueblo IV Point of Pines were more biologically distinct than those between Point of Pines and Grasshopper. Whether these are attributable to different effects of gene flow at each site, temporal differences, or a combination of both cannot be addressed.

One clear conclusion from all biological distance comparisons, though, is that biological distance in none of the trait groups correlates with geographic distance. Linear geographic distances between sites, though an imperfect proxy for the actual traversable distances between locations given topography, were calculated using approximate site latitudes and longitudes plotted in Google Earth (see Table S2.3). These linear distances have middle-to-low correlations with the biological distances presented in Table 2.5 ($r = -0.69$ to 0.47). These are not improved using the corrected D^2 values accounting for effects of sample size (Table S2.1). While this comparison is not unproblematic given noted possible bias introduced by some small sample sizes, as well as the rudimentary estimation of geographic distances (but see Betti, von Cramon-Taubadel, & Lycett, 2012, for precedent), the results nonetheless argue that gene flow from outside the region has affected local biological distances. This is because, in the absence of outside gene flow (and assuming no directional selection), group biological similarity should generally match isolation-by-distance at regionally local scales (Relethford, 2004).

Conclusion

This study set out to examine evidence for extra-regional gene flow among Pueblo III and Pueblo IV Mogollon sites in central eastern Arizona and compare these among three sets of skeletal traits. In general, the results support the presence of gene flow in both periods, namely at Turkey Creek, Grasshopper, and, more marginally, Kinishba. In the case of Grasshopper and Kinishba, other archaeological context lends further support to the presence of migrating populations mingling with local Mogollon populations. One unexpected result is the lack of support for gene flow into Point of Pines, despite archaeological evidence for a decades-long incursion of Colorado Plateau groups into that community. Biological distance analyses broadly support the impact of extra-regional gene flow on the apportionment of local biological variation.

While there are notable exceptions, the analyses presented general correspondence in the Relethford-Blangero R-matrix method results among the dental metrics, craniometrics, and postcranial metrics. Researchers should nonetheless be cautious in their choice of traits for use in these analyses, as it is evident that the signals for gene flow derived from among these skeletal regions do not always agree. The results of this study suggest that is no reason to give any one region primacy over others for indicating gene flow, which may in part be because gene flow between populations may affect the variance of parts of the body differently (e.g., as occurs in hybridization between species; Ackermann et al., 2016). Parceling the different signals of gene flow among parts of the skeleton awaits future study.

Table 2.1. Context of Groups Used in Analysis

Site	<i>N</i> (dental)	<i>N</i> (cranial & postcranial)	Estimated Date	Source of Date
Point of Pines	F: 25 M: 18	F: 31 M: 17	Pueblo IV period A.D. 1260-1450	Haury (1989)
Turkey Creek	F: 16 M: 16	F: 25 M: 20	Pueblo III period A.D. 1240-1300	Johnson (1965)
Grasshopper	F: 29 M: 14	F: 98 M: 60	Pueblo IV period A.D. 1275-1400	Longacre & Reid (1974)
Kinishba	<i>NA</i>	F: 9 M: 9	Pueblo III-IV period A.D. 1200-1400	Adler & Johnson (1996)
Slade Ruin	F: 8 M: 3	F: 11 M: 3	Pueblo III period A.D. 1100-1300	Byrd & Garcia (2015)

Table 2.2. Standard Metrics Used in Analysis

Category	Measurement	Citation
Dental	Mesiodistal Length – UM1-3, LM1-3, UI1, UI2	Moorrees & Reed 1964, Hillson 1996
	Buccolingual Breadth – UM1-3, LM1-3, UI1, UI2	Kieser 1990, Hillson 1996
Cranial	Nasal Height (NLH)	Howells 1973; Buikstra & Ubelaker 1994
	Nasal Breadth (NLB)	Howells 1973; Buikstra & Ubelaker 1994
	Interorbital Breadth (DKB)	Howells 1973
	Orbital Breadth (OBB)	Howells 1973; Buikstra & Ubelaker 1994
	Orbital Height (OBH)	Howells 1973; Buikstra & Ubelaker 1994
	Minimum Frontal Breadth (WFB)	Buikstra & Ubelaker 1994
Postcranial	Clavicle Maximum Length	Buikstra & Ubelaker 1994
	Humerus Maximum Length	Buikstra & Ubelaker 1994
	Humerus Epicondylar Breadth	Buikstra & Ubelaker 1994
	Radius Maximum Length	Buikstra & Ubelaker 1994
	Ulna Physiological Length	Buikstra & Ubelaker 1994
	Os Coxae Height	Buikstra & Ubelaker 1994
	Os Coxae Iliac Breadth	Buikstra & Ubelaker 1994
	Femur Maximum Length	Buikstra & Ubelaker 1994
	Tibia Physiological Length	Buikstra & Ubelaker 1994
	Calcaneus Maximum Length	Buikstra & Ubelaker 1994
	Calcaneus Middle Breadth	Buikstra & Ubelaker 1994

Table 2.3. Heat Map of Relethford-Blangero Residuals by Site and Sex.

Group	Sex	Dental	Cranial	Postcranial	Upper Limb	Lower Limb
Point of Pines	F	-0.147	0.103	-0.340	-0.094	-0.519
	M	0.284	-0.104	-0.427	-0.671	-0.229
Turkey Creek	F	0.053	0.396	0.005	0.710	-0.607
	M	0.040	0.341	-0.350	-0.443	-0.252
Grasshopper	F	0.022	0.401	0.037	0.051	0.019
	M	0.057	0.211	0.261	0.337	0.196
Kinishba	F	NA	-0.583	0.967	-0.194	1.952
	M	NA	-0.239	0.950	1.318	0.614
Slade Ruin	F	0.071	-0.318	-0.668	-0.474	-0.845
	M	-0.381	-0.209	-0.433	-0.542	-0.329

Key: Colors are distinguished by quartile, with the lightest indicating a low $|0-0.25|$ residual and the darkest indicating a high $|0.75+|$ residual. Positive residuals are colored shades of orange, negative residuals are colored shades of purple.

Table 2.4. R-Matrix Diagonals by Data Type & Sex.

a. cranial - female

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.337204	0.321075	0.048339
Turkey Creek	0.689859	0.669859	0.076992
Grasshopper	0.150084	0.144982	0.018138
Kinishba	0.270196	0.214641	0.080307
Slade Ruin	0.330375	0.284920	0.080324
<i>Total F_{st}</i>	<i>0.355544</i> <i>(biased)</i>	<i>0.327095</i> <i>(unbiased)</i>	<i>0.018897</i> <i>(SE)</i>

b. cranial - male

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.385173	0.355761	0.070031
Turkey Creek	0.379359	0.354359	0.065076
Grasshopper	0.132838	0.124505	0.021891
Kinishba	0.299977	0.244422	0.084939
Slade Ruin	0.555796	0.389130	0.200255
<i>Total F_{st}</i>	<i>0.350629</i> <i>(biased)</i>	<i>0.293635</i> <i>(unbiased)</i>	<i>0.030954</i> <i>(SE)</i>

c. dental - female

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.055361	0.035361	0.015548
Turkey Creek	0.145239	0.113989	0.031480
Grasshopper	0.114766	0.097524	0.020785
Slade Ruin	0.191216	0.128716	0.051082
<i>Total F_{st}</i>	<i>0.126645</i> <i>(biased)</i>	<i>0.093898</i> <i>(unbiased)</i>	<i>0.014274</i> <i>(SE)</i>

d. dental - male

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.172406	0.144628	0.031096
Turkey Creek	0.217956	0.186706	0.037084
Grasshopper	0.115879	0.080165	0.028907
Slade Ruin	0.263220	0.096554	0.094116
<i>Total F_{st}</i>	<i>0.192365</i> <i>(biased)</i>	<i>0.127013</i> <i>(unbiased)</i>	<i>0.022151</i> <i>(SE)</i>

e. postcranial – female

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.144206	0.128077	0.027258
Turkey Creek	0.113538	0.093538	0.026933
Grasshopper	0.172657	0.167555	0.016775
Kinishba	0.073511	0.017955	0.036119
Slade Ruin	0.103830	0.058375	0.038828
<i>Total F_{st}</i>	<i>0.121548</i> <i>(biased)</i>	<i>0.093100</i> <i>(unbiased)</i>	<i>0.011866</i> <i>(SE)</i>

f. postcranial - male

Population	Biased r_{ii}	Unbiased r_{ii}	SE
Point of Pines	0.109055	0.079644	0.031137
Turkey Creek	0.047800	0.022800	0.019005
Grasshopper	0.178986	0.170652	0.021233
Kinishba	0.365741	0.310185	0.078369
Slade Ruin	0.142314	0.000000	0.084672
<i>Total F_{st}</i>	<i>0.168779</i> <i>(biased)</i>	<i>0.116656</i> <i>(unbiased)</i>	<i>0.020423</i> <i>(SE)</i>

Table 2.5. Mahalanobis D^2 Results by Data Type and Sex.

a. cranial - female

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	1.603868			
Grasshopper	0.335868	1.167293		
Slade Ruin	0.863242	1.106564	0.423140	
Kinishba	0.470173	1.147145	0.444334	0.758140

b. cranial – male

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.947165			
Grasshopper	0.370137	0.695374		
Slade Ruin	1.237997	1.045512	0.528266	
Kinishba	0.750505	0.601919	0.513589	0.935382

c. dental – female

	Point of Pines	Turkey Creek	Grasshopper
Turkey Creek	0.192788		
Grasshopper	0.106640	0.318471	
Slade Ruin	0.257608	0.382786	0.375060

d. dental – male

	Point of Pines	Turkey Creek	Grasshopper
Turkey Creek	0.474207		
Grasshopper	0.319105	0.272708	
Slade Ruin	0.348809	0.570463	0.308328

e. postcranial – female

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.133090			
Grasshopper	0.414323	0.498932		
Slade Ruin	0.369664	0.263201	0.124145	
Kinishba	0.221066	0.077966	0.276078	0.091276

f. postcranial – male

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.090337			
Grasshopper	0.026230	0.192166		
Slade Ruin	0.188778	0.129561	0.304632	
Kinishba	0.734978	0.335219	0.930182	0.244940



Figure 2.1. Map of Mogollon Rim mountain region proveniences. *Image adapted from Google Earth (<https://www.google.com/earth/>).*

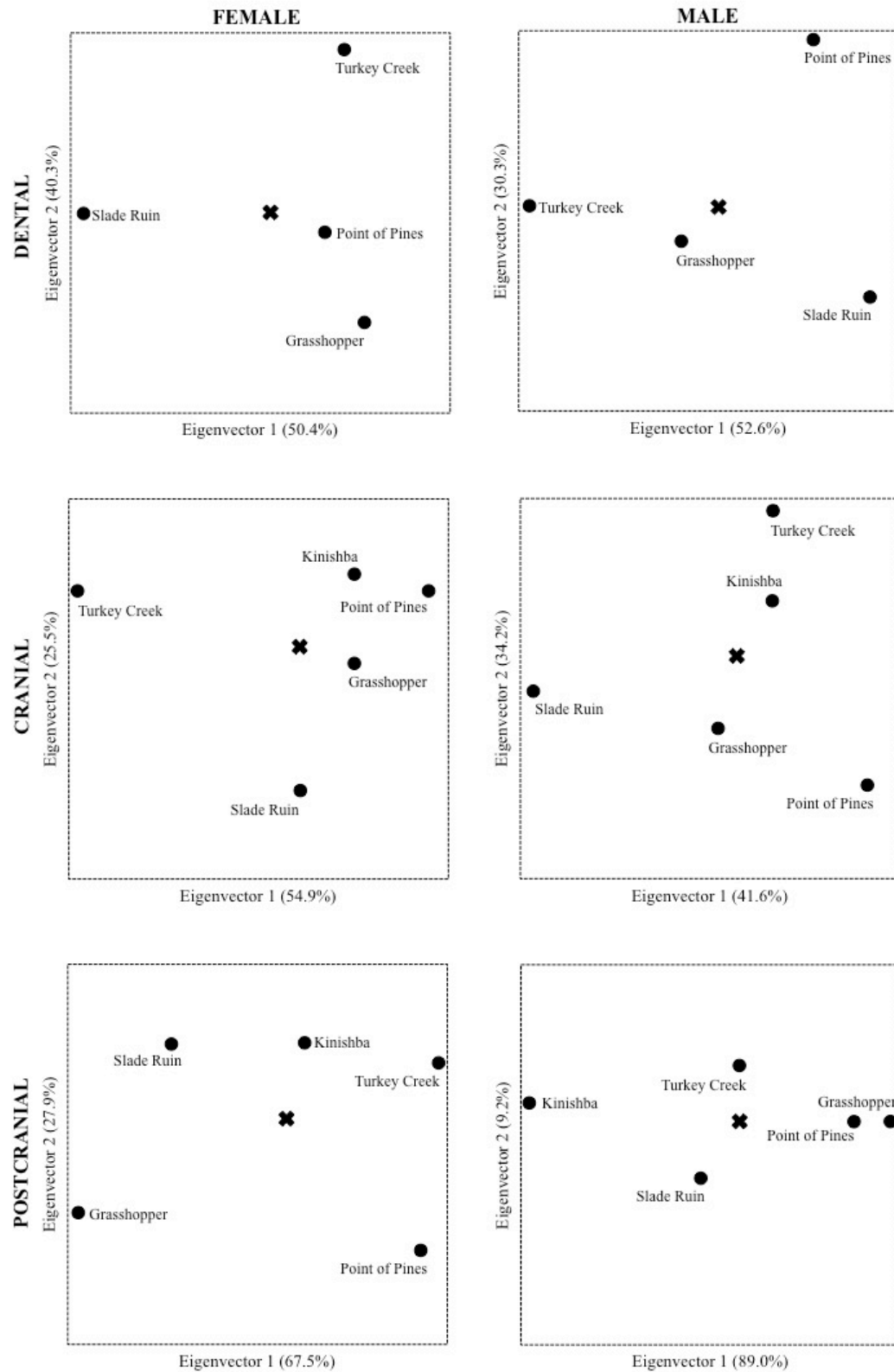


Figure 2.2. Principal coordinates plots of Mogollon Rim mountain region groups by sex and data type. Key: 'x' denotes centroid, circle denotes site.

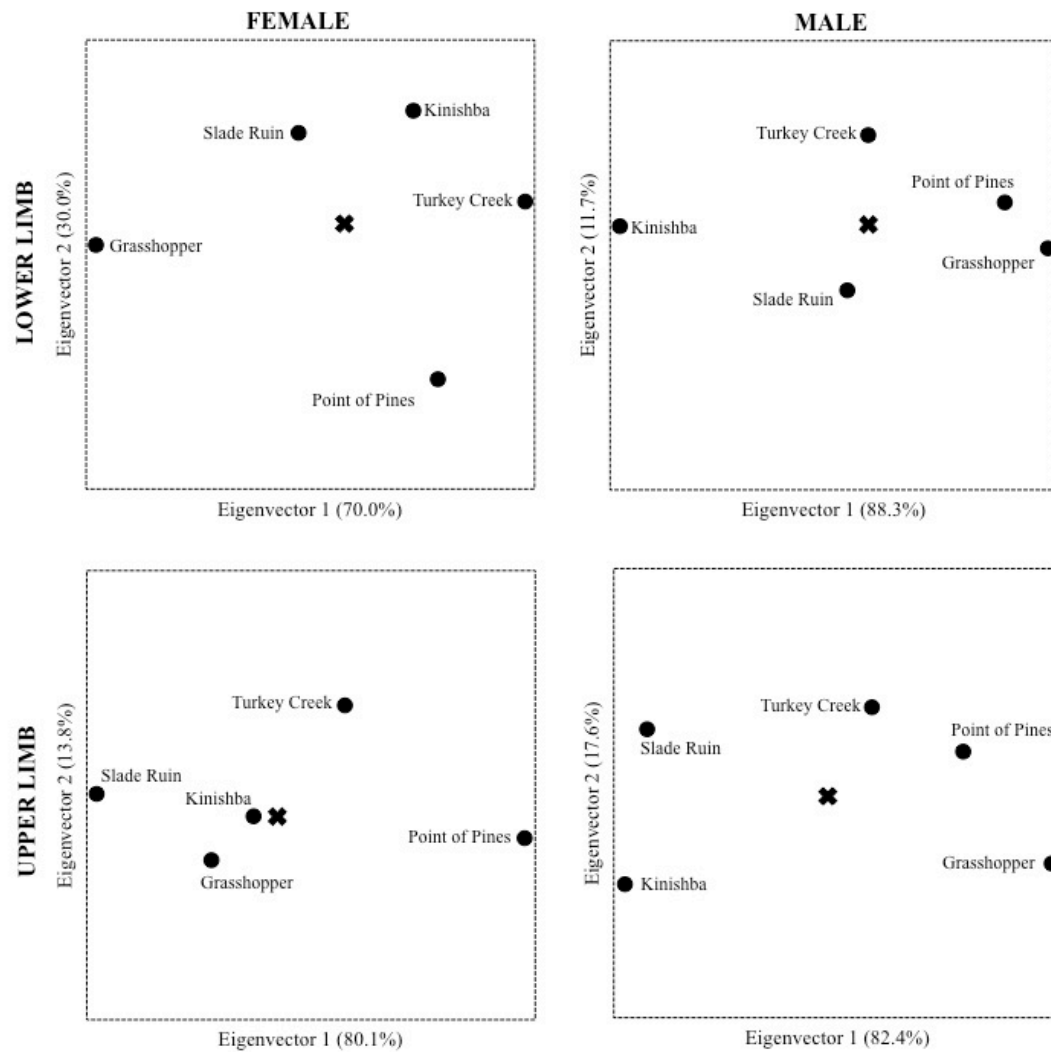


Figure 2.3. Principal coordinates plots of Mogollon Rim mountain region groups by sex and limb group. Key: 'x' denotes centroid, circle denotes site.

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Supplemental Information from Article 2

Table S2.1. Corrected Mahalanobis D^2 Values by Skeletal Region and Sex.

a. cranial - female

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	1.170319613			
Grasshopper	0.081095123	0.866068510		
Slade Ruin	0.124239067	0.321109455	0.183539035	
Kinishba	0.390042054	0.240478333	0.283557156	0.453981212

b. cranial – male

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.294223824			
Grasshopper	0.082804176	0.295374000		
Slade Ruin	1.114944176	1.254488000	1.571734000	
Kinishba	0.269102843	0.364747667	0.253077667	1.731284667

c. dental – female

	Point of Pines	Turkey Creek	Grasshopper
Turkey Creek	0.422212000		
Grasshopper	0.340256552	0.263425552	
Slade Ruin	0.732392000	0.742214000	0.581836552

d. dental – male

	Point of Pines	Turkey Creek	Grasshopper
Turkey Creek	0.234126333		
Grasshopper	0.442799762	0.530863429	
Slade Ruin	1.984524333	1.804537000	2.120243429

e. postcranial – female

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.300458387			
Grasshopper	0.159550123	0.197707510		
Slade Ruin	0.369338933	0.522253545	0.482534035	
Kinishba	0.639149054	0.828700667	0.451813156	1.120845212

f. postcranial – male

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	0.562604176			
Grasshopper	0.426711176	0.207834000		
Slade Ruin	2.164163176	2.170439000	1.795368000	
Kinishba	0.284629843	0.631447667	0.163515333	2.421726667

Table S2.2. Complete Relethford-Blangero Results by Data Type & Sex.

a. cranial - female

		Within-Group Phenotypic Variance ($\mu = 0.539$)		
Population	r_{ii}	Observed	Expected	Residual
Point of Pines	0.321075	0.647	0.544	0.103
Turkey Creek	0.669859	0.661	0.265	0.396
Grasshopper	0.144982	1.086	0.685	0.401
Kinishba	0.214641	0.047	0.629	-0.583
Slade Ruin	0.284920	0.255	0.573	-0.318

b. cranial - male

		Within-Group Phenotypic Variance ($\mu = 0.655$)		
Population	r_{ii}	Observed	Expected	Residual
Point of Pines	0.355761	0.493	0.597	-0.104
Turkey Creek	0.354359	0.939	0.599	0.341
Grasshopper	0.124505	1.022	0.812	0.211
Kinishba	0.244422	0.462	0.701	-0.239
Slade Ruin	0.389130	0.358	0.566	-0.209

c. dental - female

		Within-Group Phenotypic Variance ($\mu = 0.949$)		
Population	r_{ii}	Observed	Expected	Residual
Point of Pines	0.035361	0.864	1.011	-0.147
Turkey Creek	0.113989	0.981	0.928	0.053
Grasshopper	0.097524	0.968	0.945	0.022
Slade Ruin	0.128716	0.984	0.913	0.071

d. dental - male

		Within-Group Phenotypic Variance ($\mu = 0.847$)		
Population	r_{ii}	Observed	Expected	Residual
Point of Pines	0.144628	1.113	0.830	0.284
Turkey Creek	0.080165	0.829	0.789	0.040
Grasshopper	0.080165	0.949	0.892	0.057
Slade Ruin	0.096554	0.495	0.876	-0.381

e. postcranial - female

		Within-Group Phenotypic Variance ($\mu = 0.996$)		
Population	r_{ii}	Observed	Expected	Residual
Point of Pines	0.128077	0.618	0.958	-0.340
Turkey Creek	0.093538	1.000	0.996	0.005
Grasshopper	0.167555	0.951	0.915	0.037
Kinishba	0.017955	2.045	1.079	0.967
Slade Ruin	0.058375	0.367	1.034	-0.668

f. postcranial - male

Population	r_{ii}	Within-Group Phenotypic Variance ($\mu = 0.852$)		
		Observed	Expected	Residual
Point of Pines	0.079644	0.460	0.887	-0.427
Turkey Creek	0.022800	0.592	0.942	-0.350
Grasshopper	0.170652	1.060	0.799	0.261
Kinishba	0.310185	1.615	0.665	0.950
Slade Ruin	0.000000	0.530	0.964	-0.433

Table S2.3. Approximate linear geographic distances (kilometers) between sites

	Point of Pines	Turkey Creek	Grasshopper	Slade Ruin
Turkey Creek	12			
Grasshopper	118	107		
Slade Ruin	79	71	132	
Kinishba	56	45	70	69

Chapter 4

USING POSTCRANIAL DATA AS INDICATORS OF POPULATION HISTORY AND GENE FLOW ACROSS SPACE AND TIME IN THE PUEBLOAN SOUTHWESTERN U.S.

Disclosure Statement & Introduction to Article 3

In Article 3, I analyze gene flow on a larger regional scale. Using most of the sites from the previous analysis (Article 2 from Chapter 3) and adding sites from both New Mexico and Arizona, I compare gene flow analysis results to archaeological and ethnographic models separating the Eastern and Western Pueblo. This Puebloan cultural split was proposed over a century ago by Alfred Kidder (1917). Using Relethford-Blangero analysis, I evaluate whether that split is mirrored biologically through skeletal trait variance.

Following a recent precedent set by Agostini, Holt, & Relethford (2018), this study uses only postcranial data from Auerbach (2007). Though most studies questioning biological relationships in the Southwest have used craniometrics, this study looks to the compatibility of postcranial data with previous studies of biodistance and archaeological material, and furthermore examines the relationship of the lower limb and pelvic girdle as well as the upper limb and shoulder girdle to the overall trait variance seen in the postcrania. While biodistance is not the subject here as it was in Chapter 3, principal coordinates plots created from the R-matrix were also examined to take note of any patterns that would agree or disagree with the Relethford-Blangero results.

I performed the analysis (including coding and interpretation) as well as the initial writing of this manuscript, which incorporates archival data from my coauthor (BMA), who also edited this paper. It is written and organized in the style of the *American Journal of Physical Anthropology*, to be submitted under the following citation:

Mallard, A.M., & Auerbach, B.M. (In prep). Using Postcranial Data as Indicators of Population History and Gene Flow Across Space and Time in the Puebloan Southwestern U.S.

Abstract

Well-supported archaeological models serve as useful templates to estimate biological relationships, particularly where gene flow is concerned. This study uses postcranial data for the first time to assess possible gene flow relationships across the Ancestral Puebloan world (c. A.D. 840-1590), specifically comparing how well these data mirror the barrier of the Continental Divide as well as archaeological and ethnographic models dividing the Eastern Pueblo and Western Pueblo. Using the Relethford-Blangero method as well as Mahalanobis' D^2 , we use skeletal traits from groups of fourteen site proveniences to address the congruence of these models. While consistency between the skeletal and archaeological models varied, the Relethford-Blangero method yielded a pattern suggesting that patterns of mating for the two Ancestral Puebloan groups was different. This supports the separate cultural classifications devised by ethnographers and supported by archaeologists, as well as hypotheses of two separate Basketmaker migrations from northern Mexico to the Four Corners region. The Mahalanobis' D^2 method, meanwhile, had poor resolution for most sites, with the exception of Chaco Canyon. Chaco Canyon, according to this analyses, was phenotypically distinct from other populations, indicating a likely gene flow event that supports hypotheses that the site was a major cultural center for the surrounding region. Looking to the postcranial data as a source, the overall postcranial signal seems to be driven by the lower limb and pelvic girdle more than the upper

limb and shoulder girdle, which may have implications for the usefulness of particular traits in performing population history studies.

Introduction

The primary focus of this paper is to examine regional gene flow using osteometric data from archaeological contexts in the Southwestern United States dated to a limited temporal range. Previous studies have examined biological distance among portions of the archaeological context we include herein, using craniometric (Schillaci & Stojanowski, 2005; Byrd, 2019a) and dental (Schillaci, 2003) data, and Byrd (2019b) performed a region-wide analysis using craniometric data. While these and other researchers have performed significant archaeological investigations of the movement of artifacts and, potentially, people in the U.S. Southwest dating to the Puebloan periods, they do not often address the impact of the Continental Divide (Figure 3.1) as a geological feature that could have potentially impeded or otherwise affected population interaction. However, there is cause to consider that the Continental Divide affected gene flow across the region. For example, Auerbach (2007) noted some skeletal morphological differences between the east and the west that may be the result of recent common ancestry followed by geographic separation, resulting in a lack of gene flow. Here, we explore this hypothesis further using different methods from Auerbach's (2007) postcranial metric data analysis.

Patterns of variation, such as those described by Auerbach (2007), are poor indicators of the evolutionary processes responsible for shaping them (Roseman and Auerbach, 2015; Savell, Auerbach, & Roseman, 2016). Differences in limb and body proportions as well as stature, for instance, could arise through multiple causes—e.g., differences in diet, generalized stress from environmental factors, or genetic distinction—and cannot indicate if gene flow could have occurred between or among populations. Nevertheless, the long bones of the limbs may be invariant enough over short temporal periods to be useful for model-bound approaches to modeling gene flow (Relethford and Blangero, 1990). Agostini, Holt, and Relethford (2017) recently showed that long bone diaphyseal measurements do retain a signal of population history, making the use of postcranial data an appropriate application of biological distance and quantitative genetic methods. While some question the efficacy of some of these metrics in the study of human gene flow on a global scale (e.g., Betti, von Cramon-Taubadel, & Lycett, 2012), here we use them in a region hypothesized to be mostly interconnected (Wilcox, 1996; Mills et al., 2013) within a restricted timeline. Within this framework, we examine different patterns of gene flow in sites from Arizona and New Mexico.

Archaeological Context

As a result of geographic and cultural distinctions, Puebloan groups living on either side of the Continental Divide in the Southwest likely experienced distinctive patterns of potential interaction. Archaeological studies of social networks and population interaction by Wilcox (1996), Mills and colleagues (2013), Borck and colleagues (2015), as well as others focused on the Puebloan influence at Chaco Canyon or around the Little Colorado River and mountains of the Mogollon Rim, generally have not extended their models past the Continental Divide. Studies of the far Eastern Pueblo likewise focus eastward, examining the degree of interaction between Eastern Puebloan groups and nomadic groups from the Plains (e.g., Spielmann, Schoeninger, & Moore, 1990). In these studies, the dichotomy of “Eastern vs. Western Pueblo” represents a distinction in both material culture and ethnography between two groups potentially founded by different groups from Mesoamerica. The origins of Basketmaker II peoples (c. A.D.

400) in the Colorado Plateau region to the west and Four Corners region to the east have been popularly hypothesized to be from Mesoamerica, representing two separate migrations (Morris & Burgh, 1954; Matson, 2016; Whiteley, 2016) that became more differentiated from each other as time passed. Though they shared recent common ancestors in Mexico and occupied nearby territories in the Southwestern U.S., residents of sites such as Mesa Verde and Chaco Canyon in New Mexico are considered, from both an archaeological and ethnographic standpoint, to be different from Western Puebloan groups such as Kayenta (Kidder, 1917; Parsons, 1932; Hawley, 1937; Ellis, 1951; Dean, 1996). Western Pueblos, for instance, tend to be organized primarily by matrilineal kinship, whereas Eastern Pueblos are organized more in accordance to ritual structure (Whiteley, 2016). Styles of ceramics (Colton & Hargrave, 1937; Breternitz, Rohn, & Morris, 1974) and architecture (Dean, 1969) are archaeologically distinct, as is pueblo size, with Western pueblo structures generally smaller than those to the east (Dean, 1996).

The impact of the Continental Divide on these patterns is unclear, though perhaps implicit, as the western edge of the Divide is in the proximity of the geographic division between the Eastern and Western Pueblo (Figure 3.1). Based on a comprehensive study of decorated ceramics, Mills and colleagues (2013) reported a lack of production and trade connections between the regions east and west of the Continental Divide. Consequently, they did not include sites east of the Continental Divide in their demographic model at all; the easternmost location for which they acknowledged interaction is the Jemez Mountains, an important obsidian procurement locale for some Puebloan (Mills et al., 2013) and Mimbres (Roth, DiBenedetto, & Ferguson, 2019) populations. Despite a general lack of discussion surrounding interactions between groups on either side of the Divide, there are enough similarities in material culture that archaeologists often continue to group them together as one meta-group (“the Pueblo” or “the Ancestral Pueblo”), though this has received some criticism (e.g., Hawley, 1937).

The movement of material culture, of course, is not a perfect substitute for either the movement or the interaction of people. The possibility of copying or trading high-visibility and symbolic objects has made archaeologists cautious of the types of objects they track to demonstrate migrations or social ties (Carr, 1995; Clark, 2011). Material goods also do not perfectly track gene flow between groups. Though the culture historical paradigm equated material interactions with biological ones, the reality was almost certain to have been more nuanced. Nonetheless, using a broad archaeological context preserved in the structure, location, and dating of sites, along with their associated material culture, provides a model against which the analysis of gene flow may be assessed.

The division of Arizona versus New Mexico in this study is not one of modern political boundaries. The sites from Arizona (Table 3.1) date largely to Pueblo III-IV (c. A.D. 1000-1450), and are hypothesized to have experienced a population influx during the thirteenth-fourteenth centuries as people (Kayenta) from the Four Corners region migrated southward to the region surrounding the Little Colorado River, including the Mogollon highlands region in Arizona, and further south (Gladwin & Gladwin, 1935; Haury, 1958; Reid & Montgomery, 1998; Riggs, 2001). The New Mexico sites used in the present study include several sites that are roughly contemporaneous with the Arizona sites, with the exception of the Chaco Canyon aggregate, which includes Pueblo Bonito and any other remains whose proveniences were the Chaco Canyon group of sites. Chaco Canyon pueblos and settlements were occupied starting

approximately A.D. 800, with site depopulation initiating in the middle of the twelfth century. The Chaco Canyon sites represent groups who were living in the broader Four Corners region prior to the regional depopulation event associated with the aforementioned movement of Kayenta and other peoples to the west. Researchers largely agree that Chaco Canyon was a major crossroads of trade, migration, and culture (Wilcox, 1996; Kantner, 2004; Sebastian, 2006), and we expect to see evidence of gene flow within these sites for this reason. Following the collapse of Chaco, however, Kantner (2004) described outlying sites as increasingly isolated prior to the next wave of population movement from the Four Corners.

Thus, on both sides of the Eastern/Western Pueblo division as well as the Continental Divide, population movement occurred in a major migration southward, hypothesized to have occurred from Mesa Verde to the northern and middle Rio Grande River region in New Mexico coeval with the migration in Arizona from the Colorado Plateau into adjacent regions, such as the Mogollon Rim. As Clark and colleagues (2019) note, however, these migrations should not be considered archaeologically identical. While they hypothesize the Kayenta migration resulted in two distinct cultures in the receiving region, in contrast the Mesa Verde resettlement resulted in the migrant groups adopting the culture of the receiving groups. If we hypothesize that the gene flow should match the model scenario based on material culture, we should see signals of gene flow in later New Mexico sites such as Pottery Mound. A possible exception is Paa-Ko, which is the furthest east and sits around the eastern edge of the Continental Divide. Lambert (1954) described the site as having indirect evidence of trade (much of which is from the Plains), but did not suggest that that trade was connected to migration or gene flow.

In a previous study of Pueblo III and IV sites from within the Mogollon mountain region (Chapter Three), evidence pointed toward a mixed set of signals for gene flow among these Arizona sites. Grasshopper, for example, was on the receiving end of the Kayenta migration but retained distinct groups of material culture for both the migrants and the recipient population; study of this site within the context of just the Mogollon region suggested consistent evidence for gene flow, as well as some evidence for the geographically nearby Kinishba (Chapter Three), where material cultural also indicated limited evidence for population movement (Welch, 2013). In contrast, earlier sites (Slade Ruin), as well as the more recent Point of Pines, did not have evidence for gene flow, which could have reflected general patterns of interaction for peoples at these sites. At Point of Pines, for instance, Kayenta peoples intruded the local population for a brief period but may have never integrated with the local Mogollon population (Stone, 2000).

When placed into the broader regional context, though, it remains unknown if previously reported patterns will persist, as the context for gene flow analyses depends on the observed variation, and the Relethford-Blangero method models gene flow as occurring from outside the observed sample (Relethford & Blangero, 1990; Relethford, Crawford, & Blangero, 1997). Nevertheless, we expect that, if the sites we sample reflect the recipients of migrants following the depopulation of the Four Corners, evidence for gene flow should remain consistent for both sites in the Mogollon and in the Rio Grande regions (i.e., Arizona and New Mexico, respectively). Based on the broad review here, we expect Chaco Canyon sites to show evidence of gene flow, as well as aggregation sites like Grasshopper, Puye, and Kinishba. Sites with shorter occupations, such as Turkey Creek (a possible vanguard locality preparing the site for a larger group; Duff, 1998; Lyons, pers. comm.), or located at the edges of the Puebloan culture,

like Paa-Ko (Lambert, 1954), may have experienced less impact from the movement of Kayenta or Mesa Verde peoples.

Through the assessment of patterns of gene flow, as well as biological distances among groups, we investigate these hypotheses built on prior studies of regional gene flow and archaeological context. We examine the presence of gene flow signals at each site (see Table 3.1 for site list), as well as between Eastern and Western Pueblo groups. Furthermore, we examine how the limbs and their girdles influence the overall results. A previous study by Mallard (Chapter Three) on groups from the Mogollon mountain region suggests that overall postcranial results using these methods are only slightly more driven by the lower limb. A greater influence from one limb and its girdle over the other may have implications for the ability to discern a population history signal due to neutral evolution in different parts of the postcranial body.

Materials & Methods

All osteometric data were recorded by one of us (BMA) and are described in Auerbach (2007). Seven upper limb and eight lower limb measurements from adults (Table 3.2) were chosen for the present study. A comparison of gene flow analyses showed that, broadly, craniometric, dental, and postcranial dimensions present similar patterns, though with some notable caution (Chapter Three). Additional scholarship has indicated that, while many dimensions are subject to respond to directional selection and are not evolutionarily independent (Roseman & Auerbach, 2015; Savell et al., 2016), these traits also constrain each other's responses to selection (Savell, 2020) and likely lack notable morphological change over short periods of time (Auerbach, 2010).

All traits were measured using an osteometric board (to the nearest 0.5 mm) or sliding digital Mitutoyo calipers (to the nearest 0.01 mm) as appropriate. In all cases, the left side skeletal dimensions were used except when unobservable or affected by pathology; in these cases, the right-side dimensions were used instead. Measurements have low measurement error and high repeatability (Auerbach, 2007; 2012). Auerbach (2007) used features of the os coxae to estimate sex, relying on traits of the cranium when the os coxae were not observable. To remove the effect of sexual dimorphism on trait size, all measurements were z-score standardized.

As noted in the Introduction, the sites sampled in this study represent two broad regions, the Western and Eastern Puebloan Southwest. Sites are listed in Table 3.1 by their categorization into these regions, sample sizes by sex, and the temporal ranges of their occupation. Five sites comprise the Eastern Pueblo group: Chaco Canyon (including Pueblo Bonito), Puye, Paa-Ko, and Pottery Mound. Six sites are included in the Western Pueblo group: Grasshopper, Kinishba, Point of Pines, Turkey Creek, Carter Ranch, and Canyon del Muerto. With the exception of Chaco Canyon sites, all sites date to or after the mid-twelfth century.

Analytical Methods

Raw data were prepared using R (R Core Team, 2020) and subsequently input into RMET, a statistical software program developed by John Relethford. The two types of analyses performed by RMET (an R-matrix, or relationship matrix, and the quantitative genetic Relethford-Blangero

model) encompass different ways to demonstrate the phenotypic changes resulting from gene flow (Relethford & Blangero, 1990). The R-matrix may be transformed into a Mahalanobis D^2 matrix or its distances may be represented graphically using principal coordinates analysis to demonstrate mean population distances from a common centroid, while the Relethford-Blangero model is an analysis of trait variance (rather than means) within populations. The latter model is supported by quantitative genetic theory, which posits that interpopulation gene flow will initially bring more variation into a population than would be expected under normal circumstances. With persistent gene flow over time, the differences between those populations will decrease (Slatkin, 1987; Bohonak, 1999; Hutchison & Templeton, 1999). It is the initial signal of increased variance within populations that the Relethford-Blangero model is concerned with, as it compares a population's expected variance (based on all the populations within the model) compared to its actual variance (Relethford & Blangero, 1990).

Both of these analyses require the estimation of narrow-sense heritability (h^2). This statistic estimates the amount of genetic similarity that exists in the model within and between populations. Unless specific population data exist, this value is set at 0.55 or 1.0 for craniometric analyses (Byrd, 2014). Here, we set this value at $h^2 = 0.55$ because $h^2 = 1.0$ implies complete genetic heritability, which is unlikely for limb long bone dimensions. Relethford & Blangero (1990) demonstrated that the heritability value had only minimal effect on the models resulting from RMET, though caution should be exercised to ensure those values are not too low (defined by von Cramon-Taubadel, 2014, as 0.2 or less). It should be noted that a recent study using postcranial diaphyseal measurements in RMET set h^2 to 1.0 (Agostini, Holt, & Relethford, 2017). Census population size, rarely known for all populations in a bioarchaeological context, has been set to 1, causing the model to assume that genetic drift between groups is equivalent.

All Relethford-Blangero method analyses were performed on a combination of the upper and lower limb dimensions, as well as separately between the limbs. As indicated in a prior study by one of us (AMM) (Chapter Three), the lower limb tends to have an outsized effect on the overall residual variance calculated when both limbs are combined. If the lower limb were a more reliable reflection of gene flow than the upper limb, examination of the lower limb patterns alone, as well as in aggregate with the upper limb may add clarity to the interpretation of results.

Results

Residual variances from the Relethford-Blangero analysis are presented in Table 3.3. Broadly, these present evidence supporting gene flow within either males, females, or both sexes for most Western Pueblo sites, while, with the exception of Chaco Canyon sites, individuals from Eastern Pueblo sites do not show evidence for gene flow. While results of these analyses do not entirely correspond to hypotheses based on the archaeological models, there are some distinct patterns.

In the majority of analyses, the sign of residual variances are the same between the upper and lower limb. When there are exceptions, they either reflect a small magnitude residual for one or both limbs (e.g., Turkey Creek males, Point of Pines females), or a small aggregate residual for all postcranial dimensions (e.g., Kinishba females, Puye females). Given these results, we are

confident in primarily focusing on the results of all postcranial dimensions together, though we note exceptions.

Of the New Mexican sites, the two smaller locales, Paa-Ko and Pottery Mound, largely have negative residuals and, consequently, gene flow into these site populations is not supported. One exception is a slightly positive residual for the upper limb among males at Pottery Mound. The residual at Chaco Canyon, which includes various sites as well as Pueblo Bonito, is positive for all analyses, and the same is true for Puye with the exception of the lower limb and postcranial aggregate in females.

Among the Arizona sites, results are more mixed. Though Turkey Creek has negative residuals in all but the lower limb among males, nearby Point of Pines is negative in all but the lower limb and postcranial aggregate analyses in females. Kinishba presents positive residuals for males, and negative residuals in the female lower limb and postcranial aggregate analyses. Thus, these sites present support for sex-specific gene flow; residuals support gene flow in Point of Pines females and in Kinishba males. In both sexes, Grasshopper has relatively weak signals for all analyses, whose mixed results show a negative residual for the female postcranial aggregate but a positive one for males. Smaller sites Canyon del Muerto and Carter Ranch both have positive residuals for females and negative residuals for males, with the exception of the upper limb in females at Canyon del Muerto.

The principal coordinates analysis plots resulting from the Mahalanobis D^2 distances (Figure 3.2) generally do not suggest any clear patterns. However, Chaco Canyon is an outlier for both sexes in the lower limb and postcranial aggregate analyses. In females only, Puye and Carter Ranch are additional outliers (the upper limb for Puye, and both limbs for Carter Ranch). For the lower limb and postcranial aggregate, with the exception of Chaco Canyon, the groups cluster more tightly among males than females. This generally suggests that the regional dichotomy previously reported between the Western and Eastern Pueblo (Auerbach, 2007) may have been driven by a minority of sites within each group.

Discussion

Overall, our results show that gene flow varied across geography and time in the Puebloan Southwest between A.D. 800 and 1450. As we review below, gene flow was more evident at the large population center at Chaco Canyon than most other sites, and it is apparent in both sexes. Other sites that have archaeological contextual evidence for the presence of migrants along with local populations (e.g., Grasshopper, Point of Pines, or Puye) show a more nuanced pattern of gene flow, where evidence in support of gene flow is sex specific. In general, we conclude that patterns of gene flow as evidenced by variation in the postcranial dimensions do not indicate an easily generalizable pattern, and furthermore provide nuanced evidence for varied social dynamics within and among settlements in the Puebloan Southwest. We consider these results below in more detail with respect to the archaeological models we presented in the Introduction.

Gene Flow Analysis Results in Archaeological Context

Results of the Relethford-Blangero analysis show relatively consistent results for the four New Mexico sites, especially Chaco Canyon and Puye. The positive residuals suggest a clear signal of gene flow for both sexes at Chaco Canyon. It is important to note that our Chaco Canyon sample is aggregated from multiple locales around the complex, including Pueblo Bonito. However, numerous archaeologists have hypothesized an intricately connected regional social network among all sites considered part of the Chaco world based on size and location of great houses (Wilcox, 1996; Judge & Cordell, 2006) as well as the presence of roadways and exotic artifacts (Toll, 2006; Roth et al., 2019). Though gene flow is not inherently linked to the role of pilgrimage, Judge and Cordell (2006) interpret the Chaco world as having diverse social relationships. Chaco may have been a ritual center (Toll, 1990) or a locale solidifying a sense of cultural identity (Lekson, 2002). The results of the Relethford-Blangero analysis lend support to the conclusion that Chaco was a major political center, though there is not enough evidence to support previous hypotheses of matrilineal or patrilineal residence (Schillaci & Stojanowski, 2002). However, clear gene flow signals do suggest possible greater mobility for both sexes at Chaco Canyon.

Results from Puye, an aggregated post-Chaco site, support Schillaci and Stojanowski's (2005) conclusion based on craniometrics that at Puye males had more variation. These results, then, contrast with Corruccini's (1972) findings, which argued that variance was low among individuals at Puye, and may have indicated genetic isolation. Notably, the positive residual indicating greater than expected variance is not as high a magnitude compared to Chaco. Nevertheless, we conclude that male gene flow was present at Puye. Females, in contrast, show slightly less than expected variance, which suggests a lack of gene flow, potentially a result of less mobility than males. Based on these results, we cannot support the argument that the population living at Puye experienced a lack of genetic differentiation, as male gene flow from outside the local region negated genetic isolation.

In contrast to Chaco Canyon and Puye, both Paa-Ko and Pottery Mound show less than expected variance for both sexes. Paa-Ko was located near the Galisteo Basin and could have been somewhat isolated in comparison with the other pueblos. There is evidence for some trade into the site, particularly from the Plains, though Lambert (1954) did not conclude this as evidence for more than a long-distance trade relationship. Genetic isolation would preclude gene flow, but given its relatively short initial occupation starting in the early A.D. 1200s (Lambert, 1954), it is unclear whether genetic drift would be a factor in the lack of variance. Pottery Mound, a slightly later Pueblo IV site (A.D. 1370-1475) known for its unique kiva murals, has been hypothesized by some to represent significant western Pueblo influence based on ceramics, Sikyatki mural style, and kiva interiors (Schaafsma, 2007). Despite this influence, we find a lack of support for gene flow at this site. While this could be interpreted as a lack of support for the hypothesized social influence of the west, it could also reflect the nature of social interactions between Pottery Mound and its more distant neighbors. Rather than a migratory or intermarrying relationship, it may represent cultural borrowing. According to Hays-Gilpin and LeBlanc (2007), both are possible scenarios that may be representative of greater mobility in the Pueblo IV period, though our analysis fails to support the former.

Results from the six sites in Arizona present a more complicated picture. At most sites, with the exception of Turkey Creek, males and females differ in their residual variance patterns. Canyon

del Muerto, Point of Pines, and Carter Ranch all have greater than expected variance among females, though that signal is smaller at Canyon del Muerto in comparison with most of the other sites in this study. Grasshopper and Kinishba, in contrast, have greater than expected variance in males, though the residual at Grasshopper is also small by comparison. As a whole, these patterns may suggest differential mobility between the sexes at each of these sites.

Generally, the absolute value of the signals (greater than or less than expected variance) is not very strong at any site from Arizona, with the exceptions of males at Kinishba and females at Carter Ranch, who each have a high positive actual variance (suggesting the effect of gene flow), as well as females at Turkey Creek, who present a moderate negative variance (suggesting a lack of gene flow). A weak signal for or against gene flow could be an artifact of the populations used in the model. All are fairly closely related, resulting in similar phenotypes. If the phenotypes brought into any one group through gene flow were within the already-established range of variance for that group, a gene flow signal would be imperceptible. Likewise, if incoming phenotypes were barely beyond the established variance of the receiving group, it would result in a weak residual variance, if there was one at all.

What we do know about most of the Arizona sites is they generally occupy a temporal period marked by transition. Following the mass migration southward from the Four Corners region, specifically from the Colorado Plateau, the Mogollon Rim as well as the Phoenix and Tonto Basins undergo regional changes that are, at least partially, attributable to Puebloan migrants (Clark et al., 2019). This does not, however, mean we would immediately see a signal of gene flow – only that it is a possibility. As Mallard (Chapter Three) showed, gene flow signals can be swamped by other factors such as small population size, and Frankenberg and Konigsberg (2011) demonstrated that the time between a gene flow event and its measurement has a negative correlation to the magnitude of the residual variance. If the individuals sampled are earlier representatives of some sites, a gene flow event can be missed despite the relatively constrained temporal context.

With this in mind, several sites have been the subject of significant research in regard to whether residents of a pueblo were “local” (meaning local Mogollon populations) or “migrant” (incoming Puebloan groups, generally Kayenta), or a mix of the two residing at the same site. One site that has had a great deal of consensus among researchers about its constituent populations is Grasshopper. Evidence from architecture (Riggs, 2001), ceramics (Reid & Montgomery, 1988; Zedeño, 1994), dental non-metric morphology (McClelland, 2003), and isotopic values (Ezzo, Johnson, & Price, 1997) all have suggested the presence of at least two groups at Grasshopper. Though they could not determine from where, Ezzo and colleagues (1997) interpreted several individuals from their study of strontium isotopic values as nonlocal, and Lowell (2010) described most of the supposed migrants as female. With this largely supported presence of migrants, we expected positive residuals in the Relethford-Blangero analysis of the postcrania from Grasshopper, following results from a prior analysis (Chapter Three). However, our analysis suggests more than expected variance among males and less than expected variance among females. Given that the residuals are small for both sexes, this only provisionally supports gene flow among males, and subsequently conclusions of exogamous marriage (Reid & Whittlesey, 1997) or flight from violence (Lowell, 2007), though Baustian and colleagues (2012) did not find paleopathological evidence of greater violence against the incoming females relative

to the rest of the individuals at Grasshopper. We would argue that, given the small residuals, the results are too ambiguous to conclusively support or negate the possibility of gene flow. It is possible these results could be due to confounding effects of sampling, as individuals from all parts of the site were analyzed together, thereby potentially combining individuals from populations with different amounts of genetic isolation. It is also very possible, though, that there could be more nuance in the relationship between the original residents and the migrants than was previously thought. The presence of two groups at a site does not necessarily mean that those two groups had a mating relationship, which would result in the uncertain results indicated by this analysis.

Kinishba, which is geographically close to Grasshopper, is often analogized to larger pueblos in the region such as Grasshopper and Point of Pines (Welch, 2007). A pueblo that was initially interpreted as an Ancestral Puebloan site with early Mogollon influence (Baldwin, 1939), subsequent study has placed Kinishba as unique among Mogollon settlements. Cummings (1940) argued that the pottery of varying design influences to the north and south was evidence of trade, and Olsen (1980) stated that bone artifacts and tools were indicative of Western Puebloan traditions. More recent study (Welch, 2013) indicates that the residents of Kinishba produced ceramics using motifs and patterns found in more western groups, though this is not evidence of migration or gene flow. Nevertheless, there is circumstantial evidence for western connections among the peoples living at Kinishba during the fourteenth century. Our results indicate possible gene flow among males, but none among females. Though the magnitude of their residuals differs, Grasshopper and Kinishba do have the same pattern of sex-differentiated variance, which may suggest a regional pattern of movement.

Point of Pines and Carter Ranch present a sex-specific gene flow pattern that is opposite of Kinishba and Grasshopper pueblos. Because of disagreement in interpretations of the identity of its residents, Point of Pines is especially interesting in light of these results. While earlier studies identified Point of Pines as a clear site intrusion with cohabitating local Mogollon and nonlocal Puebloan (Kayenta) peoples (Haury, 1958; Stone, 2003), Lyons and colleagues (2018) concluded that the situation at Point of Pines was more nuanced. For example, one specific Maverick Mountain phase burned roomblock was interpreted by Haury (1958) as an incident of the locals driving out the migrant Puebloans through fire and threat of violence. Lyons and colleagues (2017), however, argued that Point of Pines was an example of successful integration of an immigrant community into a local pueblo, and later that the burning of the Maverick Mountain phase roomblock was a ritual burning performed by the Puebloan immigrants themselves to decommission the room (Lyons et al., 2018). Stone (2015) had identified this room as inhabited by locals, but more recent study (Lyons et al., 2018) suggests the Puebloan artifacts are an indication that the immigrants occupied this room. Like at Grasshopper, this is a case where we would expect to see evidence of gene flow if the incoming migrants were easily incorporated into the community as Lyons and colleagues (2017) suggested. There is greater than expected variance among females at Point of Pines, while there is less than expected variance among males, and so if there was gene flow between the two populations at Point of Pines it occurred among females only. Again, this may be the result of sampling bias, or there may be differential mobility resulting in female gene flow but not male. It is also important to consider that, as concluded in Mallard, Watson, and Auerbach (Chapter Two), small sample sizes can mask the presence of a gene flow event.

Based on ceramic analysis, Carter Ranch is another Mogollon site often presented as an example of more than one group residing in a multi-room pueblo (Longacre, 1970), though Danforth and colleagues (1994) posited a relatively small, isolated community due to high prevalence of inherited health conditions such as femoral dysplasia and Klippel-Feil syndrome. Like Point of Pines, our analysis supports gene flow among females, who have greater than expected variance, but fails to support gene flow in males. Though we cannot draw conclusions about possible differential mobility between the sexes, Longacre's (1970) initial conclusion was matrilocality at Carter Ranch; our results would support Longacre. As Carter Ranch was located in the same local region as Point of Pines (Figure 3.1), it is arguable that the former settlement provides some context by which to interpret the gene flow patterns we observe in the latter site. Were Point of Pines to have had greater female mobility, this could reflect subtle variation in mobility patterns between the sexes within the broader Mogollon Rim.

Nearby Turkey Creek has been proposed to be a vanguard population inhabited prior to and during the construction of Point of Pines (Patrick Lyons, pers. comm.). As a vanguard population at a site that lasted less than a hundred years (Johnson, 1965), or only a few generations, we would not expect to see evidence of gene flow. Indeed, that is what our analysis suggests.

Geographically apart from these locations is Canyon del Muerto, a northern Arizona locale with poorly known artifact associations (Auerbach, 2007). Like Point of Pines and Carter Ranch, females exhibit higher than expected variance and males exhibit lower than expected variance. Though these are smaller in magnitude than the residuals for the other sites with support for greater gene flow among females, the pattern nonetheless could show that the similar pattern of gene flow extends across the Western Pueblo region, with notable exceptions being Grasshopper and Kinishba.

Looking at the New Mexico and Arizona sites as a whole, a macroscopic pattern emerges. While Auerbach (2007) hypothesized a subtle separation between Puebloan peoples on either side of the Continental Divide, that hypothesis is not supported by our recent analysis. Rather, what emerges is a likely point of contact between the Western and Eastern Puebloan worlds. In the Eastern Pueblo region in New Mexico, relatively consistent patterns are present for both sexes, though they differ in whether those patterns indicate evidence for gene flow or not. Chaco Canyon has clear evidence of gene flow, which may have resulted from an early migration into the region before sites became more isolated. The six Arizona sites, in contrast, exhibit more variation in their patterns between the sexes, which may be an indication of differential mobility. Turkey Creek is the only one of these sites that clearly supports an archaeological hypothesis of the short-lived site as a vanguard population, while the greater than expected variation in females at Point of Pines could support a population influx consisting of more females than males. These differences between New Mexico and Arizona sites in regard to gene flow may be considered a point of contact between Eastern and Western Puebloan groups, supporting Kidder's (1917) assertion, and that of others, that Eastern Puebloan sites represent influence from Mesa Verde and Chaco Canyon eastward, while Western Puebloan sites were influenced primarily by Kayenta groups from the Colorado Plateau. Rather than a separation, as one might see with a mobility barrier such as the Continental Divide, we should think of this division more like a permeable frontier with differences on either side, but a demonstrated ability to cross that

frontier with trade and cultural influence (Lightfoot & Martinez, 1995). An example of this would be Pottery Mound with its influences from the Western Pueblo (Schaafsma, 2007), particularly in regions that are considered ancestral to the modern-day Hopi. Indeed, from an ethnographic perspective, Whiteley (2016) describes two major “bridges” of cultural practices and linguistic similarities uniting the Eastern and Western sides.

Influence of Limbs on Postcranial Results

The influence of the lower and upper limbs and their girdles on the postcranial Relethford-Blangero results seems to be relatively similar. However, in instances in which the aggregate sign of the residual disagrees with the residual of one of the limbs, it is almost always the upper limb and shoulder girdle group that is in disagreement. This provides some evidence that the lower limb is driving the signal more strongly than the upper limb. Given previous research that neutral evolutionary processes likely drive the evolution of femoral length (Savell et al., 2016), this is not unexpected, though it is unclear how our analyses may be influenced by this. Further studies with documented patterns of gene flow may be able to ascertain if the differences observed herein between the limbs are meaningful or artifacts of variance sampling.

Biological Distance

We performed additional analysis of Mahalanobis D^2 distances to provide a point of comparison for the quantitative genetic analyses, as biological distance is often used in bioarchaeological contexts to make conclusions regarding gene flow (Stojanowski & Schillaci, 2006). Unlike the quantitative genetic analysis, the biological distance analysis has few points of clarity. In analysis of the lower limb and pelvic girdle only, Chaco Canyon is an outlier site that does not cluster with the other sites. Given the clear signals of gene flow at this site, this makes sense. Gene flow into Chaco may have altered the trait means enough to separate it further from the other sites, effectively shadowing any other potential patterning. This pattern is not seen in the postcranial aggregate or the upper limb because the variability of the upper limb seems to swamp Chaco’s outlier status in the lower limb. While we do see Puye and Carter Ranch emerging as the outlier for females using the upper limb, in Puye’s case this isn’t evident from the quantitative genetic analysis.

Conclusion

Our analyses show that a quantitative genetic framework provides additional and critical nuance to arguments about gene flow, whether in comparison to archaeological models or biological distance analyses. While these methodological paradigms are not always in agreement, it is important to ask *why* that might be. In the case of the U.S. Southwest, archaeological relationships often have a deep and well-established history or research, but that does not mean that the relationship of populations to one another biologically follows the same pattern. The biological distances between the Western and Eastern Pueblo demonstrate a very close relationship, but the Relethford-Blangero analysis shows a difference in the patterns of gene flow that may have implications for how populations culturally moved about their landscape and whether they did or did not exchange mates extralocally.

While this research presents a broad region of variance apportionment, it is also important to remember that the Relethford-Blangero model approximates Wright's (1943) island model. It is variance from *outside* the populations in the model that provides greater than expected variance. While numerous sites are represented here, it is not exhaustive. Those sites with positive residuals supporting gene flow suggest that there is genetic influence coming from other sites, or possibly other cultures (such as the Hohokam, Mimbres, Apache, Plains nomads, etc.). Furthermore, studies that focus on a smaller region (e.g., Chapter Three) may have different results at the same site based on the same remains because of this artifact of the statistical model. Context is critical. The use of the Relethford-Blangero model in this study relies on views of the greater Pueblo world as having strong ties, whether through material culture or the exchange of mates, and the context has implications for our interpretations of how an extensive ancient social network might operate. If we see the division between Western and Eastern Puebloan peoples as more of a permeable frontier than an actual separation, it leads us towards Lightfoot and Martinez's (1995) reconceptualization that frontiers are also cultural constructs that are capable of having their own cultural interface that defies insular notions of frontiers as passive borders. Many current Southwestern archaeologists see the Puebloan world, and indeed the majority of Southwestern native history, as one of fluidity, a fact long known to their descendants (Naranjo, 1995; Bernardini, 2005, 2011).

Table 3.1. Arizona and New Mexico Sites and Contexts

	Site	N	Estimated Date	Source of Date
ARIZONA (WEST)	<i>Canyon del Muerto</i>	F: 9 M: 11	Pueblo III A.D. 1100-1225	Auerbach (2007)
	<i>Carter Ranch</i>	F: 7 M: 9	Pueblo III A.D. 1100-1225	Danforth, Cook, & Knick III (1994)
	<i>Grasshopper</i>	F: 21 M: 27	Pueblo III/IV A.D. 1275-1400	Longacre & Reid (1974)
	<i>Kinishba</i>	F: 11 M: 12	Pueblo III/IV A.D. 1200-1400	Adler & Johnson (1996)
	<i>Point of Pines</i>	F: 5 M: 4	Pueblo III/IV A.D. 1260-1450	Haury (1989)
	<i>Turkey Creek</i>	F: 4 M: 4	Pueblo III A.D. 1240-1300	Johnson (1965)
NEW MEXICO (EAST)	<i>Chaco Canyon (incl. Pueblo Bonito)</i>	F: 13 M: 5	Pueblo II A.D. 840-1150	Lekson (2006)
	<i>Paa-Ko</i>	F: 13 M: 11	Pueblo III/IV A.D. 1200-1425	Adler & Johnson (1996)
	<i>Pottery Mound</i>	F: 16 M: 24	Pueblo IV A.D. 1370-1475	Schaafsma (2007)
	<i>Puye</i>	F: 21 M: 17	Pueblo III/IV A.D. 1250-1590	Adler & Johnson (1996)

Table 3.2. Standard Postcranial Metrics* Used in Analysis

Category	Measurement	Citation
Lower Limb (& Pelvic Girdle)	Maximum Femoral Length	Martin (1928)
	Femoral Epicondylar Breadth	Martin (1928)
	Maximum Tibial Length	Martin (1928)
	Tibial Distal Articular (Tibiotalar) Surface Mediolateral Breadth	Ruff (2002)
	Maximum Iliac Blade Length	Martin (1928)
	Talus-Calcaneus Height	Raxter et al. (2006)
	Maximum Clavicular Length	Martin (1928)
Upper Limb (& Shoulder Girdle)	Maximum Humeral Length	Martin (1928)
	Maximum Humeral Epicondylar Mediolateral Breadth	Martin (1928)
	Maximum Radial Length	Martin (1928)
	Radial Head Mediolateral Diameter	Martin (1928)
	Distal Radial Articular Surface Mediolateral Breadth	Ruff (2002)

**from Auerbach (2007)*

Table 3.3. Heat Map of Residual Variances for Postcranial Data from Relethford-Blangero Analyses

Group	Sex	Postcranial Aggregate	Upper Limb	Lower Limb
Canyon del Muerto	F	0.081	0.13	-0.029
	M	-0.109	-0.16	-0.051
Carter Ranch	F	0.737	0.98	0.5
	M	-0.266	-0.23	-0.349
Grasshopper	F	-0.038	0.008	-0.075
	M	0.066	-0.044	0.187
Kinishba	F	-0.093	-0.358	0.135
	M	0.568	0.292	0.858
Point of Pines	F	0.17	0.476	-0.057
	M	-0.242	-0.179	-0.367
Turkey Creek	F	-0.302	-0.293	-0.228
	M	-0.125	0.086	-0.236
Chaco Canyon	F	0.299	0.269	0.266
	M	0.322	0.558	0.035
Paa-Ko	F	-0.414	-0.524	-0.295
	M	-0.196	-0.232	-0.223
Pottery Mound	F	-0.39	-0.441	-0.372
	M	-0.139	-0.271	0.008
Puye	F	-0.051	-0.246	0.155
	M	0.122	0.179	0.137

Key: Colors are distinguished by quartile, with the lightest indicating a low $|0-0.25|$ residual and the darkest indicating a high $|0.75+|$ residual. Positive residuals are colored shades of orange, negative residuals are colored shades of purple.



Figure 3.1. Map of sites used in analysis and important geographic features. *Red dots indicate sites from the western portion of analysis, blue dots indicate sites from the eastern portion of analysis. Image adapted from Google Earth (<https://www.google.com/earth/>).*

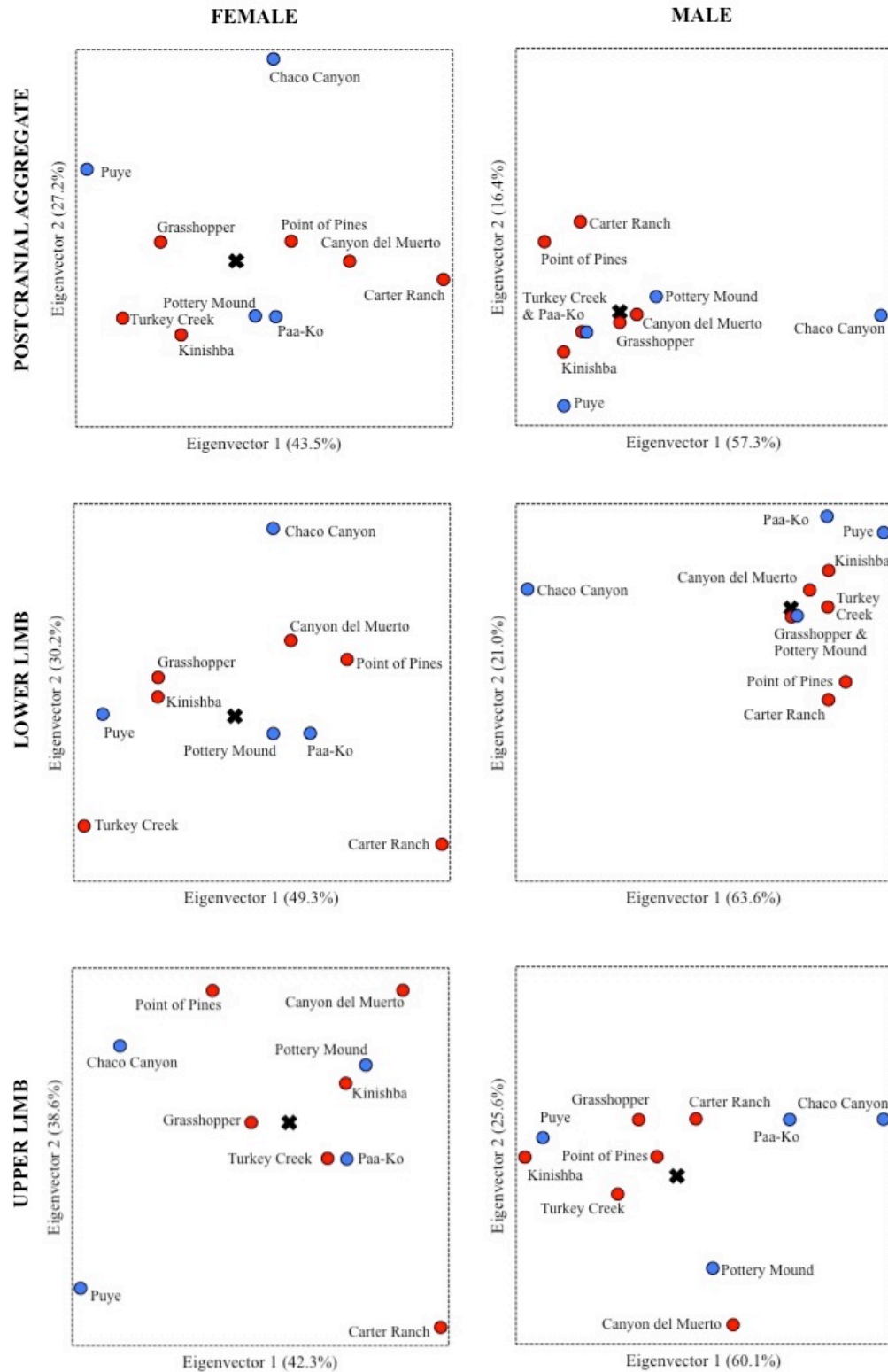


Figure 3.2. Principal coordinates plots of Southwestern groups by sex and limb group.
 Key: 'x' denotes centroid, circle denotes site; red sites are located in Arizona, blue sites are located in New Mexico.

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Chapter 5
DISCUSSION

I. Returning to the Questions

Together, Chapters Two through Four provide some insight into the potential mating relationships of groups of people from the U.S. Southwest and Northwest Mexico. They also discuss the methodologies researchers use to estimate past gene flow patterns and in turn infer past human movements. Here I discuss both of these points, as well as the ethical considerations surrounding the analysis of Native American remains, non-destructive or otherwise.

Chapter One raised several major research questions that, with varying degrees of success, have been addressed by this dissertation. I return to them below:

1. *Does the inference of gene flow differ between a quantitative genetic study and a biodistance study of the same skeletal material? Are differences informative? For example, quantitative genetic estimations may support gene flow for one site in a region, so should it be expected for that site to have greater biodistance from other sites included in the model?*

Based on the results from Chapters Three and Four, there are interpretive differences between using quantitative genetic and biodistance analysis with the same skeletal material. For example, some biodistance analyses in Chapter Four resulted in a larger distance between Chaco Canyon and all other sites than any other site from each other, suggesting a possible gene flow event. Meanwhile, Turkey Creek has a larger distance from the centroid than Grasshopper does, which would suggest that Turkey Creek may have a stronger gene flow signal. Yet that is the opposite of what the Relethford-Blangero results suggest, as they fail to support a gene flow event. This difference may be informative because it may indicate that the residents of Turkey Creek were a small and relatively isolated group for the pueblo's short lifespan, leaving them without gene flow and more susceptible to small occurrences of genetic drift. It does not appear from any of the studies that support for gene flow from the quantitative genetic model always corresponds to a greater biodistance from the other sites included in the model.

2. *Are important nuances about group interactions captured using one biological method that are not inferable from the other, or do both methods need to be used in conjunction to achieve better resolution about gene flow?*

Neither method is without utility. Biodistance is useful for demonstrating which populations are more morphologically distinct, whether as a result of genetic drift, gene flow, or differences in ancestry. Chaco Canyon falls into a more morphologically distinct category, as it does not always cluster with other groups in Chapter Four. This helps researchers identify or support potential locations that may have had complex mating relationships compared to other sites in the model. The quantitative genetic method, meanwhile, gives researchers less insight into morphological distinctiveness in the population mean, but more insight into whether a population has undergone a major consequence of the process of gene flow as it pertains to trait variance. Chapter Three demonstrates this with poorly differentiating biological distances but some instances of greater or less than expected variance indicating a gene flow event (or lack thereof). Both methods are useful and provide different elements of the overall picture of possible gene flow – therefore, using them in conjunction gives researchers better resolution. This also speaks

to the need to combine approaches not just between disciplines, but within them.

3. *Do different regions of the skeleton (e.g., cranium versus dentition or postcrania) provide consistent evidence for gene flow and for biodistances?*

As demonstrated in Chapter Three, these different skeletal regions of the skeleton sometimes provide mixed results using either method. Postcranial (limb and limb girdle) results are the most dissimilar to the other two regions (cranial and dental). This may be a consequence of the different evolutionary forces affecting each. Though the study looked for consistency between skeletal groups to add justification for using any one of them for analysis, the results are not similar enough between any two to suggest that the third lacks utility. Because none of the regions tested can be considered a control group, it is not currently possible to suggest one skeletal region over another.

4. *How does each method compare to hypotheses of migration developed from the context of material culture?*

This is the most difficult question to address, in that the answer cannot, by nature, be simple. Gene flow and migration are related but not equivalent processes, and material culture and skeletal material will inherently answer different questions about each. In the sense that both categories have been applied to the same problems, their ability to tell consistent stories is mixed. This is considered further below.

There are inevitable limitations to these analyses, including issues with sampling and the nature of the models. Though they have been controlled for as much as possible, there are concerns that should be considered in any future analyses; those are also discussed below.

II. Archaeological Conclusions

Though the geographic and temporal context differs slightly between each of the three manuscripts, each provides important insight into the overall archaeological context of gene flow (and, to a certain extent, migration) in the region spanning what is today Sonora, Mexico, and Arizona and New Mexico in the United States. Broadly, the biological distances among these sites does not parallel geographic distances, which reflects potential differences in cultural structure and relatedness within the overall region across time. Likewise, though dependent on the context of which sites are included in each study, the evidence for gene flow into sites often matches expectations set using material culture for the archaeological model, though there are notable exceptions (e.g., Point of Pines in Chapters Three and Four) that bring nuances to those archaeological models that material culture alone does not provide. Thus, by combining sources of evidence, a testable model for gene flow and population relatedness emerges.

In Chapter Two, the earliest sites, La Playa and Las Capas, which date to the San Pedro phase of the Early Agricultural Period (c. 1600-800 B.C.), present greater than expected variance compared to later sites. As discussed in that study, this may suggest there was an early pulse of gene flow that stopped contributing new variance to these populations as time passed, subsequently constraining the change in variance, or the gene flow pulse decreased or was

counteracted by enough genetic drift to cease the increase in variance by the next phase at La Playa (Cienega phase, c. 800 B.C.-A.D. 50). Byrd (2019) concluded from her craniometric analysis that this time period experienced gene flow movement from the Sonoran Desert in a northeastern direction, though it cannot be concluded from the study here (Chapter Two) that gene flow was directional.

Nevertheless, this suggests that gene flow was more restricted both more recently (spanning between A.D. 840-1590) among Sonoran settlements, as well as among settlements to the north. It is notable that the single Sonoran site from the later temporal range, El Cementerio (c. A.D. 1000-1521, the Postclassic period), has slightly higher than expected variance, supporting the presence of a gene flow event (Chapter Two). Given that this is the southernmost site from these analyses, it is likely that the external gene flow detected here comes from elsewhere in Mexico. This would support hypotheses of Mesoamerican influence on the site, as noted by Watson & García (2016). This is emphasized when contrasted with the Mogollon sites used in Chapter Two—Grasshopper, Point of Pines, and Turkey Creek pueblos. Analyses of these sites within their regional context (Chapter Three) and with respect to New Mexican settlements (Chapter Four) collectively *do* suggest gene flow occurred in these sites, but that the scale of that gene flow, perhaps, was not as sizable as the evidence for gene flow into sites like La Playa and Las Capas.

The remaining sites that I analyzed in this dissertation are located in the Mogollon Rim and Canyon de Chelly regions of Arizona, as well as the north- and central-west regions of New Mexico. While Chapter Three looks to a more constrained context in the Mogollon Rim region, Chapter Four addresses a broader geographic and temporal context. Together, there is some agreement on results of the models despite parameter differences.

The earliest site, Chaco Canyon (including Pueblo Bonito), shows greater than expected variance for both sexes. Chaco has long been considered a major political and cultural center, and more importantly to this study, the center of a significant regional social network (e.g., Wilcox, 1996). The presence of external gene flow at the site supports that conclusion, as does the greater biodistance of Chaco Canyon's inhabitants compared with all of the other sites. As a major cultural and possible ritual center (Lekson, 1999), Chaco may have attracted a variety of peoples from a broad geographic range, which would have both given more opportunity for gene flow while also increasing the average biological distance of the people there from other sites in the region. It also implies that outlying sites may have remained more isolated with respect to those located within Chaco Canyon.

Following the decrease in Chaco's prominence (and population size), the models begin to disagree with each other due to their incongruent parameters. On a regional level, sites dating only to Pueblo III (c. A.D. 1150-1350), including Turkey Creek, Slade Ruin, and Carter Ranch, fail to show any regional uniformity. Carter Ranch (Chapter Four), shows greater than expected variance only for females, while Slade Ruin generally has less than expected variance for both sexes (excepting females using dental data, Chapter Three). Turkey Creek, hypothesized to be a vanguard site prior to the construction of Point of Pines, has greater than expected variance using dental and cranial data (Chapter Three) but either expected or less than expected variance using

postcranial data (Chapters Three and Four are in agreement here). It is possible that, regionally, the Pueblo III period is marked by localized traditions of marriage rather than regional trends.

The remaining sites either overlap both the Pueblo III and Pueblo IV (c. 1350-1450) periods or are dated within Pueblo IV. The sites around the Mogollon Rim, including Point of Pines, Grasshopper, and Kinishba, appear in Chapters Three and Four, though the results are sometimes difficult to compare. Grasshopper and Point of Pines are both hypothesized to be large aggregated pueblos. In Chapter Two, the analysis suggests Grasshopper had much less than expected variance, while Chapter Three shows greater than expected variance and Chapter Four generally hovers around zero (neither greater nor less than). As will be discussed further below, this is likely an artifact of the models, and one that could be particularly illuminating. Grasshopper may have been a location that experienced gene flow in agreement with migration hypotheses gleaned from the material culture, but the differing pools of variance in each model result in a different picture.

Point of Pines is similarly difficult to interpret from these models. The site is aggregated with Turkey Creek in Chapter Two because of close geography as well as overlapping temporal ranges (particularly in light of the much larger temporal range of that model as a whole), so it is not comparable to Chapters Three and Four except to suggest that the lack of expected variance at Point of Pines (Chapter Three) or Turkey Creek (Chapter Four) could be driving the aggregate signal in Chapter Two. Chapter Three largely suggests less than expected variance at Point of Pines (with exceptions for female cranial data or male dental data), while Chapter Four is split between the sexes (with greater than expected variance among females, and less than expected variance among males). Like Grasshopper, this could be an indication that the external gene flow detected in any given study is from a population present in one study but not another. For example, in Chapter Four's model, gene flow would no longer be external and would instead be part of the overall pool of variance, making it undetectable in males. Thus, the Relethford-Blangero results in Chapters Three and Four together may be revealing nuances about population interactions among these groups that would otherwise not be present using biodistance alone.

As discussed in Chapter Three, however, and reinforced in Chapter Four, broad patterns do emerge. Grasshopper and Kinishba have long been argued to show evidence for cultural interaction with groups beyond the local region, based on material culture and settlement architecture, a model that is supported by the Relethford-Blangero analysis. Like these settlements, Point of Pines was briefly occupied by populations moving from the Colorado Plateau, but unlike them there is no evidence supporting gene flow from them, though as I noted in Chapter Three, it is possible that sample bias could be driving these results. Also, while there is some lack of clarity in the analytical results, Turkey Creek has broad evidence for gene flow from outside the region (Chapter Three), perhaps from pueblos to the east, as evidenced by the shift in evidence for gene flow in Chapter Four, where these eastern sites are included.

In Chapter Four, there is an interesting split in the gene flow trends for broadly defined Western and Eastern Pueblo groups. While to the east, gene flow is largely not supported (with the exception of Chaco Canyon), to the west it is often supported in one sex. It is possible that groups to the west are drawing mates from an external gene pool (e.g., the Hohokam) in a more localized manner, while groups to the east are not exchanging mates outside the region (e.g., the

Apache or nomadic groups from the Plains). We may be seeing some evidence of different cultural practices in mate exchange by the time groups begin migrating from the Colorado Plateau and Mesa Verde regions.

Of course, these results are dependent on the assumptions of the Relethford-Blangero approach, and the nature of the samples used in each study to construct the variance-covariance relationship matrix that underlies the analysis. Furthermore, sampling biases, as well as which parts of the skeleton are used in analyses, all account for variation in the analyses, some of which may ultimately be statistical noise (in the case of sampling) but some of which is highly consequential (in the case of which measurements are used, or representation of all groups within a site). I consider these in more detail below.

III. Quantitative Genetic Modeling, Biological Distance, and Understanding Gene Flow

As we see from the analyses in Chapters Three and Four, using a quantitative genetic model like Relethford-Blangero compliments the data we can recover from more traditional models of biological distance, in this case Mahalanobis' D^2 . The biodistance analysis reinforces our understanding that these groups are closely related to each other. This is particularly clear in some of the principal coordinate analyses of Chapter Four, where close clustering occurs because of low biological distances. F_{st} values from the R-matrices in Chapter Three, meanwhile, are generally low, suggesting low genetic differentiation when all groups in the model are considered. Interpretations of biodistance are useful compliments to the Relethford-Blangero method in other ways, as well. For instance, in Chapter Four, Chaco Canyon has a greater than expected variance, supporting the likely presence of a gene flow event, and that analysis is further supported by Chaco's comparatively large biodistance (at least among males) from the other nine sites included in that model. Additionally, Point of Pines and Turkey Creek do not have a small biodistance compared to other sites in the model in Chapter Three, despite being so geographically close. This relationship is supported by the different patterns of gene flow for the two sites that we see from the Relethford-Blangero analysis. The combination of these methods provides us with interesting nuance that would otherwise be lost from using only one method. However, we must acknowledge that they are not telling us the same information. While a closer biodistance may fit the narrative of a gene flow event, it makes for a much stronger argument to use the Relethford-Blangero method as additional support. This is because, as I reviewed in Chapter One, small biodistances could be the product of multiple biological causes, including recent shared ancestry, convergence, or gene flow.

The three studies I conduct in this dissertation make it clear that the context of the model is critical when studying gene flow. There are variances among some individual sites in each of the three analyses. Grasshopper, for example, has a less than expected variance in the first analysis when the Sonoran sites are included in the model, implying a lack of gene flow. In the second analysis that included five sites in the Mogollon Rim region, however, the site has a greater than expected variance for all three skeletal regions, though the magnitude of the figure is often low. This would suggest a possible gene flow event, which also corresponds to hypotheses based on the archaeological data (e.g., Riggs, 2001). The final analysis, which included groups from across Arizona and New Mexico, results in variances close to zero, which does not support a gene flow event. It is important to realize that these differing results do not point to a lack of

meaning in this type of analysis. Rather, it demonstrates that comparing studies with different parameters can be complicated. It could be that phenotypes like those in New Mexico were the ones creating greater than expected variance at Grasshopper. If those phenotypes weren't represented by the five Arizona sites in Chapter Three, one would see greater than expected variance in that chapter, but not in Chapter Four when the New Mexico individuals were included. Different populations, trait metrics, heritability, and population size may all cause results to vary (some more than others). The first and third studies introduce a potentially wider range of variation to their respective models than the second study does, therefore the meaning of "greater or less than expected variance" takes on a different meaning. It is possible that all three models are showing that Grasshopper had gene flow from groups more closely related to the Eastern Pueblo, and potentially some gene flow from groups to the south (e.g., the Hohokam).

Likewise, though Relethford & Blangero (1990) state that having specific heritability values will not drastically alter the results of the model, we do know that changing the heritability value will yield dissimilar results. Even so, despite differences in model parameters, the results of the Relethford-Blangero analyses do have considerable overlap in interpretation when compared to the archaeological models (particularly the second and third studies), despite the potential for error introduced when changing the parameters. Comparing models responsibly is key; without understanding differences in context that may alter the results of either the quantitative genetic or biodistance models, interpretation of the results will likely be tenuous.

Other limitations of the models are difficult, if not impossible, to address. Cemetery composition, for instance, may result in the overrepresentation of familial relatives that would affect both types of analysis. In biodistance studies, the phenotypic mean might be pulled toward that of the family, and in a Relethford-Blangero analysis the variation within the group may be limited due to close relations. Factoring in this issue, though, is nearly impossible in bioarchaeology without the aid of cemetery records or aDNA. Furthermore, it is also difficult without detailed writing records to ascertain how representative a mortuary group is in relation to what was the living population (Wood, Milner, Harpending, & Weiss, 1992). With small samples sizes, this is even more of a problem, particularly when studying groups and populations. The individuals used in these models are less likely to be representative of the group's range of variation when the sample size is lower. These are limitations that must be acknowledged, but cannot ultimately be addressed using currently available methods.

IV. Multiple Lines of Evidence and Their Realities

Because researchers often find themselves in search of multiple lines of evidence in gene flow and migration research (Cabana, 2011), it is important for researchers to understand what different data types and methods are capable of showing, as described above. Biodistance methods, crucially, are not designed to demonstrate gene flow. Rather, they are most useful in conjunction with methods like Relethford-Blangero, or for studies of population structure. Common ancestry can be a major confounding factor to biodistance studies, so that analysis is also more useful in situations with a broader range of trait variance. Material culture, too, has its own analogous situations. For example, artifact similarity is not strictly evidence for migration or site intrusion; it can also be the result of trade or mimicry. The patterns we see from both of these examples do not demonstrate the process. This is a limitation to the Relethford-Blangero method

as well, but this method is based in the signature of an evolutionary process: gene flow as the source of increased variance. In contrast, biodistance compares mean similarities regardless of their source. All of these nuances are important elements to interpreting the results of these models, and it is necessary for non-practitioners as well as practitioners to realize that misinterpretation is possible with only a superficial overview of any one source (Hakenbeck, 2008; Horsburgh, 2015).

Most lines of evidence are not congruent, nor should they be; they tell us different information about different aspects of population interaction and migration. But sometimes they do align in ways that are useful. In Chapter Three, which arguably used the model most like that described by Relethford & Blangero (1990), the interpretations of material culture and the Relethford-Blangero analysis of all three skeletal regions are complementary for Grasshopper. This site, among the five, is probably the least contentious in interpretation among archaeologists, with most evidence suggesting the presence of migrants at the site. While these two types of evidence do not model the same type of interaction, putting them together results in a more complex picture of what that interaction looked like in the past.

Considering multiple lines of evidence within the skeleton, however, is more difficult to reconcile. Though there is considerable overlap in results between regions (cranial, dental, and postcranial) in Chapter Three, the lack of concordance is sometimes concerning. With the caveat that Kinishba could not be added to the model of dental dimensions, dental data were generally not varied enough to provide insight into possible extralocal gene flow among these closely related populations (contra Chapter Two, this volume). While cranial and postcranial data resulted in similar conclusions, there were some important differences. Both sexes at Kinishba, for example, had completely opposite results when cranial versus postcranial data were considered. This may be an artifact of sampling, as Kinishba had one of the lowest sample sizes in the model. Unfortunately, this is one of the realities of bioarchaeological research: sample sizes are fixed. It could also be related to the different forces acting upon different parts of the skeleton, which is beyond the scope of this dissertation, or the constraints on variation for certain skeletal elements (e.g., teeth have a small range of variation). At this time, I cannot recommend one region of the skeleton over another. The contextual constraints (sample size, preservation, and fragmentation) should be considered on a case-by-case basis. Dental metrics, for example, are often chosen to increase sample size because teeth preserve better than bones and are less likely to have been broken in the recovery process. If possible, it would be best to do metric analysis on more than one region to obtain a broader picture of how the process of gene flow might be affecting a population, but that is not always possible based on research time and budget constraints.

Cabana & Clark (2011) advocate moving toward a more robust framework for understanding past migration. If multiple lines of evidence are to be employed in this framework, there remains considerable work to do. This dissertation takes a closer look at one (albeit important) element of studying migration: gene flow. By addressing ambiguities in the toolkit for understanding human remains and what they can tell us about gene flow, it has become clear that both gene flow and migration are so nuanced that biodistance alone is insufficient as a method to arrive at a complex picture. Therefore, I recommend the use of *both* biodistance methodology (in the form of Mahalanobis' D^2) and quantitative genetic methodology (Relethford-Blangero) to address

questions of both phenotypic mean and variance using skeletal material, which is in agreement with Byrd's (2019) recommendation using craniometric data.

V. Post-NAGPRA Research

One of the most important discussions to emerge from this dissertation has been the ethical consideration of performing non-destructive research on Native American remains from museum collections. Over the course of four years, the length of time I have performed this research (including data collection, post-processing, and writing), the general dialogue surrounding traditional biological anthropological work has changed. To be clear, concerns regarding destructive analysis are not new (Kaestle & Horsburgh, 2002). For example, we may look to negative response from some academics (e.g., Cortez, Bolnick, Nicholas, Bardill, & Colwell, 2021) to the institutionally but not tribally approved harvesting of bone samples for genomic analysis pertaining to matrilineality of Pueblo Bonito's Ancestral Puebloan residents (Kennett et al., 2017), or Turner & Nelson's (2005) overview of the use and keeping of blood samples from South American Yanomami individuals against the wishes of their descendants. However, it is the dialogue surrounding non-destructive analysis, such as metric data (this volume, Chapters Two, Three, and Four), which is currently seeing a shift in academic opinion.

Though the effects of legislation related to indigenous cultural patrimony have not been felt uniformly across the United States, or even subdisciplines of anthropology, their impacts have been substantial. The National Historic Preservation Act of 1966 (54 U.S.C. §§ 300101-307108), for instance, established CRMs (cultural resource management firms and organizations) to manage archaeological sites, and a 1992 amendment established Tribal Historic Preservation Offices (THPOs). The 1990 Native American Graves Protection and Repatriation Act (NAGPRA; 25 U.S.C. §§ 3001-3013), established guidelines for the repatriation of human remains, associated funerary objects, and objects of cultural patrimony. An optimistic view of NAGPRA in particular, such as that of Silliman & Ferguson (2010), would point to an increasing climate of consultation and collaboration with native peoples in North America as a major outcome of the law's passing, in addition to the estimated 67,000 ancestral remains already returned to federally recognized tribes (National Park Service, 2020; Nash & Colwell, 2020). This is not necessarily the perspective of representatives of the descendant communities, who must simultaneously meet (often difficult) legal requirements while processing complicated feelings about their ancestors and cultural artifacts, and how they arrived on museum shelves (Kuwanwisiwma, 2018). Who can make claims based on NAGPRA, too, is a complicated matter, requiring that claimants be federally recognized tribes or lineal descendants, which Liebmann (2008) critiques as both difficult and essentialist, and others (Kirsch, 2011; Reardon & TallBear, 2012; Van Dyke, 2020) argue acts as a reinforcement of colonial power and hierarchy.

With greater attention being paid to (or at the very least, published on) Native American perspectives on NAGPRA, archaeology, and academia, pushes to decolonize how we construct and deconstruct narratives focused on Native American history are seeing greater support (Echo-Hawk & Zimmerman, 2006), though that support does not always translate to institutional change, new policy, or shifts in public opinion (Echo-Hawk & Zimmerman, 2006; Kimmerer, 2013; Simpson, 2014). Academic opinion, however, is another matter. Legally, non-destructive analyses of Native American human remains are permissible as long as they are also allowed by

the institution (i.e., museum) and not currently under NAGPRA claim. This dissertation was started and completed with this in mind. However, a critical question remains: though legal, is non-destructive analysis of human remains without the input or permission of likely descendant groups ethically sound? If this question is applied to Native American remains, what other remains housed within museum collections fall under this query?

With regard to the preceding chapters, it has become clear that despite my intentions, I did not do my due diligence in considering multiple perspectives regarding law versus ethics. Under the law, the non-destructive analysis of these studies was acceptable. Even now, this type of analysis is at an ethical crossroads among anthropologists. But it is the Indigenous perspective that is often either missing or is not given the same weight as the legal or institutional perspective (Kirsch, 2011; Kuwanwisiwma, 2018). Though many anthropologists (e.g., Watkins, 2004; Silliman & Ferguson, 2010; Adams, 2018) have encouraged collaboration in Indigenous research regarding archaeological excavations and the analysis of aDNA, in practice we are still struggling to determine what that looks like when it comes to museum collections and archival data.

As anthropologists, we have a responsibility to scientific method but also to the descendants of those in the past whom we study. When it comes to our research, it is important to ask not just, “Will my methods harm the remains, and therefore the descendant communities?” but also more simply, “Will my research harm the descendant communities?” To answer the latter question requires stronger communication with those communities, including what questions they are interested in asking. For instance, Kuwanwisiwma (2018) discusses his tribe’s (Hopi) interest in questions of diet because of their relationship to the revitalization of modern foodways. Dwight Honyouti (Hopi) (pers. comm., 2019), THPO for the Tohono O’odham Nation in southern Arizona, asserts that he and his tribal colleagues want to know from anthropologists what they, the tribe, will get out of that research. Topics assisting in repatriation and reburial of human remains and items of cultural patrimony (Kuwanwisiwma, 2018; Byrd, 2019) are important in documentation for NAGPRA. In studying Native American histories, we need to ask these questions at the beginning, not partway through the project (or dissertation). Furthermore, as anthropologists we should not be dismissing indigenous ways of understanding their own histories and their world. For example, concepts of land and boundaries are more fluid among Hopi individuals than they are white scholars, and are even fluid between Hopi groups (Bernardini, 2005; Hedquist, Hopkins, Koyiyumptewa, Lomayestewa, & Ferguson, 2018). These nuances can help construct, rather than simply inform, our research. To truly decolonize my own research, I should have performed all of these things at the outset.

VI. Forward with Archival Data

Now that NAGPRA has been around for three decades, it has become apparent that there are still some questions that are not easily answered when it comes to ethical concerns about indigenous remains and cultural artifacts. One issue that has not been significantly addressed is the use of archival data from collections that have been repatriated. The data from several groups in this dissertation are archival and either repatriated and reburied (e.g., Grasshopper and Kinishba) or are now under claim (e.g., Point of Pines and Pottery Mound). This is a crossroads anthropologists will need to address over the next several years: now that the remains are

returned, who owns the data? Legally, it is almost always the researcher and/or institution that once housed the repatriated remains or items. But ethically, what do we as a discipline do with all those measurements, scores, drawings, and descriptions? What takes primacy, their scientific value or the wishes of the descendant communities? Samples taken from living humans are now covered by consent forms mandated by institutional review boards (IRBs), especially now that misuses such as the storing of the Yanomami blood samples have come to light and the idea of “renewed consent” is a standard consideration (Turner, Wagner, & Cabana, 2018). But often the archival data generated from studies that are later repatriated are not discussed during the repatriation process.

In the same way that donors and descendant communities are required to be informed about the status of biospecimens, we need to make greater effort as researchers to provide clarity on the process of repatriation to descendant communities. Specifically, the question of who claims the archival data needs to be addressed up front. This is especially critical in an era where data sharing is becoming easier, more common, and often required by academic granting organizations and peer-reviewed journals (Turner & Mulligan, 2019). NAGPRA was passed into law more than three decades ago, and inevitably there are things that were not considered in the repatriation process that was established – one of those things is intellectual property. As researchers, we can at least open up that dialogue in order to make our processes and motivations as transparent as possible and establish a greater relationship of trust with descendant communities.

VII. Conclusions

Though ambiguities remain in the interpretation of gene flow from human skeletal remains, there are some important conclusions to be derived from this dissertation. Biodistance and quantitative genetic analysis are best used together, as each provides an important element of the overall picture of population interaction from a biological perspective. Together, they make a stronger comparison to hypotheses based on material culture. The U.S. Southwest and Northwest Mexico made for a useful context due to the robusticity of the archaeological models. However, from the standpoint of the skeletal data, further study is necessary from archaeological contexts using populations that have greater phenotypic variation. This might help with the comparison of the three skeletal regions and determining whether differences are artifacts of the model or actual meaningful diversions. While a context with strong archaeological hypotheses and phenotypic variation is ideal, such contexts may not exist in large enough sample sizes to do population analyses. The U.S. Southwest has larger numbers of individuals at numerous sites, but not every site had a large number of *usable* individuals. Furthermore, as noted above, the ethics of even non-destructive skeletal research need to be more thoughtfully considered by myself and future researchers. This factor is just as important as the context of the analysis.

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Vita

Angela Mallard is originally from Mesa, Arizona, and received her undergraduate degree in Anthropology and History from the University of Arizona in 2008. She specialized in Southwestern zooarchaeology and worked as a curatorial assistant at the Arizona State Museum. Following graduation, she completed an internship at the Illinois State Museum and then earned her master's degree in Anthropology at New York University in 2011, participating in the Human Skeletal Biology program. While in New York, she was also an intern at the American Museum of Natural History for the Biological Anthropology division. Before beginning her doctoral work, she moved back to Arizona to teach biological anthropology for Maricopa Community Colleges. In 2015, she moved to Knoxville, Tennessee to begin her PhD in Anthropology at the University of Tennessee. While pursuing her PhD, she also taught Human Anatomy at UT as well as various courses on human evolution for the Governor's School of North Carolina.