Late Chachapoya Population Structure Prior to Inka Conquest

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ABSTRACT   Archaeological and ethnohistorical documents suggest that the Chachapoya region was inhabited by a number of distinct sociopolitical groups that only united in the face of their common enemy, the Inka. The purpose of this research is to quantify the amount of internal genetic differentiation and levels of extraregional gene flow during the Late Chachapoya period, in order to obtain a better understanding of the genetic relationship between these presumed ethnic groups. Craniometric data were collected from three Late Chachapoya samples (Laguna Huayabamba, Kuelap, and Laguna de los Cóndores), in order to understand the genetic relationships between the groups and facilitate our understanding of Late Chachapoya population structure. Genetic differentiation among these series ranged from 0.047 (heritability = 1.0) to 0.090 (heritability = 0.55). The Relethford-Blangero residuals indicate that the Laguna Huayabamba and Laguna de los Cóndores populations were receiving greater than average external gene flow, while Kuelap was receiving less than average external gene flow. The correspondence between biological and archaeological data in the investigation of prehistoric ethnic identity is discussed. Am J Phys Anthropol 131:334–342, 2006.   © 2006 Wiley-Liss, Inc.

The relationship between culture and biology is a fundamental issue in physical anthropology, one that has stirred discussion essentially since the inception of the field. A consideration for both the cultural and biological facets of group, and in particular ethnic, membership should drive our research. While sometimes considered to be more objective (Jones, 1997), material culture is not isomorphic with group identity. In an archaeological context, ethnic group designations are often based on material culture, including textiles (Heckman, 2005; Rodman, 1992; Rodman and Lopez, 2005), domestic architecture (Aldenderfer and Stanish, 1993; Bawden, 1993; Hegmon, 1994; Stanish, 1989; Vaughn, 2005), ceramics (Janusek, 2005; MacEachern, 1992; Sterner, 1992), and mortuary contexts (DeCorse, 1989; Larsson, 1989). There is, however, no trait-list that will unequivocally delimit one group from another, one identity from another. While these material manifestations are indeed powerful markers of group difference, they are but a single aspect of group identity. On the other hand, studies that purport to assign ethnic affiliation solely through biological data fail to account for the situational and dynamic nature of identity. Group identity is not dictated, nor sufficiently captured, by examining trait or gene frequencies or the characterization of cranial morphology.

More recently, studies have considered both cultural and biological aspects of group identity. Biological data in the form of bone chemistry (Knudson et al., 2004), genetically controlled skeletal or dental traits (Blom et al., 1998; Lozada Cerna, 1998; Lozada and Buikstra, 2002; Sutter, 2000; Sutter and Mertz, 2004; Steadman, 1998, 2001; Stojanowski, 2005), and cranial modification (Blom et al., 1998; Hoshower et al., 1995, Torres-Rouff, 2003) were articulated with archaeological artifacts to investigate prehistoric ethnic membership. The current research hopes to add to this growing literature, in which a dynamic articulation between culture and biology is emphasized. In this study, population genetic models are used to quantify and interpret genetic differentiation and levels of gene flow in the Chachapoya region of northern Peru. The study focuses on the Late Chachapoya (AD 1100–1470) period.

Current interpretation of the archaeological record suggests that the Late Chachapoya period was a time of increased population growth, increased settlement density, and monument construction throughout the region (Schjellerup, 1997). Given the relative paucity of archaeological data, it is difficult to accurately describe the sociopolitical organization of the region, but it is perhaps best characterized as a collection of semi-independent groups that united only when faced with a common adversary (Schjellerup, 1997, p. 67). The Chachapoya appear to have shared similar geometric architectural designs, symbolic language, and ceramic traditions (Lerche, 1995; Schjellerup, 1997), but despite these regionwide commonalities in material culture, there seem to have been significant levels of intraregional differentiation. Espinoza Soriano (1967) stated that as many as 22 separate ethnic groups inhabited the region prior to Inka conquest, though his
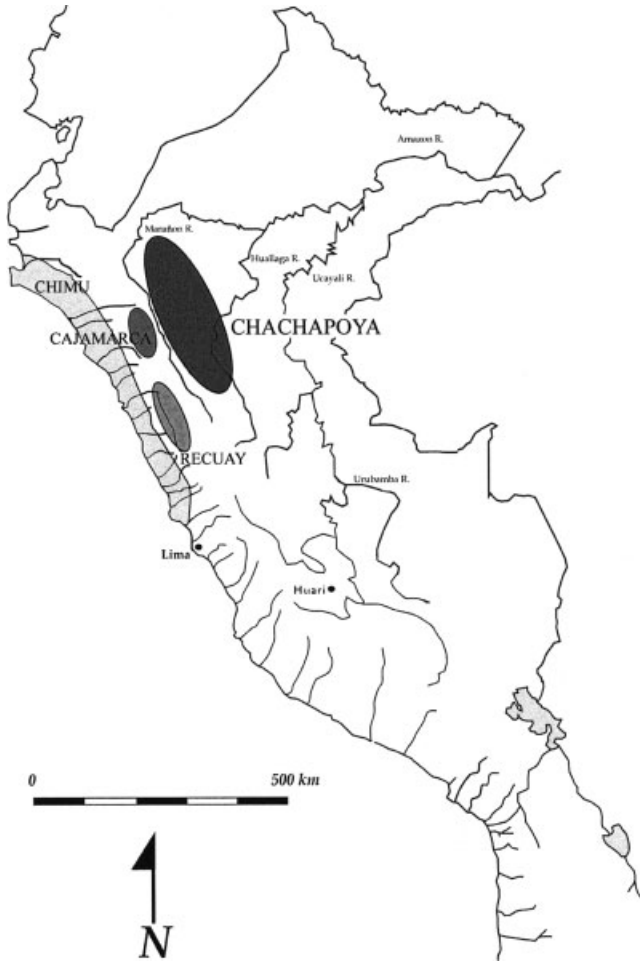
Fig. 1. Map of Chachapoya region, with sites where skeletal samples examined in this research were recovered.

TABLE 1. Age/sex distribution for Late Chachapoya skeletal samples

	0–19	20–34	35–50	50+ years	"Adult"	Total
Laguna de los Cóndores (n = 160)						
Male	0	16	31	13	0	60
Female	0	36	12	8	0	56
Indeterminate	9	11	9	5	10	44
Keulap (n = 97)						
Male	0	14	20	7	1	42
Female	0	9	6	10	2	27
Indeterminate	19	1	3	4	1	28
Laguna Huayabamba (n = 25)						
Male	0	2	6	2	0	10
Female	0	2	1	3	0	6
Indeterminate	8	1	0	0	0	0

of the available archaeologically recovered and documented collections for this time period.

Kuelap

Kuelap is situated in the Province of Luya in the Departmento Amazonas, approximately 35 km south of the modern departmental capital of Chachapoyas (Fig. 1). Narváez Vargas (1996a) placed the major construction phase of Kuelap in the Late Intermediate period, between AD 800–1200. Further, he concluded that Kuelap was affiliated with the Chillaos ethnic group, the most important group in the area before the arrival of the Inka (Narváez Vargas, 1987, 1996a).

Collected during the course of an archaeological survey of the site by Reichlen and Reichlen, (1950), the skeletal sample dates to three cultural phases: Kuelap (AD 1000–1200), Chipurik (AD 1200–1350), and Revash (AD 1350–ca. 1470). Unfortunately, Kuelap and the skeletal material that Reichlen and Reichlen (1950) collected do not figure prominently in their article. No field notes or descriptions of burial context are available. The skeletal material is in excellent condition (Table 1), and is distributed among the three times periods as follows: Kuelap, n = 6; Chipurik, n = 1; and Revash, n = 97. Only material from the Revash cultural period was included in this analysis.

Laguna Huayabamba

The second Late Chachapoya site is near Laguna Huayabamba (Fig. 2; Muscutt et al., 1994; Muscutt, 1998). The site consists of two components: 1) a residential sector set on the south side of Laguna Huayabamba, on the summit of a north-facing slope; and 2) a funerary component on the north side of the lake. The remains of approximately 48 individuals, present as both intact mummy bundles and disarticulated skeletal remains, were recovered from a single tomb from the funerary component. Radiocarbon analysis of textile fibers collected from the tomb yielded a date of ca. AD 1000–1150 (Muscutt, 2003), placing it well before the ca. AD 1472 Inka conquest. Of those 48 individuals, I was able to generate craniometric data from only 25 individuals (Table 1).

Laguna de los Cóndores

Laguna de los Cóndores is located in the northwestern corner of the Department of San Martín in the Province of Huallaga (Fig. 2). The archaeological site consists of

investigation was based on ethnohistorical documents and likely does not accurately reflect pre-Inka sociopolitical organization in Chachapoya. Archaeologically, two of the skeletal samples examined in this research, Laguna de los Cóndores and Kuelap, were attributed to the Chilcos (von Hagen, 2002) and Chillaos (Narváez Vargas, 1987, 1996a) ethnic groups, respectively. Intraregional social differentiation may have manifested in a north-south division of architectural design motifs (Lerche, 1995) and mortuary structures (von Hagen, 2002). Schjellerup (1997) suggested that mortuary custom may have been one way in which subgroup level identities were signaled. These latter factors seem to indicate that, despite material similarities between the groups that inhabited the region, there may have existed internal differentiation (Schjellerup, 1997). Thus the purpose of this study is twofold: 1) to understand Late Chachapoya population structure, and 2) to articulate the available archaeological data and results from this examination of regional phenotypic variance to further our understanding of the relationship between biology and culture.

MATERIALS AND METHODS

Craniometric data were collected from three Late Chachapoya skeletal series. These three series represent all
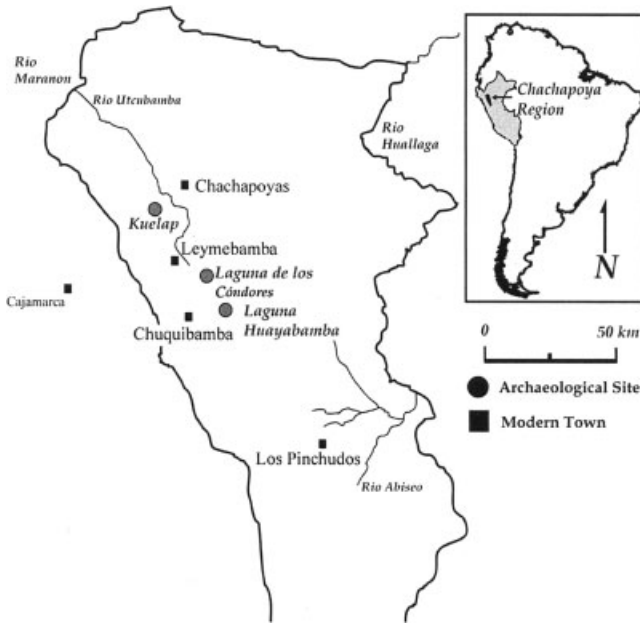
Fig. 2. Map of Peru, with groups discussed in text highlighted.

two components on opposite sides of the Laguna: 1) Llactacocha, a residential site; and 2) the funerary site, which is actually just one of a possible 18 burial sites on the cliff (von Hagen, 2002). Based on material culture recovered, the site was utilized during the late Middle Chachapoya (ca. AD 600–1000), Late Chachapoya (AD 1100–1470), Chachapoya-Inka (ca. AD 1470–1532), and Early Colonial periods (ca. AD 1532–1570) (Urton, 2001; von Hagen, 2002).

The human remains recovered from the mortuary context were divided into two subsets, based on mortuary treatment: the first consists of approximately 600–700 secondarily interred skeletonized individuals collected from a disturbed context, and the second consists of 224 mummy bundles. Some of the bundles were radiocarbon-dated to AD 1100–1420 (Guillén, 2003). Culturally, these remains were attributed to the Chilchos ethnic group (Guillén, 1998; von Hagen, 2002). According to Guillén (1998) and von Hagen (2002), skeletal remains from *chullpas* 2, 4, 5, and 6 were relocated to *chullpas* 1 and 3 after the Inka conquered the area, and therefore represent the pre-Inka local population. The crania examined for this research were from *chullpas* 1 and 3, and will therefore be considered to represent a pre-Inka Chachapoya population (Table 1).

Theoretical model

The following model is developed with the intention of discussing Late Chachapoya population structure and, more broadly, the articulation between biological and archaeological data in the description of prehistoric identity, and in particular the discussion of ethnic identity in the archaeological record. The model is based on the fundamental assumption that genetic exchange accompanies material exchange (Schillaci et al., 2001), and therefore two main points must be incorporated: 1) the degree of internal material and genetic exchange, and 2) the degree of external material and genetic exchange.

At the most basic level, based on stylistic similarities in ceramics, household construction, and symbolic motifs, it could be stated that the inhabitants of the region recognized some form of common social identity. Materially, Late Chachapoya groups appear to have a single, albeit potentially internally differentiated, social identity. If we assume that gene exchange accompanies material exchange, and given that the Chachapoya region is materially similar, it is expected that the groups will be biologically equidistant from a regional centroid, and that there will be no evidence for subgroup differentiation. Alternatively, there may be discordance between the archaeological manifestations of identity and the biological data. While the archaeological data suggest some form of overarching social identity, the biological data may indicate internal differentiation.

Evidence of extraregional material connections is relatively limited (Fig. 1). Church and Morales Gamarra (2001) recovered a single black, reduction-fired north coast Chimu pot from Los Pinchudos. Guillén (1998) also reported Chimu ceramics from the Laguna de los Cóndores. Church (1994) reported ceramics at Gran Pajatén from Callejón de Huaylas (Recuay and white-on-red), Huamachuco, and perhaps Callejón de Conchucos.

Church (1996) emphasized the importance and connection between Chachapoya and the Amazon Basin. He posited that the tropical montane societies may have acted as "primary purveyors and intermediary conveyors" in economic relations that connected other Andean regions with eastern Amazonia regions (Church, 1996, p. 7). Material recovered from the Laguna de los Cóndores provides the most concrete evidence of this connection (von Hagen, 2002). A parrot feather headdress recovered from the site, according to von Hagen (2002, p. 151), is reminiscent of contemporary lowland headdresses. Additionally, the tanned remains of two small felines (*Felis wiedii* and *Felis trigrina*) native to tropical environments were recovered (von Hagen, 2002).

The most abundant material evidence for contact exists in the Cajamarca region to the west. Initial Cajamarca ceramics (200 BC–AD 100) were recovered from a trench in Huepon (Schjellerup, 1997). Surface collections at the sites of Balsas, Pusac, Jecumbuy, and Huepon demonstrate a strong tie with Early Cajamarca (AD 100–500; Schjellerup, 1997). Late Cajamarca ceramics (AD 850–1200) were recovered from funerary caves at Huepon (Schjellerup, 1997). Late Cajamarca ceramics were also recovered from Laguna Huayabamba (Muscutt, 2003). Final Cajamarca ceramics (A.D. 1200–1532) were recovered from the Late Horizon Chachapoya site of Los Pinchudos (Morales et al., 2002).

Given the above archaeological evidence, it is suggested that the three Late Chachapoya groups examined in this research will demonstrate similar low levels of extraregional gene flow. Each group will exhibit similar levels of phenotypic variance and residuals. Alternatively, populations may exhibit differential access to extraregional gene flow.

Relethford-Blangero model

Both aspects of the above model will be examined utilizing a relationship (R) matrix, which can be utilized to address issues of prehistoric population structure (Scherer, 2005; Schillaci and Stojanowski, 2005; Steadman, 2001; Stojanowski, 2004). The R matrix characterizes the degree of genetic differentiation and the pattern

TABLE 2. Key to craniometric variable abbreviations (Buikstra and Ubelaker, 1994)

Variable	Variable abbreviation
Maximum cranial length	MCL
Maximum cranial breadth	MCB
Bizygomatic width	BIZ
Basion-bregma height	BBH
Cranial base length	CBL
Basion-prosthion length	BPL
Maximum aveolar breadth	MAB
Maximum aveolar length	MAL
Biauricular breadth	BAB
Upper facial height	UFH
Upper facial breadth	UFB
Nasal height	NH
Nasal breadth	NB
Orbital breadth	OB
Orbital height	OH
Biorbital breadth	BOB
Interorbital breadth	IOB
Frontal chord	FC
Parietal chord	PC
Occipital chord	OC
Foramen magnum length	FML
Foramen magnum breadth	FMB
Mastoid length	ML

of similarity between groups (Harpending and Ward, 1982, p. 217). The model is based on the following null hypothesis: if all populations within a region exchange migrants with an outside source at equal rates, then the relationship between average within-group phenotypic variance and the genetic distance to the regional group centroid, calculated form the diagonals of the R matrix, should be linear (Harpending and Ward, 1982). Deviations from this linear relationship indicate either that a subpopulation is very isolated and is therefore more homozygous, or that they are experiencing elevated gene flow from an outside source and are more heterozygous than expected.

Relethford and Blangero (1990) modified the model of Harpending and Ward (1982) to accommodate polygenic quantitative traits. The model retains the same null hypothesis, and should a group experience an increase in gene flow from an external source, within-group phenotypic variance will increase. Alternatively, within-group phenotypic variance may be less than expected, suggesting a greater degree of genetic isolation. The R matrix provides bias-corrected estimates of both genetic distance (d^2) and among-population genetic differentiation (F_{ST}) (Relethford and Blangero, 1990; Relethford et al., 1997; Steadman, 2001). The R matrix, F_{ST} values, and Relethford-Blangero residuals were calculated using the statistical package RMET 5.0 (http://konig.la.utk.edu/relethsoft.html).

Data collection

Data for 24 craniometric variables (Table 2), as described by Buikstra and Ubelaker (1994), were generated from the skeletal series. All measurements were taken using either a Mitutoyo digital sliding caliper or a Paleotech spreading caliper. Age estimates were based on morphological features of the skull and dental eruption patterns. Sex estimates were based on traditional cranial morphological features (Buikstra and Ubelaker, 1994). In general, there was good separation between the morphological extremes. Four of five morphological characteris-

tics reliably separated the sexes and followed the established format (Buikstra and Ubelaker, 1994). Nuchal crest development was robust for both sexes. This may have had the effect of artificially increasing the number of males in the series, but should not affect the results. Ultimately, in order to increase sample size and reduce statistical complexity, those crania categorized as "probable" males and females were treated as males and females, respectively. Further, as discussed below, the data were controlled for sex.

Statistical methods

The data were tested for significant age and sex associations using a Kruskal-Wallis nonparametric analysis of variance in SAS 8.0. Variables with significant *P*-values at the alpha = 0.05 level were removed from further analysis. While interobserver error is not a factor because all data were collected by the author, intraobserver error was assessed. Ten individuals from Laguna de los Cóndores and Kuelap were randomly selected for remeasurement after 5 days of initial data collection. The difference between the first and second trials was tested for significant difference from zero, using both parametric (Student's *t*-test) and nonparametric (sign test) methods in SAS 8.0.

Missing data are a common problem when dealing with prehistoric skeletal remains. In this instance, replacement of missing values was necessary, because RMET 5.0 requires a complete variance-covariance matrix. Missing values were imputed in SYSTAT 10.0 via an expectation-maximization (EM) algorithm which provides an unbiased estimate that does not affect levels of between-group variation (Wilkinson et al., 1996). The complete imputed data set was z-score-transformed before import into RMET 5.0.

Given that the skeletal samples are small, the R matrix was bias-corrected to reduce sampling error (Relethford et al., 1997). Analyses were performed with heritability estimates equal to 1.0 and 0.55. The former heritability estimate provides a conservative measure of the minimum amount of genetic differentiation, while the latter is generally considered a robust estimate of anthropometric variables (Konigsberg and Ousley, 1995). It was demonstrated that variation in heritability for anthropometric traits is robust and does not significantly change the pattern of Relethford-Blangero residuals (Relethford and Blangero, 1990, p. 19; Stojanowski, 2004). Additionally, given the relatively circumscribed region from which the current skeletal samples derive, it is not unreasonable to assume homogeneity of trait heritability.

Estimates of extraregional gene flow can be derived by comparing observed and expected within-group phenotypic variation. Expected within-group variation is a function of the pooled mean within-group phenotypic variation ($\bar{v}_w$), the genetic distance of population i to the centroid (r_{ii}), and the average genetic distance across all subpopulations (F_{ST}) (Relethford and Blangero, 1990; Relethford et al., 1997; Steadman, 2001).

$$E_{(\bar{v}_i)} = \frac{\bar{v}_w(1 - r_{ii})}{1 - F_{ST}}$$

The residual is the difference between the observed variance ($\bar{v}_i$) and the expected variance ($E_{(\bar{v}_i)}$), and when derived from the R matrix, reflects the relative level of extraregional gene flow (Steadman, 2001). Positive resid-

TABLE 3. *Estimated population sizes based on 1) family unit of five individuals/structure, 2) published estimates of population density (Church and Alvarez, 2002), and 3) equal population size*

Sample	Sample size	Estimated population		
		1	2	3
Cóndores	129	650	3,600	Equal
Kuelap	77	3,000	3,000	Equal
Huayabamba	16	1,000	4,595	Equal

TABLE 4. *Residuals and F_{ST} ($h^2 = 1.0$) based on 1) population estimates from associated residential sites for Late Chachapoya populations, 2) density estimates from Church and Alvarez (2002), and 3) equal population sizes*

Population estimate	(1) $\bar{v}_i - E(\bar{v}_i)$	(2) $\bar{v}_i - E(\bar{v}_i)$	(3) $\bar{v}_i - E(\bar{v}_i)$
Huayabamba	0.133	−0.010	0.017
Cóndores	0.149	0.061	0.062
Kuelap	−0.077	−0.058	−0.079
F_{ST}	0.047	0.058	0.058

uals may reflect: 1) higher levels of gene flow from an external source, 2) a higher mutation rate within a particular population (though given the relatively circumscribed temporal and spatial context of the current study, this is likely not a factor), and 3) nonrandom sample effects (Powell and Neves, 1999). The latter refer to the possibility that sampling techniques, recovery biases, and differential burial practices predicated upon social status may influence the results. Negative residuals, on the other hand, may reflect less than average external gene flow.

A measure of the minimum genetic divergence among populations, F_{ST}, is calculated as the average weighted diagonal of the R matrix (Steadman, 1998, p. 51; Williams-Blangero and Blangero, 1989).

$$F_{ST} = \sum_{i=1}^{g} w_i r_{ii}$$

where w_i is the relative population size of population i, g is the number of populations, and r_{ii} is the average genetic distance to the centroid of population i (Relethford et al., 1997).

The unbiased R matrix can be scaled by weighting each sample by estimated population size, removing the potential effects of genetic drift (Relethford, 1996). After accounting for differences in population size, any changes in heterozygosity will reflect effects of population history and migration (Relethford, 1996; Steadman, 1998). Three trials were performed ($h^2 = 1.0$) to determine the effect of different population estimates, based on: 1) published estimates of associated residential site sizes from the archaeological literature, 2) population density estimates produced by Church and Alvarez (2002), and 3) equal population sizes (Table 3).

RESULTS

Fourteen of the original 24 traits were significantly associated with age, and were removed from further analyses (MCL, BIZ, CBL, BPL, MAB, MAL, BAB, UFH, UFB, NH, OB, OH, BOB, and FMB; see Table 2). Sex-related effects were statistically removed by standardizing the raw data through a z-score transformation (Williams-Blangero and Blangero, 1989). The sexes were standardized separately within subpopulation, and combined back into subpopulation, at which point the entire data set was standardized again (Relethford and Harpending, 1994).

Only one trait (FML) demonstrated a statistically significant intraobserver error ($P = 0.0313$), though this result was not consistent. It was determined that a single set of measurements was driving this result. When this set was removed, the nonparametric sign test was no longer significant ($P = 0.0625$). Given this, FML was retained in subsequent analyses.

Individual with missing values >50% were removed from the analysis. In total, 24 individuals were removed from the Laguna de los Cóndores and Kuelap series, while only a single individual was removed from the Laguna Huayabamba series. Missing values were then imputed using SYSTAT 10.0. To determine if imputation affected within-group phenotypic variation, the original and imputed data sets were tested for significant differences, using the nonparametric Kruskal-Wallis analysis of variance. While there are small differences between the means and standard deviations between the original and imputed data sets, none of these differences reached statistical significance. Therefore, it is reasonable to conclude that the imputation of missing data will not artificially increase or decrease between-group variability.

Relethford-Blangero results

Before beginning the final analysis, the effects of three different population estimates were examined (Table 4). The results indicate that the pattern of Relethford-Blangero residuals, except for one exception, is not significantly affected by the method of population-size estimation. Further, the estimates of genetic differentiation are similar. Ultimately, because the population densities of Church and Alvarez (2002) did not include the areas surrounding Kuelap or Laguna de los Cóndores, the final results (Table 5) are based on population estimates derived from the size of associated residential components.

Estimates of genetic differentiation derived from the bias-corrected R matrix (Table 5) ranged from 0.047 (heritability = 1.0) to 0.090 (heritability = 0.55). While estimates of genetic differentiation were obviously affected by differences in trait heritability, the pattern of residuals did not change (Table 5). This suggests that the Relethford-Blangero residuals are robust despite potential variation in trait heritability. Kuelap exhibits a negative residual, suggesting that it was receiving less than average external gene flow. Laguna Huayabamba and Laguna de los Cóndores, on the other hand, exhibit positive residuals, and therefore were receiving greater than average external gene flow.

The biological distance matrices presented in Table 6 are based on the scaled R matrix. The largest genetic distance is between Kuelap and Laguna Huayabamba, followed by the distance between Laguna de los Cóndores and Kuelap. A plot (Fig. 3) of the genetic distance from Table 6 (r_{ii}) and average within-group phenotypic variance ($\bar{v}_i$) indicates that the samples violate the null hypothesis of a linear relationship. Based on the scaled principal component loadings (Fig. 4), the first principal component appears to be weighted average of all the cranial measurements, and is generally considered an overall indicator of size. Because the data were z-score-trans-

TABLE 5. Regional phenotypic distances to centroid (r_{ii}), observed mean variance ($\bar{v}_i$), expected mean variance ($E_{(\bar{v}_i)}$), and residual variance ($\bar{v}_i - E(\bar{v}_i)$) for Late Chachapoya populations under heritability = 1.0 and heritability = 0.55

	r_{ii}	$(\bar{v}_i)$	$E_{(\bar{v}_i)}$	$\bar{v}_i - E(\bar{v}_i)$
Heritability = 1.0				
Huayabamba	0.1270	0.931	0.798	0.133
Cóndores	0.0622	1.006	0.857	0.149
Kuelap	0.0173	0.821	0.898	−0.077
$F_{ST} = 0.047$,				
SE = 0.0105				
Heritability = 0.55				
Huayabamba	0.2433	0.931	0.724	0.207
Cóndores	0.1108	1.006	0.851	0.154
Kuelap	0.0348	0.821	0.924	−0.102
$F_{ST} = 0.0902$,				
SE = 0.0129				

TABLE 6. Genetic distances between Late Chachapoya populations, based on scaled R matrix[1]

	Huayabamba	Cóndores	Kuelap
Huayabamba	0.0000	0.0855	0.2438
Cóndores	0.1643	0.0000	0.0984
Kuelap	0.4471	0.1812	0.0000

[1] Distances in upper matrix are derived from heritability estimate of 1.0. Distances in lower matrix are derived from heritability estimate of 0.55.

Fig. 3. Plot of observed mean phenotypic variance ($\bar{v}_i$) vs. genetic distance from centroid (r_{ii}) for Late Chachapoya populations. Diagonal line indicates hypothetical relationship between these variables.

formed and therefore controlled for sex-related differences in size, the variation along this principal component may be related to an overall difference in size between populations.

It is also possible examine the potential effect of genetic drift on population structure by comparing scaled (Fig. 4) and unscaled (Fig. 5) distances. This comparison suggests that genetic drift had little impact on Late Chachapoya population differentiation (Relethford, 1996).

DISCUSSION

There are two primary issues to discuss in light of these results: 1) the evidence for Late Chachapoya population structure, and 2) the implications of these results for our understanding of prehistoric ethnic groups.

At the moment, it is not possible to discuss changes in regional genetic differentiation through time in Chachapoya because of the limited number of skeletal samples. Earlier Chachapoya samples are not available, and there is only a single Inka-period sample. Therefore, it is not possible to compare F_{ST} values across time to more fully discuss changes in genetic differentiation concomitant with social change. Given that, the estimates of genetic differentiation for the Late Chachapoya period range from 0.047 ($h^2 = 1$) to 0.090 ($h^2 = 0.55$), though evaluation of the significance and meaning of these estimates must await the recovery of more Chachapoya skeletal samples.

Evaluation of the pattern of Relethford-Blangero residuals can provide insights into Late Chachapoya population history. The residuals indicate that the Laguna Huayabamba and Laguna de los Cóndores populations were receiving greater than average external gene flow. Kuelap, on the other hand, was receiving less than average external gene flow. The populations are relatively equidistant from one another (Fig. 4), which seems to suggest that each was participating within an intrare-
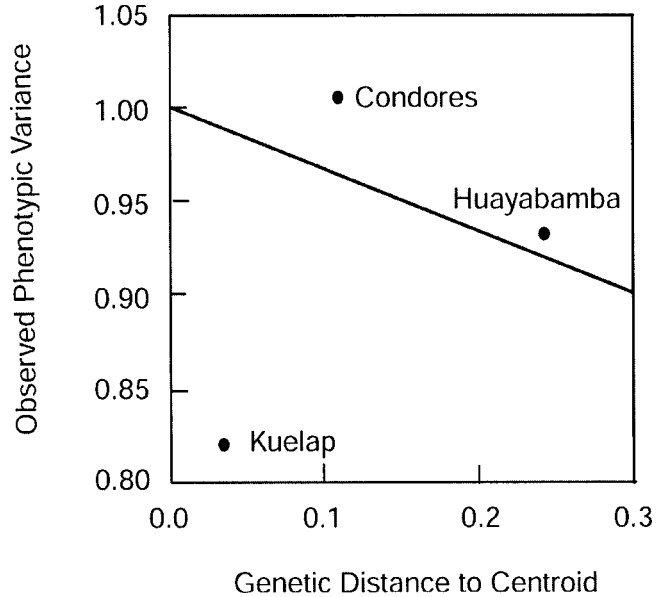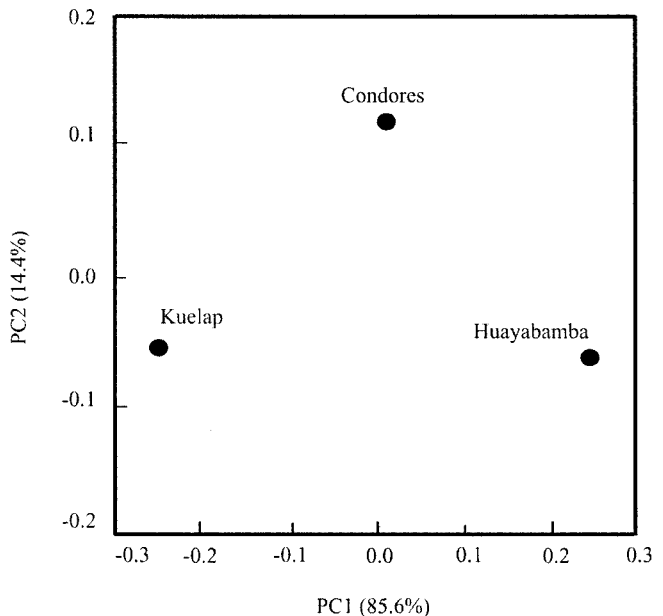

Fig. 4. Plot of first and second principal components (PCs) from scaled bias-corrected R matrix for Late Chachapoya populations ($h^2 = 1$). PC1 explains 85.6% of variation; PC2 accounts for 14.4%. Each component is scaled by square root of its corresponding eigenvalue.

gional gene-flow network equally. Additionally, the pattern of between-group biological distances suggests isolation-by-distance (Table 6), and as can be seen in Figure 2, the populations are arranged roughly along a north-south axis formed by the Río Utcubamba.

Still, when we consider the Relethford-Blangero residuals, it is apparent that two of the populations (Laguna de los Cóndores and Laguna Huayabamba) had stronger
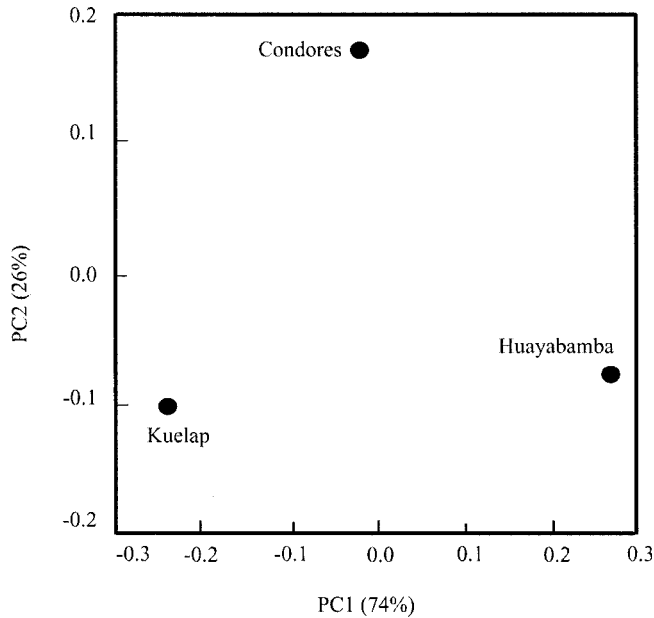
Fig. 5. Plot of first and second principal components (PCs) from unscaled bias-corrected R matrix for Late Chachapoya populations ($h^2 = 1$). PC1 explains 75% of variation; PC2 accounts for 26%. Each component is scaled by square root of its corresponding eigenvalue.

genetic interaction with extraregional sources. Given these results and the distribution of populations in Figure 3, Kuelap does seem distinct. Archaeologically, Kuelap is unique among Chachapoya sites for a number of reasons (Narváez Vargas, 1987, 1996a,b). First and most obvious is the sheer size of the walls, ranging up to 50 feet in height (Muscutt, 1998), that enclose the site. Internally, another wall divides the site into upper and lower levels, which was interpreted as evidence of sociopolitical divisions (Bradley, 2005). Finally, the range of mortuary practices evident at Kuelap encompasses the range observed across the entire Chachapoya region. The fact that Laguna de los Cóndores and Laguna Huayabamba exhibit positive Relethford-Blangero residuals may indicate that external gene flow came from the south. This is interesting in light of the presumed closer cultural ties with the Amazon Basin, based on similar iconographic motifs (von Hagen, 2002), and the stronger material ties with Cajamarca described above.

Ultimately, the population structure during the Late Chachapoya period is complex and must await further data collection for more definitive answers. As it stands, archaeological evidence suggests that Late Chachapoya settlements were located in high, defensible locations, and that population size was increasing. Increased population size may have necessitated increased extraction of resources, which ultimately may have taxed carrying capacity. Ultimately, increased resource competition may have stimulated the signaling of local, sub-group identity, but this process would have drawn from a common pool of symbolic motifs. One such form of signaling may have been in the mortuary context, through the use of anthropomorphic sarcophagi in the north, and burial *chullpas* in the south. The results from this analysis suggest that despite these archaeological indicators of "separation," there were few cultural barriers that prevented gene flow between Late Chachapoya populations. Thus,

contrary to material manifestations of subgroup reification and the existence of distinct "ethnic" groups, the results of this biological analysis seem to indicate subgroup unification despite presumed material boundaries.

The label of Chachapoya is likely a Late Horizon (AD 1472–1532) appellative applied to the inhabitants by the Inka (Muscutt, 1998), who presumably recognized some common factor among the inhabitants of the region. We must consider, however, that in attempting to maintain the ideal of their administrative infrastructure, the Inka may have collapsed internally recognized groups into a single administrative unit (D'Altroy, 1992, 2001; Julien, 1988). Internally derived definitions of "us" may have been overlooked or ignored by the externally derived Inka definitions of "them" (Jenkins, 2003). Drawing upon ethnohistoric documents, Espinoza Soriano (1967) stated that at least 22 separate ethnic groups may have occupied the region. However, the ethnic groups as discussed by Spanish chroniclers cannot be accepted at face value, for those groups observed by the Spanish were constructed by the Inkas and may not resemble their original pre-Inka configuration.

As mentioned previously, the area surrounding Laguna de los Cóndores and Kuelap was attributed to two different ethnic groups, the Chilcos (von Hagen, 2002) and Chillaos (Narváez Vargas, 1987, 1996a), respectively, based on ethnohistorical documents. We cannot assume, however, that these groups were ethnic groups as we would define them. A Western-derived understanding of social groupings may not carry any explanatory power within the Andean context. Hence we cannot assume that our archaeologically or ethnohistorically derived definitions of ethnic groups correspond to meaningful social groups, and are internally consistent or even relevant. Despite geographic and material similarities, all of which when taken in isolation would point to a common identity, genetically the picture in the Chachapoya region is more complicated. The description of identity is not as "simple" as either artifact distributions or population structure. Neither factor is predominant or inherently more correct or objective (Jones, 1997).

CONCLUSIONS

In general, physical anthropologists should approach research agendas that purport to elucidate the nature of prehistoric ethnic groups with caution. Prehistoric ethnic groups, whether defined archaeologically or from ethnohistoric documents, should not be uncritically accepted. Ethnic identity is an ascriptive, self-referential category (Barth, 1969; Nagata, 1974; Okamura, 1981), created by both "insiders" and "outsiders" (Jenkins, 2003). While a concentration on the formal, structural attributes of ethnic groups (Barth, 1969; Eriksen, 1991) strikes a positive note for archaeologists, the commonly agreed-upon criterion that ethnic group membership is self-referential limits archaeological possibilities. We are therefore left with a definitional conundrum: ethnicity is simultaneously something that people *do* (Hegmon, 1998) which makes it amenable to archaeological investigation, while it is also self-ascriptional, removing it from the realm of archaeological investigation. Therefore, it is unlikely, if not impossible, for archaeologists and bioarchaeologists to truly discuss what a prehistoric group's "ethnic identity" may have been. At a fundamental level, we can discern the existence of social boundaries that influence the exchange of both material artifacts and genes. In the

current research, archaeological and ethnohistorical documents suggest that the Chachapoya region was inhabited by a number of sociopolitically distinct groups that only united in the face of their common enemy, the Inka. On the other hand, interpretation of the biological data suggests that that these potential social boundaries did not significantly affect gene flow between groups. The pattern of biological distances suggests that gene exchange was structured roughly along the Río Utcubamba. Does this indicate that Chachapoya groups were uniting in the face of a common enemy? At the moment, it is not possible to answer this question because we do not know the population structure of the region during earlier time periods. Evaluation of population differentiation for earlier Chachapoya skeletal samples will be needed to more fully address this question.

Anthropologists must consider how best to define the concept of ethnicity, as well as the context from which the data were recovered. Because bioarchaeologists only have access to proxies of identity (classes of data that in some way capture aspects or reflections of identity), we must approach the problem from a holistic anthropological perspective, while remaining cautious in the pursuit and classification of prehistoric identity.

ACKNOWLEDGMENTS

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